ECOLOGY FOR ALL!

Gettysburg College

Ecology for All!

Written and Edited By*:

Nathan Brouwer, Hannah Connuck, Hayden Dubniczki, Natasha Gownaris, Aaron Howard,

Castilleja Olmsted, Dan Wetzel, Kyle Whittinghill, Andrew Wilson, Taylor Zallek

(*Authors listed in alphabetical order)

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (https://LibreTexts.org) and like the hundreds of other texts available within this powerful platform, it is freely available for reading, printing and "consuming." Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects.

Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.

The LibreTexts mission is to unite students, faculty and scholars in a cooperative effort to develop an easy-to-use online platform for the construction, customization, and dissemination of OER content to reduce the burdens of unreasonable textbook costs to our students and society. The LibreTexts project is a multi-institutional collaborative venture to develop the next generation of open-access texts to improve postsecondary education at all levels of higher learning by developing an Open Access Resource environment. The project currently consists of 14 independently operating and interconnected libraries that are constantly being optimized by students, faculty, and outside experts to supplant conventional paper-based books. These free textbook alternatives are organized within a central environment that is both vertically (from advance to basic level) and horizontally (across different fields) integrated.

The LibreTexts libraries are Powered by NICE CXOne and are supported by the Department of Education Open Textbook Pilot Project, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptions contact info@LibreTexts.org. More information on our activities can be found via Facebook (https://facebook.com/Libretexts), Twitter (https://twitter.com/libretexts), or our blog (http://Blog.Libretexts.org).

This text was compiled on 03/27/2025

TABLE OF CONTENTS

Licensing

A detailed breakdown of this resource's licensing can be found in ***Back Matter/Detailed Licensing****.*

CHAPTER OVERVIEW

1: Introduction to Ecology

Learning Objectives

- Introduce the scope of ecology.
- Review the nature of science and ecology's place as a branch of the natural sciences.
- Define the key levels of ecological organization: population, community, and ecosystem.
- Outline the history and expansion of ecology.

Summary

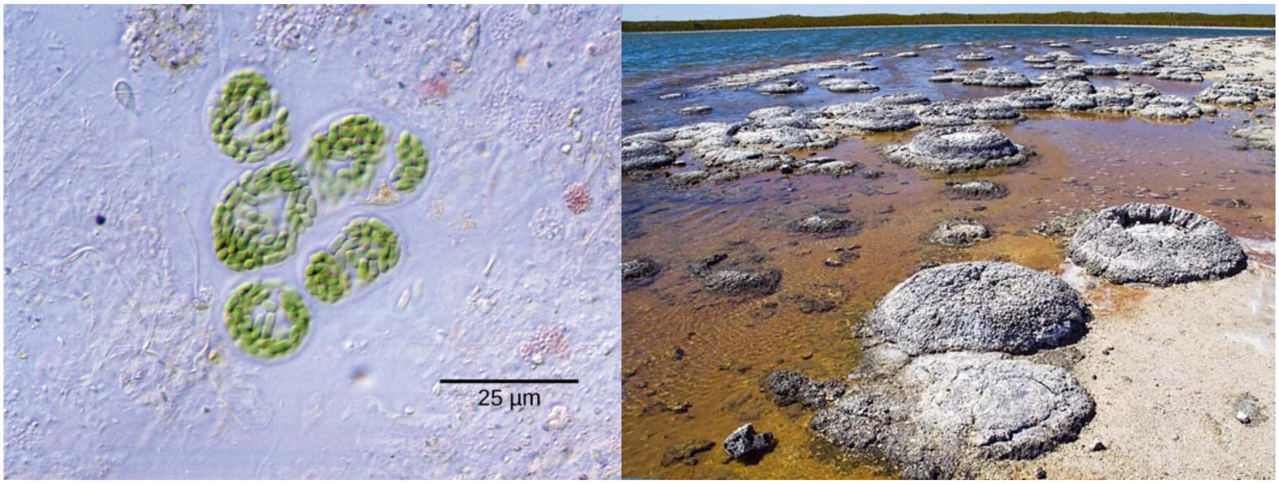
Ecology is the study of living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of ecology is vast, from the interactions of bacteria and viruses in the human gut to the ebb and flow of carbon dioxide through all the plants of the world. While ecology is a relatively young scientific discipline, it grew rapidly and now contributes to many issues important to society, such as the management of wildlife, conservation of endangered species, and mitigation of the impacts of climate change.

1.1: Biology and The Scientific Method

This textbook focuses on the field of ecology. Ecology is a sub-field of biology which studies living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of ecology is vast.

Among other things, ecology is the study of:

- Life processes, interactions, and adaptations
- The movement of materials and energy through living communities
- The successional development of ecosystems
- Cooperation, competition, and predation within and between species
- The abundance, biomass, and distribution of organisms in the context of the environment
- Patterns of biodiversity and its effect on ecosystem processes



(a) (b)

Figure 1.1.1: Formerly called blue-green algae, these (a) cyanobacteria, shown here at 300x magnification under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)

Ecology has practical applications in conservation biology, wetland management, natural resource management (agroecology, agriculture, forestry, agroforestry, fisheries), city planning (urban ecology), community health, economics, basic and applied science, and human social interaction (human ecology).

The word "ecology" ("Ökologie") was coined in 1866 by the German scientist Ernst Haeckel, and it became a rigorous science in the late 19th century. Evolutionary concepts relating to adaptation and natural selection are cornerstones of modern ecological theory.

Before we can dive into the field of ecology, we must first develop a common understanding of the practice and process of science.

1.1.1: The Process of Science

Ecology is a science, but what exactly is science? What does the study of ecology share with other scientific disciplines? Science (from the Latin *scientia*, meaning "knowledge") can be defined as knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method. It becomes clear from this definition that the application of the scientific method plays a major role in science. The scientific method is a method of research with defined steps that include experiments and careful observation.

The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses by means of repeatable experiments. A hypothesis is a suggested explanation for an event, which can be tested. Although using the scientific method is inherent to science, it is inadequate in determining what science is. This is because it is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but when it comes to disciplines like archaeology, psychology, and geology, the scientific method becomes less applicable as it becomes more difficult to repeat experiments.

These areas of study are still sciences, however. Consider archeology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, an archeologist can hypothesize that an ancient culture existed based on finding a piece of pottery. Further hypotheses could be made about various characteristics of this culture, and these hypotheses may be found to be correct or false through continued support or contradictions from other findings. A hypothesis may become a verified theory. A theory is a tested and confirmed explanation for observations or phenomena. Science may be better defined as fields of study that attempt to comprehend the nature of the universe.

1.1.1.1: Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or, maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.1.2). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

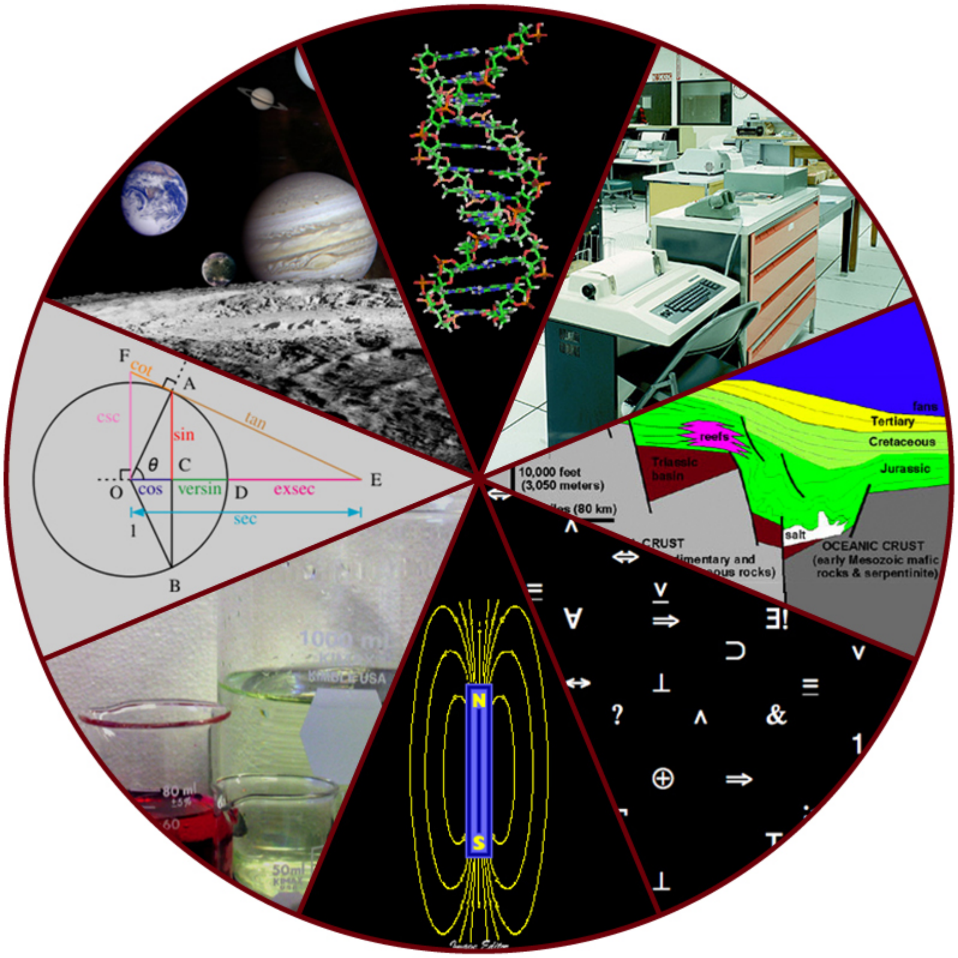


Figure 1.1.2: The natural sciences include astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: “Image Editor”/Flickr)

There is no unanimous agreement when it comes to defining what the natural sciences include, however. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into life sciences, which study living things and include biology, and physical sciences, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on both life and physical sciences and are interdisciplinary. Natural sciences are sometimes referred to as “hard science” because they rely on the use of quantitative data; social sciences that study society and human behavior are more likely to use qualitative assessments to drive investigations and findings.

Not surprisingly, the natural science of biology has many branches or subdisciplines. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals. In contrast to biologists that focus on the functioning of individual organisms or their subunits, ecologists typically treat organisms as the subunits of larger entities, such as populations, communities, or ecosystems.

1.1.1.2: Scientific Reasoning

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative or quantitative, and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies provide an example. In this type of research, many live brains are observed while people are doing a specific activity, such as viewing images of food. The part of the brain that “lights up” during this activity is then predicted to be the part controlling the response to the selected stimulus, in this case, images of food. The “lighting up” of the various areas of the brain is caused by excess absorption of radioactive sugar derivatives by active areas of the brain. The resultant increase in radioactivity is observed by a scanner. Then, researchers can stimulate that part of the brain to see if similar responses result.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reason, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. Descriptive (or discovery) science, which is usually inductive, aims to observe, explore, and discover, while hypothesis-based science, which is usually deductive, begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, and most scientific endeavors combine both approaches. The fuzzy boundary becomes apparent when thinking about how easily observation can lead to specific questions. For example, a gentleman in the 1940s observed that the burr seeds that stuck to his clothes and his dog’s fur had a tiny hook structure. On closer inspection, he discovered that the burrs’ gripping device was more reliable than a zipper. He eventually developed a company and produced the hook-and-loop fastener popularly known today as Velcro. Descriptive science and hypothesis-based science are in continuous dialogue.

1.1.1.1: The Scientific Method

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England’s Sir Francis Bacon (1561–1626) (Figure 1.1.3), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method.

Figure 1.1.3: Sir Francis Bacon (1561–1626) is credited with being the first to define the scientific method (credit: Paul van Somer).

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let’s think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: “Why is the classroom so warm?”

1.1.1.1: Proposing a Hypothesis

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, the student can make a prediction. A prediction is similar to a hypothesis but it typically has the format “If . . . then . . . .” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

1.1.1.1: Testing a Hypothesis

A valid hypothesis must be testable. It should also be falsifiable, meaning that it can be disproven by experimental results. Importantly, science does not claim to “prove” anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural, for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. The control group contains every feature of the experimental group except it is not given the manipulation that is hypothesized about. Therefore, if the results of the experimental group differ from the control group, the difference must be due to the hypothesized manipulation, rather than some outside factor. Look for the variables and controls in the examples that follow. To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure and this hypothesis should be rejected. Each hypothesis should be tested by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure $1.1.4$). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this “warm classroom” example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One observation to explain this occurrence might be, “When I eat breakfast before class, I am better able to pay attention.” The student could then design an experiment with a control to test this hypothesis.

In hypothesis-based science, specific results are predicted from a general premise. This type of reasoning is called deductive reasoning: deduction proceeds from the general to the particular. But the reverse of the process is also possible: sometimes, scientists reach a general conclusion from a number of specific observations. This type of reasoning is called inductive reasoning, and it proceeds from the particular to the general. Inductive and deductive reasoning are often used in tandem to advance scientific knowledge (Figure $1.1.5$).

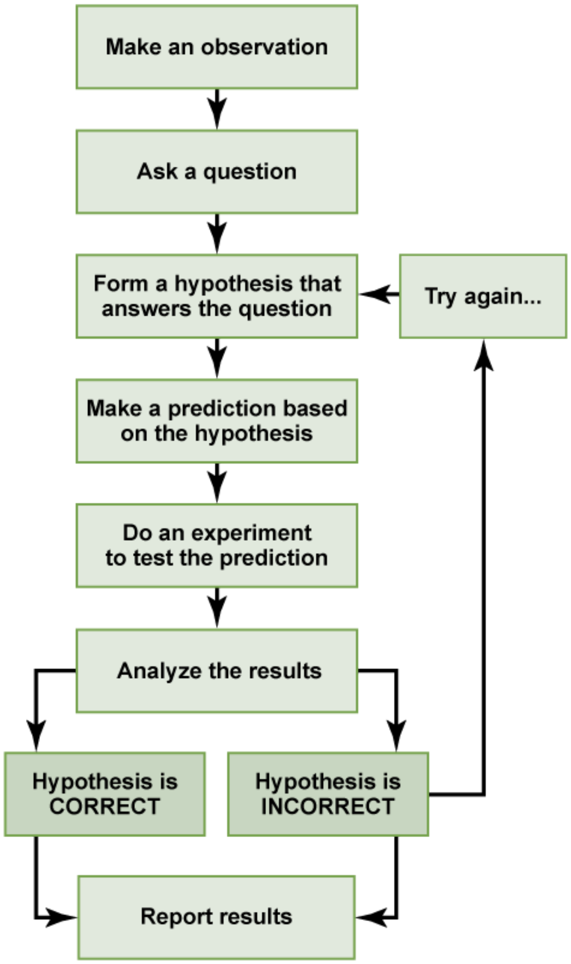
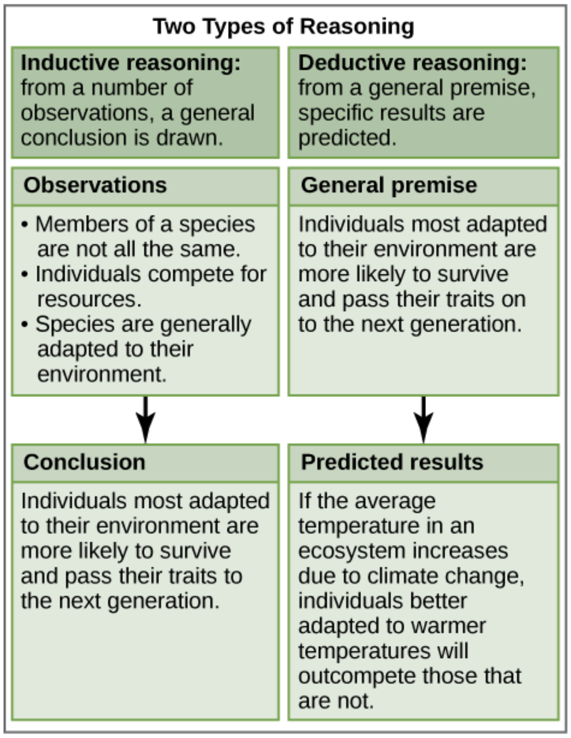


Figure 1.1.4: The scientific method consists of a series of well-defined steps. If a hypothesis is not supported by experimental data, a new hypothesis can be proposed.



Two Types of Reasoning

Inductive reasoning: from a number of observations, a general conclusion is drawn.

Deductive reasoning: from a general premise, specific results are predicted.

Observations

- Members of a species are not all the same.
- Individuals compete for resources.
- Species are generally adapted to their environment.

General premise

Individuals most adapted to their environment are more likely to survive and pass their traits on to the next generation.

Conclusion

Individuals most adapted to their environment are more likely to survive and pass their traits to the next generation.

Predicted results

If the average temperature in an ecosystem increases due to climate change, individuals better adapted to warmer temperatures will outcompete those that are not.

Figure 1.1.5: Scientists use two types of reasoning, inductive and deductive reasoning, to advance scientific knowledge. As is the case in this example, the conclusion from inductive reasoning can often become the premise for deductive reasoning.

The scientific method may seem too rigid and structured. It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

1.1.2: Two Types of Science: Basic Science and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or to bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or "pure" science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge's sake, though this does not mean that, in the end, it may not result in a practical application.

In contrast, applied science or "technology," aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster (Figure 1.1.6). In applied science, the problem is usually defined for the researcher.

Figure 1.1.6: After Hurricane Ike struck the Gulf Coast in 2008, the U.S. Fish and Wildlife Service rescued this brown pelican. Thanks to applied science, scientists knew how to rehabilitate the bird (credit: FEMA).

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the wide knowledge foundation generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, DNA makes new copies of itself, shortly before a cell divides. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual’s complete collection of genes is his or her genome.) Other less complex organisms have also been studied as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.1.7) relied on basic research carried out with simple organisms and, later, with the human genome. An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.

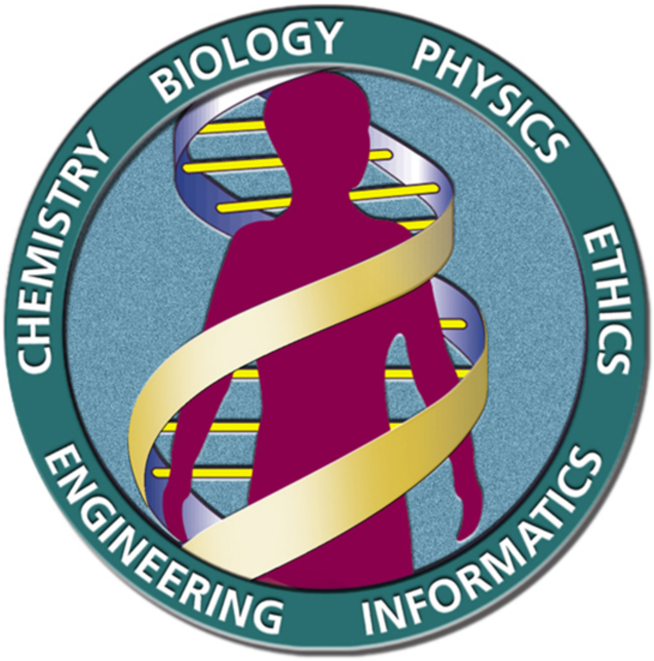


Figure 1.1.7: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003 (credit: U.S. Department of Energy Genome Programs).

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew on the dish, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

1.1.3: Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that are reviewed by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. First, scientific writing must be brief, concise, and accurate. A scientific paper needs to be succinct but detailed enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections—introduction, materials and methods, results, and discussion. This structure is sometimes called the "IMRaD" format. There are usually acknowledgment and reference sections as well as an abstract (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The introduction starts with brief, but broad, background information about what is known in the field. A good introduction also gives the rationale of the work; it justifies the work carried out and also briefly mentions the end of the paper, where the hypothesis or research question driving the research will be presented. The introduction refers to the published scientific work of others and therefore requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered plagiarism.

The materials and methods section includes a complete and accurate description of the substances used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Some journals require a results section followed by a discussion section, but it is more common to combine both. If the journal does not allow the combination of both sections, the results section simply narrates the findings without any further interpretation. The results are presented by means of tables or graphs, but no duplicate information should be presented. In the discussion section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously published scientific research. Therefore, proper citations are included in this section as well.

Finally, the conclusion section summarizes the importance of the experimental findings. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. Therefore, a well-done scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRAD format because they do not present original scientific findings, or primary literature; instead, they summarize and comment on findings that were published as primary literature and typically include extensive reference sections.

1.1.4: Contributors and Attributions

Modified from the following sources:

- **1.1: The Science of Biology** by OpenStax is licensed CC BY 4.0.
- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

1.2: What is Ecology?

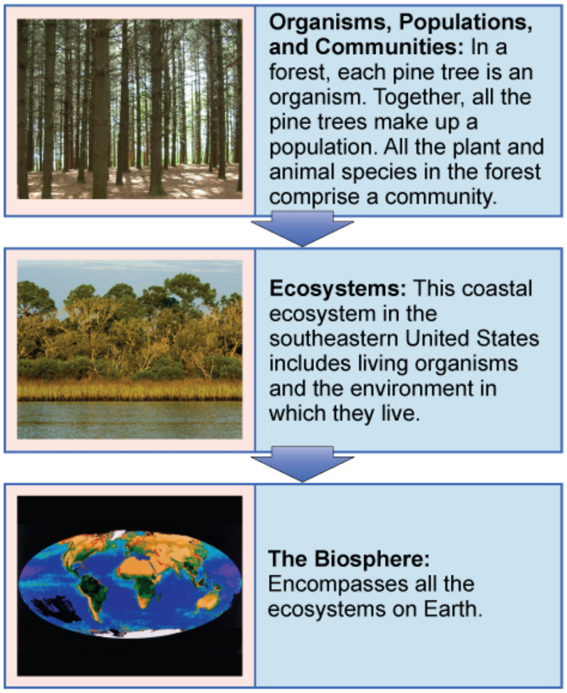
Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models.

Link to Learning

Climate change can alter where organisms live, which can sometimes directly affect human health. Watch the PBS video “Feeling the Effects of Climate Change” in which researchers discover a pathogenic organism living far outside of its normal range (https://www.pbs.org/video/need-to-know-feeling-the-effects-of-climate-change/).

Levels of Ecological Study

When a discipline such as biology is studied, it is often helpful to subdivide it into smaller, related areas. For instance, cell biologists interested in cell signaling need to understand the chemistry of the signal molecules (which are usually proteins) as well as the result of cell signaling. Ecologists interested in the factors that influence the survival of an endangered species might use mathematical models to predict how current conservation efforts affect endangered organisms. To produce a sound set of management options, a conservation biologist needs to collect accurate data, including current population size, factors affecting reproduction (like physiology and behavior), habitat requirements (such as plants and soils), and potential human influences on the endangered population and its habitat (which might be derived through studies in sociology and urban ecology). Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap: organism, population, community, and ecosystem (Figure 1.2.1).



Organisms, Populations, and Communities: In a forest, each pine tree is an organism. Together, all the pine trees make up a population. All the plant and animal species in the forest comprise a community.

Ecosystems: This coastal ecosystem in the southeastern United States includes living organisms and the environment in which they live.

The Biosphere: Encompasses all the ecosystems on Earth.

Figure 1.2.1: Ecologists study within several biological levels of organization (credit “organisms”: modification of work by "Crystl"/Flickr; credit “ecosystems”: modification of work by Tom Carlisle, US Fish and Wildlife Service Headquarters; credit “biosphere”: NASA).

Organismal Ecology

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological, physiological, and behavioral. For instance, the Karner blue butterfly *Lycaeides melissa samuelis* (Figure 1.2.2) is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine. This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.

Figure 1.2.2: The Karner blue butterfly *Lycaeides melissa samuelis* is a rare butterfly that lives only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It can only lay its eggs on lupine plants (credit: modification of work by J & K Hollingsworth, USFWS).

After hatching, the larval caterpillars emerge and spend four to six weeks feeding solely on wild lupine (Figure 1.2.3). The caterpillars pupate (undergo metamorphosis) and emerge as butterflies after about four weeks. The adult butterflies feed on the nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies’ preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).

Figure 1.2.3: The wild lupine *Lupinus perennis* is the host plant for the Karner blue butterfly.

Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. (Organisms that are all members of the same species are called conspecifics.) A population is identified, in part, by where it lives, and its area of population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called heterospecifics. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

For example, Karner blue butterfly larvae form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants. This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the biotic components (living things) in an area along with the abiotic components (non-living things) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored and how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat. Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, through the biotic and abiotic portions of the ecosystem.

Career Connection

Ecologist

A career in ecology contributes to many facets of human society. Understanding ecological issues can help society meet the basic human needs of food, shelter, and health care. Ecologists can conduct their research in the laboratory and outside in natural environments (Figure 1.2.4). These natural environments can be as close to home as the stream running through your campus or as far away as the hydrothermal vents at the bottom of the Pacific Ocean. Ecologists manage natural resources such as white-tailed deer populations *Odocoileus virginianus* for hunting or aspen *Populus* spp. timber stands for paper production. Ecologists also work as educators who teach children and adults at various institutions including universities, high schools, museums, and nature centers. Ecologists may also work in advisory positions assisting local, state, and federal policymakers to develop laws that are ecologically sound, or they may develop those policies and legislation themselves. To become an ecologist requires an undergraduate degree, usually in a natural science. The undergraduate degree is often followed by specialized training or an advanced degree, depending on the area of ecology selected. Ecologists should also have a broad background in the physical sciences, as well as a sound foundation in mathematics and statistics.

Figure 1.2.4: This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study (credit: USFWS Mountain Prairie Region, NPS).

Link to Learning

Visit this site to see Stephen Wing, a marine ecologist from the University of Otago, discuss the role of an ecologist and the types of issues ecologists explore.

Contributors and Attributions

Modified from the following sources:

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- **44.1: The Scope of Ecology** by OpenStax is licensed CC BY 4.0.

1.3: History of Ecology

Ecology is a new science and considered an important branch of biological science, having only become prominent during the second half of the 20th century (McIntosh, 1985). Ecological thought is derivative of established currents in philosophy, particularly from ethics and politics (Laferrière & Stoett, 2003).

Its history stems all the way back to the 4th century. One of the first ecologists whose writings survive may have been Aristotle or perhaps his student, Theophrastus, both of whom had an interest in many species of animals and plants. Theophrastus described interrelationships between animals and their environment as early as the 4th century BC (Ramalay, 1940). Ecology developed substantially in the 18th and 19th centuries. It began with Carl Linnaeus and his work with the economy of nature (Reid, 2009). Soon after came Alexander von Humboldt and his work with botanical geography (Silvertown et al., 2006). Alexander von Humboldt and Karl Möbius then contributed with the notion of biocoenosis. Eugenius Warming's work with ecological plant geography led to the founding of ecology as a discipline (Coleman, 1986). Charles Darwin's work also contributed to the science of ecology, and Darwin is often attributed with progressing the discipline more than anyone else in its young history. Ecological thought expanded even more in the early 20th century (Acot, 1997). Major contributions included Eduard Suess' and Vladimir Vernadsky's work with the biosphere, Arthur Tansley's ecosystem, Charles Elton's *Animal Ecology*, and Henry Cowles' ecological succession (Cowles, 1911).

Ecology influenced the social sciences and humanities. Human ecology began in the early 20th century, recognizing humans as an ecological factor. Later, James Lovelock advanced views on Earth as a macro-organism with the Gaia hypothesis (Egerton, 1973; Egerton, 2001). Conservation stemmed from the science of ecology. Important figures and movements include Shelford and the ESA, the National Environmental Policy Act, George Perkins Marsh, Theodore Roosevelt, Stephen A. Forbes, and post-Dust Bowl conservation. Later in the 20th century, world governments collaborated on human effects on the biosphere and Earth's environment.

The history of ecology is intertwined with the history of conservation efforts, in particular the founding of the Nature Conservancy (Smith & Mark, 2009).

18th and 19th century Ecological murmurs

Arcadian and Imperial Ecology

In the early Eighteenth century, preceding Carl Linnaeus, two rival schools of thought dominated the growing scientific discipline of ecology. First, Gilbert White a "parson-naturalist" is attributed with developing and endorsing the view of Arcadian ecology. Arcadian ecology advocates for a "simple, humble life for man" and a harmonious relationship with humans and nature (Worster, 1994). Opposing the Arcadian view is Francis Bacon's ideology, "imperial ecology". Imperialists work "to establish through the exercise of reason and by hard work, man's dominance over nature" (Worster, 1994). Imperial ecologists also believe that man should become a dominant figure over nature and all other organisms as "once enjoyed in the Garden of Eden" (Worster, 1994). Both views continued their rivalry through the early eighteenth century until Carl Linnaeus's support of imperialism; and in short time due to Linnaeus's popularity, imperial ecology became the dominant view within the discipline.

Carl Linnaeus and Systema Naturae

Carl Linnaeus, a Swedish naturalist, is well known for his work with taxonomy but his ideas helped to lay the groundwork for modern ecology. He developed a two part naming system for classifying plants and animals. Binomial Nomenclature was used to classify, describe, and name different genera and species. The compiled editions of *Systema Naturae* developed and popularized the naming system for plants and animals in modern biology. Reid suggests "Linnaeus can fairly be regarded as the originator of systematic and ecological studies in biodiversity," due to his naming and classifying of thousands of plant and animal species. Linnaeus also influenced the foundations of Darwinian evolution, he believed that there could be change in or between different species within fixed genera. Linnaeus was also one of the first naturalists to place men in the same category as primates (Reid, 2009).

The botanical geography and Alexander von Humboldt

Throughout the 18th and the beginning of the 19th century, European empires began to feel the pressure of their growing populations to expand, leading to an explosion of maritime exploration for territory, commerce, discover and catelog natural resources, and gain global influence. The great maritime powers such as Britain, Spain, and Portugal launched multiple world exploratory expeditions in this time leading to a vast growth of human knowledge: at the beginning of the 18th century, about twenty thousand plant species were known, versus forty thousand at the beginning of the 19th century, and about 300,000 today.

These expeditions were joined by many scientists, including botanists, such as the German explorer Alexander von Humboldt. Humboldt is often considered as father of ecology. He was the first to take on the study of the relationship between organisms and their environment. He exposed the existing relationships between observed plant species and climate, and described vegetation zones using latitude and altitude, a discipline now known as geobotany. Von Humboldt was accompanied on his expedition by the botanist Aimé Bonpland.

In 1856, the Park Grass Experiment was established at the Rothamsted Experimental Station to test the effect of fertilizers and manures on hay yields. This is the longest-running field experiment in the world (Silvertown et al., 2006).

The notion of biocoenosis: Wallace and Möbius

Alfred Russel Wallace, contemporary and colleague of Darwin, was first to propose a "geography" of animal species. Several authors recognized at the time that species were not independent of each other, and grouped them into plant species, animal species, and later into communities of living beings or biocoenosis. The first use of this term is usually attributed to Karl Möbius in 1877, but already in 1825, the French naturalist Adolphe Dureau de la Malle used the term *societé* about an assemblage of plant individuals of different species.

Warming and the foundation of ecology as discipline

While Darwin focused exclusively on competition as a selective force, Eugen Warming devised a new discipline that took abiotic factors, that is drought, fire, salt, cold etc., as seriously as biotic factors in the assembly of biotic communities. Biogeography before Warming was largely of descriptive nature – faunistic or floristic. Warming's aim was, through the study of organism (plant) morphology and anatomy, i.e. adaptation, to explain why a species occurred under a certain set of environmental conditions. Moreover, the goal of the new discipline was to explain why species occupying similar habitats, experiencing similar hazards, would solve problems in similar ways, despite often being of widely different phylogenetic descent. Based on his personal observations in Brazilian cerrado, in Denmark, Norwegian Finnmark and Greenland, Warming gave the first university course in ecological plant geography. Based on his lectures, he wrote the book ‘Plantesamfund’, which was immediate translated to German, Polish and Russian, later to English as ‘Oecology of Plants’. Through its German edition, the book had an immense effect on British and North American scientists like Arthur Tansley, Henry Chandler Cowles and Frederic Clements (Coleman, 1986).

Malthusian influence

Thomas Robert Malthus was an influential writer on the subject of population and population limits in the early 19th century. His works were very important in shaping the ways in which Darwin saw the world worked. Malthus wrote:

> *That the increase of population is necessarily limited by the means of subsistence,*
>
> *That population does invariably increase when the means of subsistence increase, and,*
>
> *That the superior power of population is repressed, and the actual population kept equal to the means of subsistence, by misery and vice (Malthus, 1798).*

In An Essay on the Principle of Population Malthus argues for the reining in of rising population through 2 checks: Positive and Preventive checks. The first raising death rates, the latter lowers birthing rates (Gilbert, n.d.). Malthus also brings forth the idea that the world population will move past the sustainable number of people (Malthus, 1798). This form of thought still continues to influences debates on birth and marriage rates to this theory brought forth by Malthus (Gilbert, n.d.) The essay had a major influence on Charles Darwin and helped him to theories his theory of Natural Selection (van Wyha, 2008). This struggle proposed by Malthusian thought not only influenced the ecological work of Charles Darwin, but helped bring about an economic theory of world of ecology (Todes, 1987).

Darwinism and the science of ecology

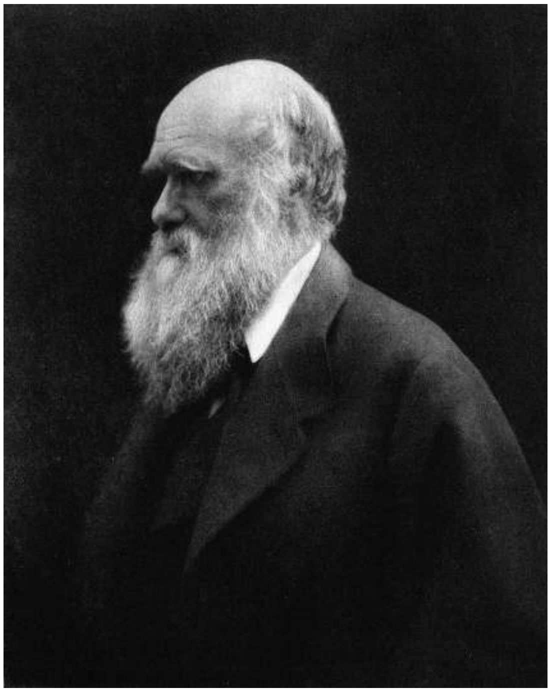


Figure 1.3.1: Julia Margaret Cameron’s portrait of Darwin.

It is often held that the roots of scientific ecology may be traced back to Darwin (Stauffer, 1957). This contention may look convincing at first glance inasmuch as *On the Origin of Species* is full of observations and proposed mechanisms that clearly fit within the boundaries of modern ecology (e.g. the cat-to-clover chain – an ecological cascade) and because the term ecology was coined in 1866 by a strong proponent of Darwinism, Ernst Haeckel. However, Darwin never used the word in his writings after this year, not even in his most "ecological" writings such as the foreword to the English edition of Hermann Müller’s *The Fertilization of Flowers* (1883) or in his own treatise of earthworms and mull formation in forest soils (The formation of vegetable mould through the action of worms, 1881). Moreover, the pioneers founding ecology as a scientific discipline, such as Eugen Warming, A. F. W. Schimper, Gaston Bonnier, F.A. Forel, S.A. Forbes and Karl Möbius, made almost no reference to Darwin’s ideas in their works (Acot, 1997). This was clearly not out of ignorance or because the works of Darwin were not widespread. Some such as S.A.Forbes studying intricate food webs asked questions as yet unanswered about the instability of food chains that might persist if dominant competitors were not adapted to have self-constraint (Forbes, 1887). Others focused on the dominant themes at the beginning, concern with the relationship between organism morphology and physiology on one side and environment on the other, mainly abiotic environment, hence environmental selection. Darwin’s concept of natural selection on the other hand focused primarily on competition (Paterson, 2005). The mechanisms other than competition that he described, primarily the divergence of character which can reduce competition and his statement that "struggle" as he used it was metaphorical and thus included environmental selection, were given less emphasis in the Origin than competition (Worster, 1994). Despite most portrayals of Darwin conveying him as a non-aggressive recluse who let others fight his battles, Darwin remained all his life a man nearly obsessed with the ideas of competition, struggle and conquest – with all forms of human contact as confrontation (Worster, 1994; Kormondy, 1978).

Although there is nothing incorrect in the details presented in the paragraph above, the fact that Darwinism used a particularly ecological view of adaptation and Haeckel's use and definitions of the term were steeped in Darwinism should not be ignored. According to ecologist and historian Robert P. McIntosh, "the relationship of ecology to Darwinian evolution is explicit in the title of the work in which ecology first appeared," (McIntosh, 1985; Haeckel, 1866). A more elaborate definition by Haeckel in 1870 is translated on the frontispiece of the influential ecology text known as 'Great Apes' as "… ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence," (Allee et al., 1949; McIntosh, 1985). The issues brought up in the above paragraph are covered in more detail in the Early Beginnings section underneath that of History in the Wikipedia page on Ecology.

Early 20th century ~ Expansion of ecological thought

The biosphere – Eduard Suess and Vladimir Vernadsky

By the 19th century, ecology blossomed due to new discoveries in chemistry by Lavoisier and de Saussure, notably the nitrogen cycle. After observing the fact that life developed only within strict limits of each compartment that makes up the atmosphere, hydrosphere, and lithosphere, the Austrian geologist Eduard Suess proposed the term biosphere in 1875. Suess proposed the name biosphere for the conditions promoting life, such as those found on Earth, which includes flora, fauna, minerals, matter cycles, et cetera.

In the 1920s Vladimir I. Vernadsky, a Russian geologist who had defected to France, detailed the idea of the biosphere in his work "The biosphere" (1926), and described the fundamental principles of the biogeochemical cycles. He thus redefined the biosphere as the sum of all ecosystems.

First ecological damages were reported in the 18th century, as the multiplication of colonies caused deforestation. Since the 19th century, with the industrial revolution, more and more pressing concerns have grown about the impact of human activity on the environment. The term ecologist has been in use since the end of the 19th century.

The ecosystem: Arthur Tansley

Over the 19th century, botanical geography and zoogeography combined to form the basis of biogeography. This science, which deals with habitats of species, seeks to explain the reasons for the presence of certain species in a given location.

It was in 1935 that Arthur Tansley, the British ecologist, coined the term ecosystem, the interactive system established between the biocoenosis (the group of living creatures), and their biotope, the environment in which they live. Ecology thus became the science of ecosystems.

Tansley's concept of the ecosystem was adopted by the energetic and influential biology educator Eugene Odum. Along with his brother, Howard T. Odum, Eugene P. Odum wrote a textbook which (starting in 1953) educated more than one generation of biologists and ecologists in North America.

Ecological succession – Henry Chandler Cowles

Figure 1.3.2: The Indiana Dunes on Lake Michigan, which Cowles referred to in his development of his theories of ecological succession.

At the turn of the 20th century, Henry Chandler Cowles was one of the founders of the emerging study of "dynamic ecology", through his study of ecological succession at the Indiana Dunes, sand dunes at the southern end of Lake Michigan. Here Cowles found evidence of ecological succession in the vegetation and the soil with relation to age. Cowles was very aware of the roots of the concept and of his (primordial) predecessors (Cowles, 1911). Thus, he attributes the first use of the word to the French naturalist Adolphe Dureau de la Malle, who had described the vegetation development after forest clear-felling, and the first comprehensive study of successional processes to the Finnish botanist Ragnar Hult (1881).

Animal Ecology - Charles Elton

20th century English zoologist and ecologist, Charles Elton, is commonly credited as “the father of animal ecology” (Southwood & Clark, 1999). Elton influenced by Victor Shelford's *Animal Communities in Temperate America* began his research on animal ecology as an assistant to his colleague, Julian Huxley, on an ecological survey of the fauna in Spitsbergen in 1921. Elton's most famous studies were conducted during his time as a biological consultant to the Hudson Bay Company to help understand the fluctuations in the company's fur harvests. Elton studied the population fluctuations and dynamics of snowshoe hare, Canadian lynx, and other mammals of the region. Elton is also considered the first to coin the terms, food chain and food cycle in his famous book *Animal Ecology* (Elton, 2011). Elton is also attributed with contributing to disciplines of invasion ecology, community ecology, and wildlife disease ecology (Wilson, 2011).

G. Evelyn Hutchinson - father of modern ecology

George “G” Evelyn Hutchinson was a 20th-century ecologist who is commonly recognized as the “Father of Modern Ecology”. Hutchinson is of English descent but spent most of professional career studying in New Haven, Connecticut at Yale University. Throughout his career, over six decades, Hutchinson contributed to the sciences of limnology, entomology, genetics, biogeochemistry, mathematical theory of population dynamics and many more (Lovejoy, 2011). Hutchinson is also attributed as being the first to infuse science with theory within the discipline of ecology (McIntosh, 1985). Hutchinson was also one of the first credited with combining ecology with mathematics. Another major contribution of Hutchinson was his development of the current definition of an organism's “niche” – as he recognized the role of an organism within its community. Finally, along with his great impact within the discipline of ecology throughout his professional years, Hutchinson also left a lasting impact in ecology through his many students he inspired. Foremost among them were Robert H. MacArthur, who received his PhD under Hutchinson, and Raymond L. Lindemann, who finished his PhD dissertation during a fellowship under him. MacArthur became the leader of theoretical ecology and, with E. O. Wilson, developed island biography theory. Raymond Lindemann was instrumental in the development of modern ecosystem science (Dritschilo, 2008).

20th century transition to modern ecology

“What is ecology?” was a question that was asked in almost every decade of the 20th century (McIntosh, 1985). Unfortunately, the answer most often was that it was mainly a point of view to be used in other areas of biology and also “soft,” like sociology, for example, rather than “hard,” like physics. Although autecology (essentially physiological ecology) could progress through the typical scientific method of observation and hypothesis testing, synecology (the study of animal and plant communities) and genecology (evolutionary ecology), for which experimentation was as limited as it was for, say, geology, continued with much the same inductive gathering of data as did natural history studies (Cook, 1977). Most often, patterns, present and historical, were used to develop theories having explanatory power, but which had little actual data in support. Darwin's theory, as much as it is a foundation of modern biology, is a prime example.

G. E. Hutchinson, identified above as the “father of modern ecology,” through his influence raised the status of much of ecology to that of a rigorous science. By shepherding of Raymond Lindemann's work on the trophic-dynamic concept of ecosystems through the publication process after Lindemann's untimely death, Hutchinson set the groundwork for what became modern ecosystem science. With his two famous papers in the late 1950s, “Closing remarks,” and “Homage to Santa Rosalia,” as they are now known, Hutchinson launched the theoretical ecology which Robert MacArthur championed (Hutchinson, 1957; Hutchinson, 1959; Bocking, 1997).

Ecosystem science became rapidly and sensibly associated with the “Big Science”—and obviously “hard” science—of atomic testing and nuclear energy. It was brought in by Stanley Auerbach, who established the Environmental Sciences Division at Oak Ridge National Laboratory, to trace the routes of radionuclides through the environment, and by the Odum brothers, Howard and Eugene, much of whose early work was supported by the Atomic Energy Commission (Craige, 2001; Golley, 1993). Eugene Odum's textbook, *Fundamentals of Ecology*, has become something of a bible today. When, in the 1960s, the International Biological Program (IBP) took on an ecosystem character, ecology, with its foundation in systems science, forever entered the realm of Big Science, with projects having large scopes and big budgets (BioScience, 1964). Just two years after the publication of Rachel Carson's *Silent Spring* in 1962, ecosystem ecology was trumpeted as THE science of the environment in a series of articles in a special edition of *BioScience* (Dritschilo, 2019).

Theoretical ecology took a different path to establish its legitimacy, especially at eastern universities and certain West Coast campuses (MacArthur, 1955). It was the path of Robert MacArthur, who used simple mathematics in his “Three Influential Papers, also published in the late 1950s, on population and community ecology (MacArthur, 1957; MacArthur, 1958; Van Valen & Pitelka, 1974). Although the simple equations of theoretical ecology at the time, were unsupported by data, they still were still deemed to be “heuristic.” They were resisted by a number of traditional ecologists, however, whose complaints of “intellectual censorship” of studies that did not fit into the hypothetico-deductive structure of the new ecology might be seen as evidence of the stature to which the Hutchinson-MacArthur approach had risen by the 1970s (Peters, 1976).

Timeline of ecologists

A list of founders, innovators and their significant contributions to ecology, from Romanticism onward.

Notable figure	Lifespan	Major contribution & citation
Antonie van Leeuwenhoek	1632–1723	First to develop concept of food chains
Carl Linnaeus	1707–1778	Influential naturalist, inventor of science on the economy of nature[64][65]
Alexander Humboldt	1769–1859	First to describe ecological gradient of latitudinal biodiversity increase toward the tropics in 1807 (Darwin, 1859)
Charles Darwin	1809–1882	Founder of the hypothesis of evolution by means of natural selection, founder of ecological studies of soils[67]

Elizabeth Catherine Thomas Carne	1817-1873	Geologist, mineralogist and philosopher who observed rural vs urban living, spatially and culturally, finding in country living the best attack on suffocating class divides, healthier living, and best access to natural education (Hardie-Budden, 2014; Futuyma, 2005).
Herbert Spencer	1820–1903	Early founder of social ecology, coined the phrase 'survival of the fittest' (Egerton, 2007; Glaubrecht, 2008)
Karl Möbius	1825–1908	First to develop concept of ecological community, biocenosis, or living community (Baker, 1966; Nyhart, 1998; Palamar, 2008)
Ernst Haeckel	1834–1919	Invented the term ecology, popularized research links between ecology and evolution
Victor Hensen	1835–1924	Invented term plankton, developed quantitative and statistical measures of productivity in the seas
Eugenius Warming	1841–1924	Early founder of Ecological Plant Geography (Coleman, 1986)
Ellen Swallow Richards	1842–1911	Pioneer and educator who linked urban ecology to human health (Forbes, 1915)
Stephen Forbes	1844–1930	Early founder of entomology and ecological concepts in 1887 (Forbes, 1887; Cohen, 1987)
Vito Volterra	1860–1940	Independently pioneered mathematical populations models around the same time as Alfred J. Lotka (Volterra, 1926; Adams & Fuller, 1940).
Vladimir Vernadsky	1869–1939	Founded the biosphere concept
Henry C. Cowles	1869–1939	Pioneering studies and conceptual development in studies of ecological succession (Smuts, 1926)
Jan Christiaan Smuts	1870–1950	Coined the term holism in a 1926 book *Holism and Evolution* (Cooper, 1957)
Arthur G. Tansley	1871–1955	First to coin the term ecosystem in 1936 and notable researcher (Nyhart, 1998; Kingsland, 1994; Ilerbaig, 1999)
Charles Christopher Adams	1873–1955	Animal ecologist, biogeographer, author of first American book on animal ecology in 1913, founded ecological energetics (Raup, 1959; Simberloff, 1980)
Friedrich Ratzel	1844–1904	German geographer who first coined the term biogeography in 1891

Frederic Clements	1874–1945	Authored the first influential American ecology book in 1905 (Ellison, 2006)
Victor Ernest Shelford	1877–1968	Founded physiological ecology, pioneered food-web and biome concepts, founded The Nature Conservancy (Kendeigh, 1968; Berryman, 1992)
Alfred J. Lotka	1880–1949	First to pioneer mathematical populations models explaining trophic (predator-prey) interactions using logistic equation (McIntosh, 1975)
Henry Gleason	1882–1975	Early ecology pioneer, quantitative theorist, author, and founder of the individualistic concept of ecology[84][88]
Charles S. Elton	1900–1991	'Father' of animal ecology, pioneered food-web & niche concepts and authored influential *Animal Ecology* text (Ellison, 2006; Flannery, 2003)
G. Evelyn Hutchinson	1903–1991	Limnologist and conceptually advanced the niche concept[90][91][92]
Eugene P. Odum	1913–2002	Co-founder of ecosystem ecology and ecological thermodynamic concepts (Edmondson, 1991; Patrick, 1994; Gunderson et al., 2002)
Howard T. Odum	1924–2002	Co-founder of ecosystem ecology and ecological thermodynamic concepts (Ilerbaig, 1999; Kendeigh, 1968; Rotabi, 2007; Patten, 1993; Ewel, 2003; Brown, 1999)
Robert MacArthur	1930–1972	Co-founder on Theory of Island Biogeography and innovator of ecological statistical methods (Levin, 1998)

Ecological Influence on the Social Sciences and Humanities

Human ecology

Human ecology began in the 1920s, through the study of changes in vegetation succession in the city of Chicago. It became a distinct field of study in the 1970s. This marked the first recognition that humans, who had colonized all of the Earth's continents, were a major ecological factor. Humans greatly modify the environment through the development of the habitat (in particular urban planning), by intensive exploitation activities such as logging and fishing, and as side effects of agriculture, mining, and industry. Besides ecology and biology, this discipline involved many other natural and social sciences, such as anthropology and ethnology, economics, demography, architecture and urban planning, medicine and psychology, and many more. The development of human ecology led to the increasing role of ecological science in the design and management of cities.

In recent years human ecology has been a topic that has interested organizational researchers. Hannan and Freeman (*Population Ecology of Organizations (1977)*, American Journal of Sociology) argue that organizations do not only adapt to an environment. Instead it is also the environment that selects or rejects populations of organizations. In any given environment (in equilibrium) there will only be one form of organization (isomorphism). Organizational ecology has been a prominent theory in accounting for diversities of organizations and their changing composition over time.

James Lovelock and the Gaia hypothesis

The Gaia theory, proposed by James Lovelock, in his work *Gaia: A New Look at Life on Earth*, advanced the view that the Earth should be regarded as a single living macro-organism. In particular, it argued that the ensemble of living organisms has jointly evolved an ability to control the global environment — by influencing major physical parameters as the composition of the atmosphere, the evaporation rate, the chemistry of soils and oceans — so as to maintain conditions favorable to life. The idea has been supported by Lynn Margulis who extended her endosymbiotic theory which suggests that cell organelles originated from free living organisms to the idea that individual organisms of many species could be considered as symbionts within a larger metaphorical "super-organism" (Allee et al., 1949).

This vision was largely a sign of the times, in particular the growing perception after the Second World War that human activities such as nuclear energy, industrialization, pollution, and overexploitation of natural resources, fueled by exponential population growth, were threatening to create catastrophes on a planetary scale, and has influenced many in the environmental movement since then.

History and relationship between ecology and conservation and environmental movements

Environmentalists and other conservationists have used ecology and other sciences (e.g., climatology) to support their advocacy positions. Environmentalist views are often controversial for political or economic reasons. As a result, some scientific work in ecology directly influences policy and political debate; these in turn often direct ecological research.

The history of ecology, however, should not be conflated with that of environmental thought. Ecology as a modern science traces only from Darwin's publication of Origin of Species and Haeckel's subsequent naming of the science needed to study Darwin's theory. Awareness of humankind's effect on its environment has been traced to Gilbert White in 18th-century Selborne, England (Worster, 1994). Awareness of nature and its interactions can be traced back even farther in time (Egerton, 1973; Egerton, 2001). Ecology before Darwin, however, is analogous to medicine prior to Pasteur's discovery of the infectious nature of disease. The history is there, but it is only partly relevant.

Neither Darwin nor Haeckel, it is true, did self-avowed ecological studies. The same can be said for researchers in a number of fields who contributed to ecological thought well into the 1940s without avowedly being ecologists (McIntosh, 1985; Kingsland, 1985). Raymond Pearl's population studies are a case in point (Huxley, 1942). Ecology in subject matter and techniques grew out of studies by botanists and plant geographers in the late 19th and early 20th centuries that paradoxically lacked Darwinian evolutionary perspectives. Until Mendel's studies with peas were rediscovered and melded into the Modern Synthesis, Darwinism suffered in credibility (Kingsland, 2005). Many early plant ecologists had a Lamarckian view of inheritance, as did Darwin, at times. Ecological studies of animals and plants, preferably live and in the field, continued apace however (Coker, 1991).

Conservation and environmental movements - 20th Century

When the Ecological Society of America (ESA) was chartered in 1915, it already had a conservation perspective (Shelford, 1917). Victor E. Shelford, a leader in the society's formation, had as one of its goals the preservation of the natural areas that were then the objects of study by ecologists, but were in danger of being degraded by human incursion (Forbes, 1922). Human ecology had also been a visible part of the ESA at its inception, as evident by publications such as: "The Control of Pneumonia and Influenza by the Weather," "An Overlook of the Relations of Dust to Humanity," "The Ecological Relations of the Polar Eskimo," and "City Street Dust and Infectious Diseases," in early pages of Ecology and Ecological Monographs. The ESA's second president, Ellsworth Huntington, was a human ecologist. Stephen Forbes, another early president, called for "humanizing" ecology in 1921, since man was clearly the dominant species on the Earth (Adams, 1935).

This auspicious start actually was the first of a series of fitful progressions and reversions by the new science with regard to conservation. Human ecology necessarily focused on man-influenced environments and their practical problems. Ecologists in general, however, were trying to establish ecology as a basic science, one with enough prestige to make inroads into Ivy League faculties. Disturbed environments, it was thought, would not reveal nature's secrets.

Interest in the environment created by the American Dust Bowl produced a flurry of calls in 1935 for ecology to take a look at practical issues. Pioneering ecologist C. C. Adams wanted to return human ecology to the science (Adams, 1935). Frederic E.

Clements, the dominant plant ecologist of the day, reviewed land use issues leading to the Dust Bowl in terms of his ideas on plant succession and climax (Clements, 1935). Paul Sears reached a wide audience with his book, *Deserts on the March* (Sears, 1935). World War II, perhaps, caused the issue to be put aside.

The tension between pure ecology, seeking to understand and explain, and applied ecology, seeking to describe and repair, came to a head after World War II. Adams again tried to push the ESA into applied areas by having it raise an endowment to promote ecology. He predicted that "a great expansion of ecology" was imminent "because of its integrating tendency."[109] Ecologists, however, were sensitive to the perception that ecology was still not considered a rigorous, quantitative science. Those who pushed for applied studies and active involvement in conservation were once more discreetly rebuffed. Human ecology became subsumed by sociology. It was sociologist Lewis Mumford who brought the ideas of George Perkins Marsh to modern attention in the 1955 conference, "Man's Role in Changing the Face of the Earth." That prestigious conclave was dominated by social scientists. At it, ecology was accused of "lacking experimental methods" and neglecting "man as an ecological agent." One participant dismissed ecology as "archaic and sterile," (Hagen, 1992). Within the ESA, a frustrated Shelford started the Ecologists' Union when his Committee on Preservation of Natural Conditions ceased to function due to the political infighting over the ESA stance on conservation (Shelford, 1917). In 1950, the fledgling organization was renamed and incorporated as the Nature Conservancy, a name borrowed from the British government agency for the same purpose.

Two events, however, brought ecology's course back to applied problems. One was the Manhattan Project. It had become the Nuclear Energy Commission after the war. It is now the Department of Energy (DOE). Its ample budget included studies of the impacts of nuclear weapon use and production. That brought ecology to the issue, and it made a "Big Science" of it (Worster, 1994; Dritschilo, 2004). Ecosystem science, both basic and applied, began to compete with theoretical ecology (then called evolutionary ecology and also mathematical ecology). Eugene Odum, who published a very popular ecology textbook in 1953, became the champion of the ecosystem. In his publications, Odum called for ecology to have an ecosystem and applied focus (Miller, 1965).

The second event was the publication of Silent Spring. Rachel Carson's book brought ecology as a word and concept to the public. Her influence was instant. A study committee, prodded by the publication of the book, reported to the ESA that their science was not ready to take on the responsibility being given to it (Dritschilo, 2006).

Carson's concept of ecology was very similar to Gene Odum's (Blair, 1977). As a result, ecosystem science dominated the International Biological Program of the 1960s and 1970s, bringing both money and prestige to ecology (Kwa, 1987; Curlin, 1972). Silent Spring was also the impetus for the environmental protection programs that were started in the Kennedy and Johnson administrations and passed into law just before the first Earth Day. Ecologists' input was welcomed. Former ESA President Stanley Cain, for example, was appointed an Assistant Secretary in the Department of the Interior.

The environmental assessment requirement of the 1969 National Environmental Policy Act (NEPA), "legitimized ecology," in the words of one environmental lawyer (Auerbach, 1972). An ESA President called it "an ecological 'Magna Carta,'" (Schindler, 1976). A prominent Canadian ecologist declared it a "boondoggle," (Dritschilo, 2016). NEPA and similar state statutes, if nothing else, provided much employment for ecologists. Therein was the issue. Neither ecology nor ecologists were ready for the task. Not enough ecologists were available to work on impact assessment, outside of the DOE laboratories, leading to the rise of "instant ecologists," having dubious credentials and capabilities (Dritschilo, 2016). Calls began to arise for the professionalization of ecology. Maverick scientist Frank Egler, in particular, devoted his sharp prose to the task (Dale et al., 2000). Again, a schism arose between basic and applied scientists in the ESA, this time exacerbated by the question of environmental advocacy. The controversy, whose history has yet to receive adequate treatment, lasted through the 1970s and 1980s, ending with a voluntary certification process by the ESA, along with lobbying arm in Washington (Suter, 1981).

Post-Earth Day, besides questions of advocacy and professionalism, ecology also had to deal with questions having to do with its basic principles. Many of the theoretical principles and methods of both ecosystem science and evolutionary ecology began to show little value in environmental analysis and assessment (Peters, 1976). Ecologists, in general, started to question the methods and logic of their science under the pressure of its new notoriety (Ellison, 2006; Peters, 1991; Simberloff & Abele 1976). Meanwhile, personnel with government agencies and environmental advocacy groups were accused of religiously applying dubious principles in their conservation work (Chase, 1995). Management of endangered Spotted Owl populations brought the controversy to a head (Takacs, 1996).

Conservation for ecologists created travails paralleling those nuclear power gave former Manhattan Project scientists. In each case, science had to be reconciled with individual politics, religious beliefs, and worldviews, a difficult process. Some ecologists managed to keep their science separate from their advocacy; others unrepentantly became avowed environmentalists.[128]

Roosevelt & American conservation

Theodore Roosevelt was interested in nature from a young age. He carried his passion for nature into his political policies. Roosevelt felt it was necessary to preserve the resources of the nation and its environment. In 1902 he created the federal reclamation service, which reclaimed land for agriculture. He also created the Bureau of Forestry. This organization, headed by Gifford Pinchot, was formed to manage and maintain the nations timberlands.[129] Roosevelt signed the Act for the Preservation of American Antiquities in 1906. This act allowed for him to "declare by public proclamation historic landmarks, historic and prehistoric structures, and other objects of historic and scientific interest that are situated upon lands owned or controlled by the Government of the United States to be national monuments." Under this act he created up to 18 national monuments. During his presidency, Roosevelt established 51 Federal Bird Reservations, 4 National Game Preserves, 150 National Forests, and 5 National Parks. Overall he protected over 200 million acres of land (“Theodore Roosevelt and the Environment," n.d.; “Theodore Roosevelt and conservation,” n.d.).

Ecology and global policy

Ecology became a central part of the World's politics as early as 1971, UNESCO launched a research program called *Man and Biosphere*, with the objective of increasing knowledge about the mutual relationship between humans and nature. A few years later it defined the concept of Biosphere Reserve.

In 1972, the United Nations held the first international Conference on the Human Environment in Stockholm, prepared by Rene Dubos and other experts. This conference was the origin of the phrase "Think Globally, Act Locally". The next major events in ecology were the development of the concept of biosphere and the appearance of terms "biological diversity"—or now more commonly biodiversity—in the 1980s. These terms were developed during the Earth Summit in Rio de Janeiro in 1992, where the concept of the biosphere was recognized by the major international organizations, and risks associated with reductions in biodiversity were publicly acknowledged.

Then, in 1997, the dangers the biosphere was facing were recognized all over the world at the conference leading to the Kyoto Protocol. In particular, this conference highlighted the increasing dangers of the greenhouse effect – related to the increasing concentration of greenhouse gases in the atmosphere, leading to global changes in climate. In Kyoto, most of the world's nations recognized the importance of looking at ecology from a global point of view, on a worldwide scale, and to take into account the impact of humans on the Earth's environment.

Sources

1. McIntosh, R. P. (1985). *The background of ecology: Concept and theory*. Cambridge University Press.
2. Laferrière, E., & Stoett, P. J. (2003). *International relations theory and ecological thought: Towards a synthesis*. Routledge. pp. 25–. https://doi.org/10.4324/9781134710683
3. Ramalay, F. (1940). The growth of a science. *University of Colorado Studies*, 26, 3–14.
4. Reid, G. M. (2009). Carolus Linnaeus (1707–1778): His life, philosophy and science and its relationship to modern biology and medicine. *Taxon*, *58*(1), 18–31. https://doi.org/10.1002/tax.581005
5. Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M., & Biss, P. M. (2006). The Park Grass Experiment 1856–2006: Its contribution to ecology. *Journal of Ecology*, 94(4), 801–814. https://doi.org/10.1111/j.1365-2745.2006.01145.x
6. Coleman, W. (1986). Evolution into ecology? The strategy of Warming's ecological plant geography. *Journal of the History of Biology*, 19(2), 181–196. https://doi.org/10.1007/BF00138875
7. Acot, P. (1997). The Lamarckian cradle of scientific ecology. *Acta Biotheoretica*, 45(3/4), 185–193. https://doi.org/10.1023/A:1000631103244
8. Cowles, H. C. (1911). The causes of vegetational cycles. *Annals of the Association of American Geographers*, 1(1), 3–20. https://doi.org/10.2307/2560843
9. Egerton, F. N. (1973). Changing concepts of the balance of nature. *Quarterly Review of Biology*, 48(2), 322–350. https://doi.org/10.1086/407594

10. Egerton, F. N. (2001). A history of the ecological sciences, Part 1: Early Greek origins. *Bulletin of the Ecological Society of America*, 82, 93–97.
11. Smith, S. H. I., & Mark, S. (2009). The historical roots of the Nature Conservancy in the Northwest Indiana/Chicagoland region: From science to preservation. *The South Shore Journal*, 3, 1–10. Archived from the original on January 1, 2016.
12. Worster, D. (1994). *Nature's economy: A history of ecological ideas*. Cambridge University Press. ISBN 978-0-521-46834-3.
13. Malthus, T. R. (1798). *An essay on the principle of population* (Oxford World's Classics reprint, p. 61, end of Chapter VII).
14. Gilbert, G. (n.d.). Introduction to Malthus, T. R. (1798). *An essay on the principle of population* (Oxford World's Classics reprint, p. viii).
15. Malthus, T. R. (1798). *An essay on the principle of population* (Oxford World's Classics reprint, p. 13).
16. Gilbert, G. (n.d.). Introduction to Malthus, T. R. (1798). *An essay on the principle of population* (Oxford World's Classics reprint, p. xviii).
17. van Wyhe, J. (2008). *Darwin: The story of the man and his theories of evolution*. London: Andre Deutsch Ltd. ISBN 0-233-00251-0.
18. Todes, D. P. (1987). Darwin's Malthusian metaphor and Russian evolutionary thought, 1859-1917. *Isis*, *78*(4) pages 537-540.
19. Stauffer, R. C. (1957). Haeckel, Darwin and ecology. *Quarterly Review of Biology*, 32(2), 138–144. https://doi.org/10.1086/401754
20. Forbes, S. A. (1887). The lake as microcosm. *Bulletin of the Scientific Association*, 77–87. Archived from the original (PDF) on September 27, 2011. Retrieved January 19, 2010.
21. Paterson, H. (2005). The competitive Darwin. *Paleobiology*, *31*(2), 56–76. https://doi.org/10.1666/0094-8373(20...6:TCD]2.0.CO;2
22. Kormondy, E. J. (1978). Ecology/economy of nature—synonyms? *Ecology*, *59*(6), 1292–1294. https://doi.org/10.2307/1938247
23. McIntosh, R. P. (1985). *The background of ecology: Concept and theory*. Cambridge University Press.
24. Haeckel, E. (1866). *Generelle morphologie der organismen: Allgemeine grundzüge der organischen formen-wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte descendenz-theorie* (2 vols.). Reimer.
25. Allee, W. C., Emerson, A. E., Park, O., Park, T., & Schmidt, K. P. (1949). *Principles of animal ecology*. Saunders.
26. Southwood, R., & Clarke, J. R. (1999). Charles Sutherland Elton. *29 March 1900 – 1 May: Elected F.R.S. 1953*.
27. Elton, C. S. (1968). *Animal ecology* (Reprint). Great Britain: William Clowes and Sons Ltd.
28. Wilson, K. (2011). *Animal ecology: Legacy of Charles S. Elton*. Journal of Animal Ecology. Retrieved from http://www.journalofanimalecology.org/view/0/virtualissuelegacyofcharlesselton.html
29. Slobodkin, L. B. (1993). An appreciation: George Evelyn Hutchinson. *Journal of Animal Ecology*, *62*(2), 390–394. https://doi.org/10.2307/5370
30. Lovejoy, T. E. (2011). George Evelyn Hutchinson (13 January 1903 – 17 May 1991). *Biographical Memoirs of Fellows of the Royal Society*, *57*, 167–177. https://doi.org/10.1098/rsbm.2010.0016
31. See 23
32. Dritschilo, W. (2008). Bringing statistical methods to community and evolutionary ecology. In O. Harman & M. R. Dietrich (Eds.), *Rebels, mavericks, and heretics in biology* (pp. 356–371). Yale University Press.
33. See 23
34. Cook, R. E. (1977). Raymond Lindeman and the trophic-dynamic concept in ecology. *Science*, *198*(4312), 22–26. https://doi.org/10.1126/science.198.4312.22
35. Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/sqb.1957.022.01.039
36. Hutchinson, G. E. (1959). Homage to Santa Rosalia; or, why are there so many kinds of animals? *American Naturalist*, *93*(870), 145–159. https://doi.org/10.1086/282070
37. Bocking, S. (1997). *Ecologists and environmental politics: A history of contemporary ecology*. Yale University Press.
38. Craige, B. J. (2001). *Eugene Odum: Ecosystem ecologist and environmentalist*. University of Georgia Press.
39. Golley, F. B. (1993). *A history of the ecosystem concept in ecology*. Yale University Press.
40. BioScience. (1964). *BioScience*, 14(7).
41. Dritschilo, W. (2019). *Earth days reprised* (p. 161). Amazon.com.
42. MacArthur, R. H. (1955). Fluctuations of animal populations, and a measure of stability. *Ecology*, *36*(4), 533–536. https://doi.org/10.2307/1929601
43. MacArthur, R. H. (1957). On the relative abundance of bird species. *Proceedings of the National Academy of Sciences, USA*, *43*(3), 293–295. https://doi.org/10.1073/pnas.43.3.293

44. MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology, 39*(4), 599–619. https://doi.org/10.2307/1931600
45. Van Valen, L., & Pitelka, F. (1974). Commentary: Intellectual censorship in ecology. *Ecology, 55*, 925–926. https://doi.org/10.2307/1940345
46. Peters, R. H. (1976). Tautology in evolution and ecology. *American Naturalist, 110*(971), 1–12. https://doi.org/10.1086/283045
47. Engleberg, J., & Boyarsky, L. L. (1979). The noncybernetic nature of ecosystems. *The American Naturalist, 114*, 317–324.
48. Suter, G. W. (1981). Ecosystem theory and NEPA assessment. *Bulletin of the Ecological Society of America, 62*, 186–192.
49. Lewin, R. (1983). Santa Rosalia was a goat. *Science, 221*(4611), 636–639. https://doi.org/10.1126/science.221.4611.636
50. Cody, M. L., & Diamond, J. M. (Eds.). (1975). *Ecology and evolution of communities*. Harvard University Press.
51. Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Harvard University Press.
52. Quammen, D. (1996). *The song of the dodo: Island biogeography in an age of extinction*. Simon & Schuster.
53. Allen, T. F. H. (1981). The noble art of philosophical ecology. *Ecology, 62*(3), 870–871. https://doi.org/10.2307/1937754
54. Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Smithsonian Institution Press.
55. Strong, D. R., Jr., Simberloff, D., Abele, L. G., & Thistle, A. B. (Eds.). (1984). *Ecological communities: Conceptual issues and the evidence*. Princeton University Press.
56. Gilpin, M. E., & Diamond, J. M. (1984). Are species co-occurrences on islands non-random? In D. R. Strong, Jr., D. Simberloff, L. G. Abele, & A. B. Thistle (Eds.), *Ecological communities: Conceptual issues and the evidence* (pp. 297–315). Princeton University Press.
57. Roughgarden, J. (1983). Competition and theory in community ecology. *The American Naturalist, 122*(5), 583–601. https://doi.org/10.1086/284160
58. MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
59. Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of nature reserves. *Biological Conservation, 7*(2), 129–146. https://doi.org/10.1016/0006-3207(75)90052-x
60. Simberloff, D. S., & Wilson, E. O. (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology, 50*(2), 278–296. https://doi.org/10.2307/1934856
61. Simberloff, D. S., & Abele, L. G. (1976). Island biogeography theory and conservation practice. *Science, 191*(4224), 285–286. https://doi.org/10.1126/science.191.4224.285
62. Laurance, W. F. (2008). Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation, 141*(7), 1731–1744. https://doi.org/10.1016/j.biocon.2008.05.011
63. Kormondy, E. J. (1978). Ecology/economy of nature—synonyms? *Ecology, 59*(6), 1292–1294. https://doi.org/10.2307/1938247
64. Egerton, F. N. (2007). A history of the ecological sciences, part 23: Linnaeus and the economy of nature. *Bulletin of the Ecological Society of America, 88*(1), 72–88. https://doi.org/10.1890/0012-9623(20...HOTES]2.0.CO;2
65. ^ [1][*dead link*]
66. ^ *Darwin, C. (1859). On the Origin of Species (1st ed.). London: John Murray. ISBN 978-0-8014-1319-3.*
67. ^ *Country Towns, and the Place They Fill in Modern Civilization. Covent Garden: Bell & Daldy. 1868.*
68. ^ *Hardie-Budden, M. (2014). "Elizabeth Catherine Thomas Carne: A 19th century Hypatia and her circle". Transactions of the Royal Geological Society of Cornwall.* ***23*** *(1): 16–39. ISSN 0372-1108.*
69. ^ *Futuyma, D. J. (2005). "The Nature of Natural Selection". In Cracraft, J.; Bybee, R. W. (eds.). Evolutionary Science and Society: Educating a New Generation. American Institute of Biological Sciences. pp. 93–98.*
70. ^ *Glaubrecht, M. (2008). "Homage to Karl August Möbius (1825–1908) and his contributions to biology: zoologist, ecologist, and director at the Museum für Naturkunde in Berlin". Zoosystematics and Evolution.* ***84*** *(1): 9–30. doi:10.1002/zoos.200700010.*
71. ^ Jump up to:[a] [b] *Baker, H. G. (1966). "Reasoning about adaptations in ecosystems". BioScience.* ***16*** *(1): 35–37. doi:10.2307/1293551. JSTOR 1293551.*
72. ^ *Nyhart, L. K. (1998). "Civic and Economic Zoology in Nineteenth-Century Germany: The "Living Communities" of Karl Mobius". Isis.* ***89*** *(4): 605–630. doi:10.1086/384157. JSTOR 236735. S2CID 144650169.*
73. ^ *Palamar, C. R. (2008). "The Justice of Ecological Restoration: Environmental History, Health, Ecology, and Justice in the United States" (PDF). Human Ecology Review.* ***15*** *(1): 82–94.*
74. ^ *Forbes, S. A. (1915). "The ecological foundations of applied entomology" (PDF). Annals of the Entomological Society of America.* ***8*** *(1): 1–19. doi:10.1093/aesa/8.1.1. Archived from the original (PDF) on 27 September 2011. Retrieved 19 January2010.*

75. ^ Cohen, J. E. (1987). "Lotka, Alfred James (1880–1949)"(PDF). In Eatwell, J.; Newman, P. (eds.). The New Palgrave Dictionary of Economics. New York: Stockton Press. pp. 245–247. Archived from the original (PDF) on 26 June 2009.
76. ^ Volterra, V. (1926). "Fluctuations in the Abundance of a Species considered Mathematically". Nature. **118** (2972): 558–560. Bibcode:1926Natur.118..558V. doi:10.1038/118558a0. S2CID 4007591.
77. ^ Adams, C. C.; Fuller, G. D. (1940). "Henry Chandler Cowles, Physiographic Plant Ecologist". Annals of the Association of American Geographers. **31** (1): 39–43. doi:10.1080/00045604009357195. JSTOR 2561130.
78. ^ Smuts, Jan Christiaan (1926). "Holism and Evolution". Nature. **119** (2991): 307–309. Bibcode:1927Natur.119..307K. doi:10.1038/119307a0. S2CID 33107208.
79. ^ Cooper, W. S. (1957). "Sir Arthur Tansley and the Science of Ecology". Ecology. **38** (4): 658–659. doi:10.2307/1943136. JSTOR 1943136.
80. ^ Jump up to:[a] [b] [c] Kingsland, S. E. (1994). "Review: The History of Ecology". Journal of the History of Biology. **27** (2): 349–357. doi:10.1007/BF01062566. PMID 11639332. S2CID 6125993.
81. ^ Ilerbaig, J. (1999). "Allied Sciences and Fundamental Problems: C.C. Adams and the Search for Method in Early American Ecology". Journal of the History of Biology. **32** (3): 439–463. doi:10.1023/A:1004737021541. JSTOR 4331545. S2CID 82928157.
82. ^ Raup, H. M. (1959). "Charles C. Adams, 1873–1955". Annals of the Association of American Geographers. **49** (2): 164–167. doi:10.1111/j.1467-8306.1959.tb01607.x. JSTOR 2561526.
83. ^ Jump up to:[a] [b] [c] Simberloff, D. (1980). "A succession of paradigms in ecology: Essentialism to materialism and probalism". Synthese. **43**: 3–39. doi:10.1007/BF00413854. S2CID 46962930.
84. ^ Jump up to:[a] [b] [c] [d] Ellison, A. M. (2006). "What Makes an Ecological Icon". Bulletin of the Ecological Society of America. **87** (4): 380–386. doi:10.1890/0012-9623(2006)87[380:WMAEI]2.0.CO;2. S2CID 84751493.
85. ^ Kendeigh, S. C. (1968). "Victor Ernest Shelford, Eminent Ecologist, 1968". Bulletin of the Ecological Society of America. **49**(3): 97–100. JSTOR 20165761.
86. ^ Berryman, A. A. (1992). "The Origins and Evolution of Predator-Prey Theory" (PDF). Ecology. **73** (5): 1530–1535. doi:10.2307/1940005. JSTOR 1940005. Archived from the original (PDF) on 31 May 2010.
87. ^ McIntosh, R. P. (1975). "H. A. Gleason-"Individualistic Ecologist" 1882–1975: His Contributions to Ecological Theory". Bulletin of the Torrey Botanical Club. **105** (5): 253–278. doi:10.2307/2484142. JSTOR 2484142.
88. ^ Southwood, R.; Clarke, J. R. (1999). "Charles Sutherland Elton. 29 March 1900-1 May 1991". Biographical Memoirs of Fellows of the Royal Society. **45**: 131–146. doi:10.1098/rsbm.1999.0043. JSTOR 770268.
89. ^ Flannery, M. C. (2003). "Evelyn Hutchinson: A Wonderful Mind". The American Biology Teacher. **65** (6): 462–467. doi:10.1662/0002-7685(2003)065[0462:EHAWM]2.0.CO;2. JSTOR 4451536.
90. ^ Edmondson, Y. H. (1991). "In Memoriam: G. Evelyn Hutchinson, 1903–1991". Limnology and Oceanography. **36** (3): 618. doi:10.4319/lo.1991.36.3.0618. JSTOR 2837527.
91. ^ Patrick, R. (1994). "George Evelyn Hutchinson (30 January 1903–17 May 1991)". Proceedings of the American Philosophical Society. **138** (4): 531–535. JSTOR 986851.
92. ^ Jump up to:[a] [b] Gunderson, L.; Folke, C.; Lee, M.; Holling, C. S. (2002). "In memory of mavericks". Conservation Ecology. **6** (2): 19. doi:10.5751/ES-00423-060219.
93. ^ Jump up to:[a] [b] Rotabi, K. S. (2007). "Ecological Theory Origin from Natural to Social Science or Vice Versa? A Brief Conceptual History for Social Work". Advances in Social Work. **8** (1): 113–129. doi:10.18060/135.
94. ^ Patten, B. C. (1993). "Toward a more holistic ecology, and science: the contribution of H.T. Odum". Oecologia. **93** (4): 597–602. Bibcode:1993Oecol..93..597P. doi:10.1007/BF00328970. PMID 28313830. S2CID 230601.
95. ^ Ewel, J. J. (2003). "Howard Thomas Odum (1924–2002)". Bulletin of the Ecological Society of America. **84** (1): 13–15. doi:10.1890/0012-9623(2003)84[13:HTO]2.0.CO;2.
96. ^ Brown, J. H. (1999). "The Legacy of Robert Macarthur: From Geographical Ecology to Macroecology". Journal of Mammalogy. **80** (2): 333–344. doi:10.2307/1383283. JSTOR 1383283.
97. ^ Levin, Simon A. (1998). "Ecosystems and the Biosphere as Complex Adaptive Systems". Ecosystems. **1** (5): 431–436. doi:10.1007/s100219900037. S2CID 29793247.
98. ^ Allee, W. C.; Emerson, A. E.; Park, O.; Park, T.; Schmidt, K. P. (1949). Principles of Animal Ecology. Philadelphia: W. B. Saunders Company.
99. ^ Kingsland, S. E. (1985). Modeling Nature: Episodes in the History of Ecology. Chicago: University of Chicago Press.
100. ^ Huxley, J. S. (1942). Evolution: The Modern Synthesis. London: Allen & Unwin.
101. ^ Kingsland, S. E. (2005). The Evolution of American Ecology: 1890–2000. Baltimore: Johns Hopkins University Press.

102. ^ Jump up to:[a] [b] *Coker, R. A. (1991). Pioneer Ecologist: The Life and Work of Victor Ernest Shelford, 1877–1968. Washington: Smithsonian Institution Press.*
103. ^ *Shelford, V. E. (1917). "The Ideals and Aims of the Ecological Society of America". Bulletin of the Ecological Society of America. **1**: 1–2.*
104. ^ *Forbes, S. A. (1922). "The Humanizing of Ecology". Ecology. **3**(2): 89–92. doi:10.2307/1929143. JSTOR 1929143.*
105. ^ *Adams, C. C. (1935). "The Relation of General Ecology to Human Ecology". Ecology. **16** (3): 316–335. doi:10.2307/1930072. JSTOR 1930072.*
106. ^ *Clements, F. E. (1935). "Experimental Ecology in the Public Service". Ecology. **16** (3): 342–63. doi:10.2307/1930074. JSTOR 1930074.*
107. ^ *Sears, P. B. (1935). Deserts on the March. Norman: University of Oklahoma Press.*
108. ^ *Adams, C. C. (1947). "First Report of the committee of the Ecological Society of America for an Endowment Policy and Program". Ecological Society of America.*
109. ^ *Thomas, W. L. Jr., ed. (1956). Man's Role in Changing the Face of the Earth. Chicago: University of Chicago Press.*
110. ^ *Hagen, J. B. (1992). An Entangled Bank, The Origins of Ecosystem Ecology. New Brunswick, NJ: Rutgers University Press.*
111. ^ *Dritschilo, W. (2004). Earth Days: Ecology Comes of Age as a Science. iUniverse.*
112. ^ *Miller, R. S. (1965). "Summary Report of the Ecological Study Committee with Recommendations for the Future of Ecology and the Ecological Society of America". Bulletin of the Ecological Society of America. **46**: 61–81.*
113. ^ *Dritschilo, W. (2006). "Rachel Carson and Mid-Twentieth Century Ecology". Bulletin of the Ecological Society of America. **87** (4): 357–367. doi:10.1890/0012-9623(2006)87[357:RCAMCE]2.0.CO;2.*
114. ^ *Blair, W. F. (1977). Big Biology: The US/IBP. Stroudsburg, PA: Hutchinson & Ross.*
115. ^ *Kwa, C. (1987). "Representations of Nature Mediating between Ecology and Science Policy: The Case of the International Biological Programme". Social Studies of Science. **17** (3): 413–442. doi:10.1177/030631287017003002. S2CID 143156381.*
116. ^ *Curlin, J. W. (1972). "Courts, Ecology, and Environmental Planning". Ecology. **53** (3): 373–374. doi:10.2307/1934222. JSTOR 1934222.*
117. ^ *Auerbach, S. I. (1972). "Ecology, Ecologists and the E.S.A". Ecology. **53** (2): 204–207. doi:10.2307/1934073. JSTOR 1934073.*
118. ^ *Schindler, D. W. (1976). "The Impact Statement Boondoggle". Science. **192** (4239): 506. Bibcode:1976Sci...192..509S. doi:10.1126/science.192.4239.509. PMID 17745634.*
119. ^ Dritschilo, W. (2016) *Magnificent Failure: Frank Egler and the Greening of American Ecology, An Epistolary Biography*. Samizdat 2016 (Available from Amazon.com) p 360.
120. ^ Dritschilo, W. (2016) *Magnificent Failure: Frank Egler and the Greening of American Ecology, An Epistolary Biography*. Samizdat 2016 (Available from Amazon.com) pp 358-368.
121. ^ *Dale, V. H.; Barrett, G. W.; Carpenter, A. T.; Hinkle, C. R.; Mitsch, W. J.; Pitelka, L. F. (2000). "ESA's Professional Certification Program: Let's Make It Work". Bulletin of the Ecological Society of America. **81** (4): 255–257. doi:10.1890/0012-9623(2000)081[0255:C]2.0.CO;2.*
122. ^ *Suter, G. W. (1981). "Ecosystem Theory and NEPA Assessment". Bulletin of the Ecological Society of America. **62**: 186–192.*
123. ^ *Peters, R. H. (1976). "Tautology in Evolution and Ecology". The American Naturalist. **110** (971): 1–12. doi:10.1086/283045. S2CID 84636015.*
124. ^ *Peters, R. H. (1991). A Critique for Ecology. Cambridge: Cambridge University Press.*
125. ^ *Simberloff, D. S.; Abele, L. G. (1976). "Island Biogeography Theory and Conservation Practice". Science. **191** (4224): 285–6. Bibcode:1976Sci...191..285S. doi:10.1126/science.191.4224.285. PMID 17832147. S2CID 12912668.*
126. ^ *Chase, A. (1995). In a Dark Wood: The Fight Over Forests and the Rising Tyranny of Ecology. New York: Houghton Mifflin Company.*
127. ^ *Takacs, D. (1996). The Idea of Biodiversity: Philosophies of Paradise. Baltimore: Johns Hopkins University Press.*
128. ^ *"Theodore Roosevelt and the Environment". PBS. Retrieved 7 April 2014.*
129. ^ *"Theodore Roosevelt and conservation". National Park Service. Retrieved 7 April 2014.*

1.4: Subdisciplines of Ecology

Skills to Develop:

- Appreciate the diversity of ecological studies
- Understand how ecology interacts with other fields

Subdisciplines of ecology, and subdiscipline classification

Ecology is a broad discipline comprising many subdisciplines. The field of ecology can be subdivided according to several classification schemes:

By methodology used for investigation

- Field ecology – collection of information outside a laboratory, library or workplace setting
- Quantitative ecology – the application of advanced mathematical and statistical tools to any number of problems in the field of ecology
- Theoretical ecology – the development of ecological theory, usually with mathematical, statistical and/or computer modeling tools

By spatial scale of ecological system under study

- Global ecology – the global sum of all biospheres on Earth
- Macroecology – study of relationships between organisms and their environment at large spatial scales
- Microecology – microbial ecology or ecology of a microhabitat

By level of organisation or scope

Arranged from lowest to highest level of organisation:[1]

- Autecology – the study of individual organisms of a single species in relation to their environment
- Synecology – the study of homogenous or heterogenous groups of organisms in relation to their environment
    - Population ecology – study of the dynamics of species populations and how these populations interact with the environment – the study of homogenous groups of organisms related as a single species
    - Community ecology – associated populations of species in a given area – the study of heterogenous groups of organisms comprised of multiple associated species
    - Ecosystem ecology – study of living and non-living components of ecosystems and their interactions

By biological classification or taxon under study

- Human ecology – study of the relationship between humans and their natural, social, and built environments
- Animal ecology – scientific study of the relationships between living animals and their environment
- Insect ecology – the study of how insects interact with the surrounding environment
- Microbial ecology – study of the relationship of microorganisms with their environment
- Plant ecology – the study of effect of the environment on the abundance and distribution of plants.

By biome under study

- Benthic ecology – the study of the interaction of deep-dwelling aquatic organisms with each other and with the environment
- Desert ecology – the study of interactions between both biotic and abiotic components of desert environments
- Forest ecology – study of interactions between the biota and environment in forests
- Grassland ecology – study of area with vegetation dominated by grasses
- Marine ecology – the study of the interactions between organisms and environment in the sea
- Aquatic ecology – the study of interactions between organisms and the environment in water
- Urban ecology – study of the relation of living organisms with each other and their surroundings in the context of an urban environment

By biogeographic realm or climatic area under study

- Arctic ecology – the study of the relationships between biotic and abiotic factors in the arctic
- Polar ecology – the relationship between plants and animals and a polar environment
- Tropical ecology – the study of the relationships between the biotic and abiotic components of the tropics.

By ecological aspects or phenomena under investigation

- Behavioral ecology – study of the evolutionary basis for animal behavior due to ecological pressures
- Chemical ecology – study of chemically-mediated interactions between living organisms – which deals with the ecological role of biological chemicals used in a wide range of areas including defense against predators and attraction of mates
- Disease ecology – sub-discipline of ecology – which studies host-pathogen interactions, particularly those of infectious diseases, within the context of environmental factors;
- Ecophysiology – study of adaptation of an organism's physiology (studies the interaction of physiological traits with the abiotic environment) to environmental conditions
- Ecotoxicology – which looks at the ecological role of toxic chemicals (often pollutants, but also naturally occurring compounds)
- Evolutionary ecology – interaction of biology and evolution – or ecoevolution which looks at evolutionary changes in the context of the populations and communities in which the organisms exist
- Fire ecology – study of fire in ecosystems, which looks at the role of fire in the environment of plants and animals and its effect on ecological communities
- Functional ecology – the study of the roles, or functions, that certain species (or groups thereof) play in an ecosystem
- Genetic ecology – study of genetic material in the environment
- Landscape ecology – science of relationships between ecological processes in the environment and particular ecosystems
    - Landscape limnology – spatially explicit study of lakes, streams, and wetlands as they interact with freshwater, terrestrial, and human landscapes to determine the effects of pattern on ecosystem processes across temporal and spatial scales
- Molecular ecology – a field of evolutionary biology that applies molecular population genetics, molecular phylogenetics, and genomics to traditional ecological questions
- Paleoecology – study of interactions between organisms and their environments across geologic timescales
- Social ecology – study of relationships between people and their environment
- Soil ecology – the ecology of the pedosphere
- Spatial ecology – study of the distribution or space occupied by species
- Thermal ecology – the study of the relationship between temperature and organisms

Ecology-involved interdisciplinary fields

- Agroecology – study of ecological processes in agriculture
- Applied ecology – the practice of employing ecological principles and understanding to solve real world problems
    - Conservation ecology – study of threats to biological diversity, which studies how to reduce the risk of species extinction
    - Restoration ecology – scientific study of renewing and restoring ecosystems, which attempts to understand the ecological basis needed to restore impaired or damaged ecosystems
- Biogeochemistry – study of chemical cycles of the earth that are either driven by or influence biological activity
- Biogeography – study of the distribution of species and ecosystems in geographic space and through geological time
- Ecological design – design that minimizes environmentally destructive impacts by integrating itself with living processes
- Ecological economics – interdependence of human economies and natural ecosystems
- Ecological engineering – environmental engineering
- Ecological anthropology – study of cultural adaptations to environments
    - Festive ecology – study of the relationships between the symbolism and the ecology of the plants, fungi and animals associated with cultural events
- Ecological health
- Ecosophy – philosophy of ecological harmony or equilibrium as developed by Arne Næss or Félix Guattari
- Environmental psychology – academic study of the mind's relationship to one's immediate surroundings
- Natural history – study of organisms including plants or animals in their environment
- Systems ecology – holistic approach to the study of ecological systems

Other disciplines

Ecology has also inspired (and lent its name to) other non-biological disciplines such as:

- Media ecology
- Industrial ecology
- Information ecology

SECTION OVERVIEW

1.5: An Overview of Essential Mathematics Used in Science

Mathematics is the abstract science of numbers, quantity and space. Mathematics may be studied in its own right (pure mathematics), or as it is applied to scientific disciplines such as (applied mathematics).

Statistics is a mathematical body of science that pertains to the collection, analysis, interpretation or explanation, and presentation of data, or as a branch of mathematics.

Quantitative ecology is the application of advanced mathematical and statistical tools to any number of problems in the field of ecology. It is a small but growing subfield in ecology, reflecting the demand among practicing ecologists to interpret ever larger and more complex data sets using quantitative reasoning. Quantitative ecologists might apply some combination of deterministic or stochastic mathematical models to theoretical questions or they might use sophisticated methods in applied statistics for experimental design and hypothesis testing. Typical problems in quantitative ecology include estimating the dynamics and status of wild populations, modeling the impacts of anthropogenic or climatic change on ecological communities, and predicting the spread of invasive species or disease outbreaks.

Quantitative ecology, which mainly focuses on statistical and computational methods for addressing applied problems, is distinct from theoretical ecology which tends to explore focus on understanding the dynamics of simple mechanistic models and their implications for a general set of biological systems using mathematical arguments.

How does mathematics and statistics integrate into the scientific method?

Mathematics and statistics are vital for scientific inquiry. It is an especially imperative tool for disciplines that are inherently variable and require extensive collection of data. Ideally scientists would like to collect data from every individual in the population of interest, but this is rarely possible. As a result, scientists often must use data collected from a representative sample of individuals to draw inferences about basic biological phenomena for a population. This is where mathematics and statistics steps into the party.

What are the most important functions of statistics?

Some of the most important functions of statistics include:

- Description and summary of basic findings (Descriptive statistics).
- Testing hypotheses regarding relationships between variables so the cause and effect can begin to be understood (Inferential statistics).
- Presenting findings in an easily understood manner – misunderstandings keep science from moving forward!

Contributors and Attribution

Modified by Melissa Ha and Rachel Schleiger (CC-BY-NC) and Quantitative ecology From Wikipedia, the free encyclopedia

1.5.2: Summarizing data--Descriptive statistics

1.5.3: Testing hypotheses--Inferential statistics

1.5.1: Essential mathematical and statistical terms and concepts

General terms:

- Data – Systematically recorded information.
- Value – Each measurement or observation
- Variable – The object being controlled, manipulated, measured or observed. There are two main types:
  - Independent (explanatory) – The variable that you think will affect what is being measured/observed.
  - Dependent (response) – The variable that is being measured.
- Population – Entire set of objects to be studied.
  - Parameter – Numerical characteristic of population.
- Sample – Sub-collection of objects from population.
  - Statistic – Numerical characteristic of sample from population.

Example

You are a biologist who studies how monarch butterfly (*Danaus plexippus*) populations are affected by habitat destruction. You set up a long-term study to monitor populations in degraded, intact, and restored habitats where monarchs historically have been recorded/observed.

- Population: All monarch butterflies.
- Parameter: Not possible to collect a population worth of data for monarchs. Thus, no parameters can be calculated.
- Sample: Total monarchs observed at each field site during each year of the study.
- Statistic: Any calculations/manipulations from the field site data.

Types of statistics:

- Descriptive statistics – Are calculations to summarize trends in the data. Minimally, measures of center (averages) and spread (standard deviations) from data recorded.
- Inferential statistics – The point of inferential statistics is to take data from the sample to make inferences about the population. Calculations here test hypotheses and try to find/infer cause-and-effect relationships and/or correlations.

It is important to note that statistics can only be helpful if the data from the sample is representative of the population and the interpretation of the data is unbiased!

Types of data:

- Qualitative (categorical) data – Data expressed not in terms of numbers, but rather by means of a natural language description. There are two main types of qualitative data:
  - Ordinal – When categories are in a particular order (ex: large, medium, small)
  - Nominal – When categories have no natural ordering (ex: dog breed, color)

  Graphs types used: Pie, bar
- Quantitative (numerical) data – Data expressed not by means of a natural language description, but rather in terms of numbers. There are two main types of quantitative data:
  - Continuous – Numbers where any integer or fraction can be observed (ex: time, height, or weight)
  - Discrete – A fixed number of outcomes is possible such that there are only whole integers possible (ex: counts)

  Graphs types used: Histograms, line-graphs, scatterplots

Attribution

Rachel Schleiger (CC-BY-NC)

1.5.2: Summarizing data--Descriptive statistics

How do you summarize data?

Data is summarized in two main ways: summary calculations and summary visualizations.

Calculations: What types of measures are used?

To be able to interpret patterns in the data, raw data must first be manipulated and summarized into two categories of measurements: measures of central tendency and measures of variability. These two categories of measurements encapsulate the first step of scientific inquiry, descriptive statistics.

Measures of central tendency (center) – Provides information of how data cluster around some single middle value. While there are several ways to measure central tendency, the two measures most often used in Ecology are the mean and the median:

- **Mean** (average) – Sum of all individual values (Σx_i) divided by total number of values in sample/population (n). This is the most commonly used measure of central tendency under symmetrical (normal) distribution. It is sensitive to outliers. The sample mean is usually denoted $\bar{x}$.
- **Median** – The middle value when the data set is ordered in sequential rank. This is commonly used when data is skewed and is resistant to outliers. Notice that if there is an even number of values, the median is calculated by adding the middle two values, and dividing by 2:

  for an odd number of values, ranked smallest to largest: 1, 3, 3, **6**, 7, 8, 9. The median is **6**.

  for an even number of values, ranked smallest to largest: 1, 2, 3, **4, 5**, 6, 7, 9. The median is $(4+5) \div 2 \; = 4.5$.

- **Mode** – The most frequently occurring value in the sample. This is less often used in Ecology.

Measures of variability (spread) – Describes how spread out or dispersed the data are. There are two main measures of spread used in biological inquiry:

- **Range** – Quantifies the distance between the largest and smallest data values.
- **Standard deviation** – Quantifies the variation or dispersion from the average of a dataset. A low standard deviation indicates that the data tends to be very close to the mean; a high standard deviation indicates that the data points are spread out over a large range of values. This calculation is sensitive to outliers. The standard deviation of a sample is denoted with a lower case s and is calculated as follows:

$$s = \sqrt{\frac{(x_i - \bar{x})^2}{n-1}} \tag{1.5.2.1}$$

  Notice that the numerator in the formula for the standard deviation includes the term $(x_i - \bar{x})$ which measures how far each individual value (x_i) is from the sample mean $\bar{x}$. If the data are highly dispersed/variable, some of these values will be larger, and hence the standard deviation will be large.

- **Standard error (SE)** – Quantifies how different the sample mean (the average of the data values you have) is likely to be from the mean for the whole population mean (i.e., what you are trying to estimate). It tells you how much the sample mean would vary if you were to repeat a study using new samples from within a single population. The standard error is calculated by dividing the standard deviation by the square root of the sample size:

$$SE = \frac{s}{\sqrt{n}} \tag{1.5.2.2}$$

Visualizing the data: How are tables and graphs used?

After all desired descriptive statistics are calculated, they are typically visually summarized into either a table or graph.

Tables:

A **table** is a set of data values arranged into columns and rows. Typically the columns encompass a broad data category, and the rows encompass another. Within each broad category, there are subcategories that determine how many columns and rows the table consists of. Tables are used to both collect and summarize data. However, most of the time when tables are presented, they consist of summarized data, not raw data. Although tables allow summarized data to be presented in an orderly manner, most people prefer to translate tables into the more powerful data visualization tool, a graph.

Graphs:

A **graph** is a diagram showing the relation between variable quantities, typically of two variables, each measured along one of a pair of axes at right angles. Graphs can look like a chart or drawing. Most graphs use bars, lines, or parts of a circle to display data. However, there are sometimes when graphs are overlaid on top of maps to also display geographical location, or are even animated to be interactive.

Major graph type categories:

- **Circle/Pie –** A circular chart divided into slices to illustrate numerical proportion. In a pie chart, the arc length of each slice (and consequently its central angle and area), is proportional to the quantity it represents. While it is named for its resemblance to a pie that has been sliced, there are variations on the way it can be presented.
- **Line** – A type of chart which displays information as a series of data points called 'markers' connected by straight line segments. It is a basic type of chart common in many fields. It is similar to a scatter plot except that the measurement points are ordered in sequence (typically by their x-axis value) and joined with straight line segments. A line chart is often used to visualize a trend in data over intervals of time – a time series – thus the line is often drawn chronologically.

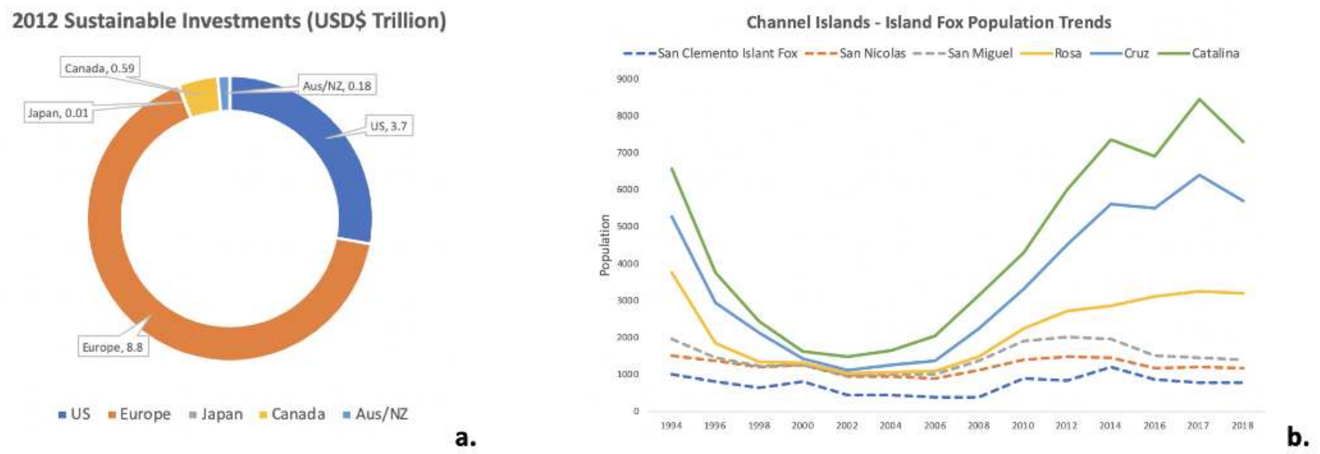


Figure 1.5.2.1 : Examples of a circle/pie graph (a.) and a line graph (b.). Image created by Rachel Schleiger (CC-BY-NC).

- **Scatter plot** – A graph in which the values of two variables are plotted along the horizontal and vertical axes, the pattern of the resulting points revealing any correlation preset. The data are displayed as a collection of points, each having the value of one variable determining the position on the horizontal axis and the value of the other variable determining the position on the vertical axis.

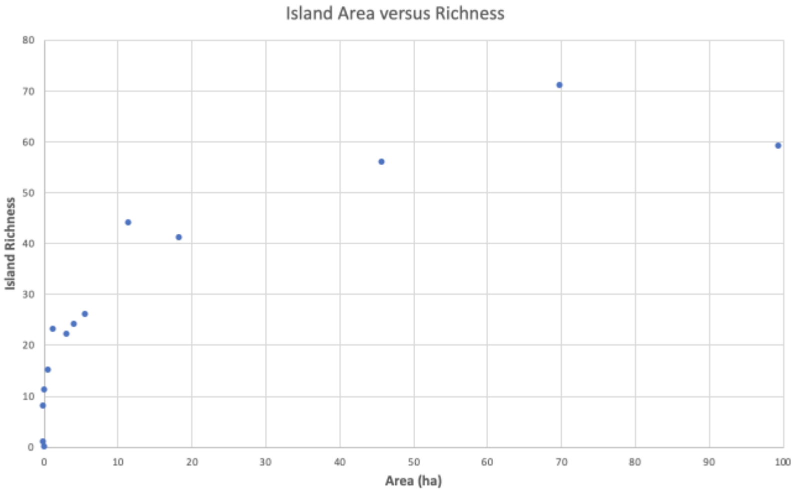


Figure 1.5.2.2 : Example of a scatter plot. Image created by Rachel Schleiger (CC-BY-NC).

- **Bar** – A chart or graph that presents categorical data with rectangular bars with heights or lengths proportional to the values that they represent. The bars can be plotted vertically or horizontally.
- **Histogram** – Is an approximate representation of the distribution of numerical data. To construct a histogram, the first step is to "bin" (or "bucket") the range of values—that is, divide the entire range of values into a series of intervals—and then count how many values fall into each interval. The bins are usually specified as consecutive, non-overlapping intervals of a variable. The bins (intervals) must be adjacent (meaning there are not spaces between them like there are in bar graphs), and are often (but not required to be) of equal size. If the bins are of equal size, a rectangle is erected over the bin with height proportional to the frequency—the number of cases in each bin.

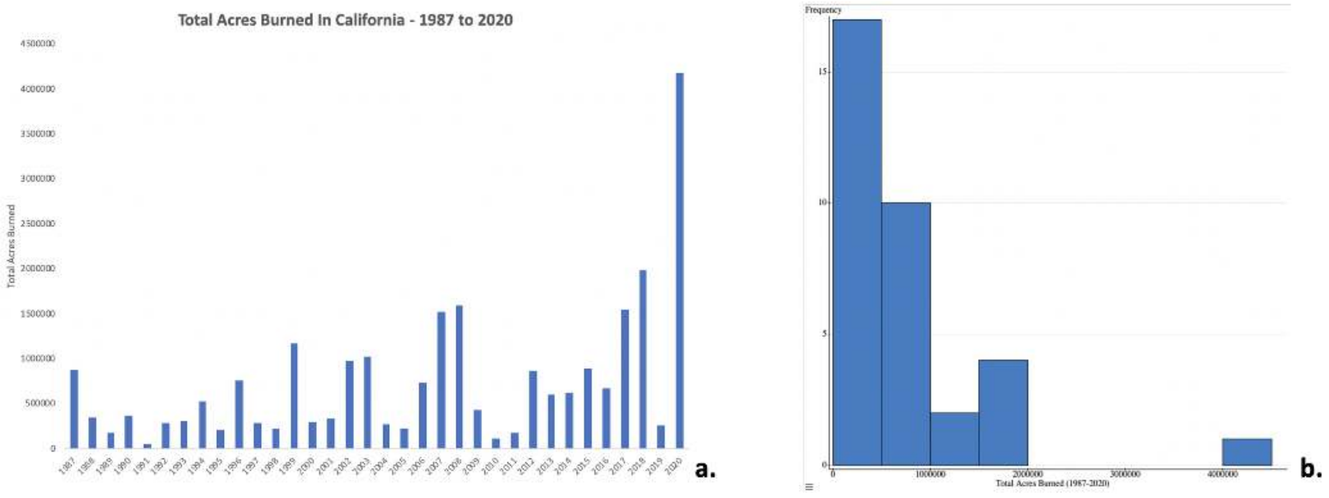


Figure 1.5.2.3 : Examples of a bar graph (a.) and a histogram (b.) using the same dataset. Image created by Rachel Schleiger (CC-BY-NC).

Characteristics of effective graphical displays

> *The greatest value of a picture is when it forces us to notice what we never expected to see.*

Professor Edward Tufte explained that users of information displays are executing particular *analytical tasks* such as making comparisons. The *design principle* of the information graphic should support the analytical task.[1] As William Cleveland and

Robert McGill show, different graphical elements accomplish this more or less effectively. For example, dot plots and bar charts outperform pie charts.[12]

In his 1983 book *The Visual Display of Quantitative Information*, Edward Tufte defines 'graphical displays' and principles for effective graphical display in the following passage: "Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency. Graphical displays should:

- show the data
- induce the viewer to think about the substance rather than about methodology, graphic design, the technology of graphic production, or something else
- avoid distorting what the data has to say
- present many numbers in a small space
- make large data sets coherent
- encourage the eye to compare different pieces of data
- reveal the data at several levels of detail, from a broad overview to the fine structure
- serve a reasonably clear purpose: description, exploration, tabulation, or decoration
- be closely integrated with the statistical and verbal descriptions of a data set.

Graphics *reveal* data. Indeed graphics can be more precise and revealing than conventional statistical computations."[3]

1. *techatstate (7 August 2013). "Tech@State: Data Visualization - Keynote by Dr Edward Tufte". Archived from the original on 29 March 2017. Retrieved 29 November 2016 – via YouTube.*
2. *leveland, W. S.; McGill, R. (1985). "Graphical perception and graphical methods for analyzing scientific data". Science.* ***229*** *(4716): 828–833. Bibcode:1985Sci...229..828C. doi:10.1126/science.229.4716.828. PMID 17777913. S2CID 16342041.*
3. *Tufte, Edward (1983). The Visual Display of Quantitative Information. Cheshire, Connecticut: Graphics Press. ISBN 0-9613921-4-2. Archived from the original on 2013-01-14. Retrieved 2019-08-10.*

Explore data visualizations at from data to viz.

Attribution

Rachel Schleiger (CC-BY-NC) and Data Visualization From Wikipedia, the free encyclopedia, modified by Andy Wilson.

1.5.3: Testing hypotheses--Inferential statistics

What is a hypothesis and are there different kinds?

Biological (Scientific) hypothesis: An idea that proposes a tentative explanation about a phenomenon or a narrow set of phenomena observed in the natural world. This is the backbone of all scientific inquiry! As such it is important to have a solid biological hypothesis before moving forward in the scientific method (i.e. procedures, results, discussion). After the creation of a solid biological hypothesis, it can then be simplified into a statistical hypothesis (as defined below) that will become the basis for how the data will be analyzed and interpreted.

Statistical hypotheses: After defining a strong biological hypothesis, a statistical hypothesis can be created based on what youp predict will be the measured outcome(s) (dependent variable(s)). If a study has multiple measured outcomes there can be multiple statistical hypotheses. Each statistical hypothesis will have two components (Null and Alternative).

- **Null hypothesis** (H_0) – This hypothesis states that there is no relationship (or no pattern) between the independent and dependent variables.
- **Alternative hypothesis** (H_1) – This hypothesis states that there is a relationship (or is a pattern) between the independent and dependent variables.

Independent versus dependent variables: For both biological and statistical hypotheses there should be two basic variables defined:

- **Independent (explanatory) variable** – It is usually what phenomena you think will affect the measure you are interested in (dependent variable).
- **Dependent (response) variable** – A dependent variable is what you measure in the experiment and what is affected during the experiment. The dependent variable responds to (depends on) the independent variable. In a scientific experiment, you cannot have a dependent variable without an independent variable.

Example

Yellow-billed Cuckoo nests were counted during breeding season in degraded, restored, and intact riparian habitats to see overall habitat preference for nesting sites increased with habitat health.

- Scientific hypothesis: yellow-billed Cuckoo will have habitat preferences because of habitat health/status
- Statistical hypotheses: (H_0) there will be no differences in number of nests between habitats with different health/status; (H_1) there will be more nests in restored and intact habitats compared to degraded
- Independent variable = habitat health/status
- Dependent variable = number of nests counted

How do you reach conclusions?

Finally, after defining the biological hypothesis, statistical hypothesis, and collecting all your data, a researcher can begin statistical analysis. A statistical test will mathematically “test” your data against the statistical hypothesis. The type of statistical test that is used depends on the type and quantity of variables in the study, as well as the question the researcher wants to ask. After computing the statistical test, the outcome will indicate which statistical hypothesis is more likely. This, in turn indicates to scientists what level of inference can be gained from the data compared to the biological hypothesis (the focus point of the study). Then a conclusion can be made based on the sample about the entire population. It is important to note that the process does not stop here. Scientists will want to continue to test this conclusion until a clear pattern emerges (or not) or to investigate similar but different questions.

Types of Basic Statistical Tests

Inferential statistics generally provide a test statistic, the degrees of freedom (related to the number of individuals in each sample) and a p-value. Significance (acceptance of the alternative hypothesis) is generally based on the p-value. Depending on the field, scientists will often use a cut-off of 0.01 or 0.05 to determine significance. If the test returns a p-value that is less than this value, the relationship is deemed significant.

- **Chi-Square – Are two categorical variables related?**
  - (e.g. do different habitats different in the numbers of species of each type?)
- **T-Test – Does the mean (continuous data) of one group (a categorical variable) differ from the mean of another group?**
  - (e.g. are oak trees taller than hickory trees, on average?)
- **ANOVA – Does the mean of several groups differ? A post-hoc test is used to run pairwise comparisons if so**
  - (e.g. does height differ across tree species, on average?)
- **Linear regression - Are two continuous variables linearly related?**
  - (e.g. do taller trees have a larger circumference?)

The “Magic” level of Significance

- **p-value** – probability of achieving the observed result given no experimental effect

If $p \leq 0.05$ – accept alternative hypothesis

- There is less than 5% chance that the samples are from the same population
- There is a significant difference between the samples

If $p > 0.05$ – accept null hypothesis

- There is no significant difference between the samples

Attribution

Rachel Schleiger (CC-BY-NC)

CHAPTER OVERVIEW

2: The Physical Environment

Learning Objectives

- Outline the properties of water that are essential for life as we know it on Earth.
- Describe the hydrologic cycle including the important reservoirs for water on Earth and processes that move water between reservoirs (or pools).
- Define characteristics of soils and the factors that determine what type of soil develops in a given location.
- Discuss the layers in Earth's atmosphere and distinguish between climate and weather in Ecology.
- Illustrate the important factors in Earth's energy balance.
- Communicate the causes and climate consequences of Atmospheric and Oceanic circulation.
- Delineate the natural causes of climate change on Earth.
- Summarize some important changes in Earth's climate through geologic time.

Summary

This chapter describes the physical environment of the planet Earth and the importance of the physical environment for the field of Ecology. Sections 2.1 and 2.2 discuss important properties of water and they hydrologic cycle. Section 2.3 characterizes soils, their importance for ecology, and how they form. Earth's atmosphere, energy balance and atmospheric and oceanic circulation are detailed in sections 2.4, 2.5, and 2.6. Finally Sections 2.7 and 2.8 illustrate the natural causes of climate change on earth and some of the important past changes in Earth's climate. For a description of the human impact on current and future global climate, see the chapter on "Human Impact on Global Climate".

2.1: Properties of Water

Do you ever wonder why scientists spend time looking for water on other planets? It is because water is essential to life, as we understand it; even minute traces of it on another planet can indicate that life could or did exist on that planet. Water is one of the more abundant molecules in living cells and the one most critical to life as we know it. Approximately 60–70 percent of your body is made up of water. Without it, life simply would not exist.

Water Is a Polar Molecule

The hydrogen and oxygen atoms within water molecules form polar covalent bonds. The shared electrons spend more time associated with the oxygen atom than they do with hydrogen atoms. There is no overall charge to a water molecule, but there is a slight positive charge on each hydrogen atom and a slight negative charge on the oxygen atom. Because of these charges, the slightly positive hydrogen atoms repel each other and form the unique shape seen in (Figure $2.1.1$).

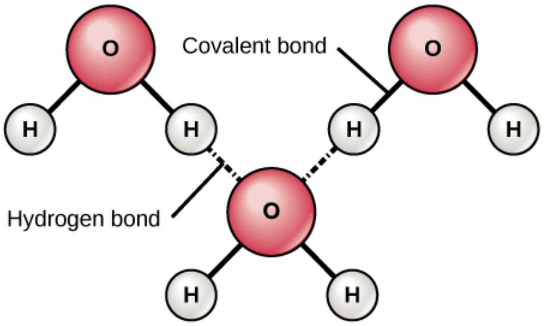


Figure $2.1.1$: Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water.

Each water molecule attracts other water molecules because of the positive and negative charges in the different parts of the molecule allowing the formation of hydrogen bonds. Water also attracts and form hydrogen bonds with other polar molecules (such as sugars). When a substance readily forms hydrogen bonds with water, it can dissolve in water and is referred to as hydrophilic (“water-loving”). Hydrogen bonds are not readily formed with nonpolar substances like oils and fats. These nonpolar compounds are hydrophobic (“water-fearing”) and will not dissolve in water.

Water Stabilizes Temperature

Temperature is a measure of the motion (kinetic energy) of molecules. As the motion increases, energy is higher and thus temperature is higher. Water absorbs a great deal of energy before its temperature rises. Increased energy disrupts the hydrogen bonds between water molecules. The hydrogen bonds in water allow it to absorb and release heat energy more slowly than many other substances (giving water a high specific heat). Because these bonds can be created and disrupted rapidly, water absorbs an increase in energy and temperature changes only minimally. This means that water moderates temperature changes within organisms and in their environments. As energy input continues, the balance between hydrogen-bond formation and destruction swings toward the destruction side. More bonds are broken than are formed. This process results in the release of individual water molecules at the surface of the liquid (such as a body of water, the leaves of a plant, or the skin of an organism) in a process called evaporation. Evaporation of sweat, which is 90 percent water, allows for cooling of an organism, because breaking hydrogen bonds requires an input of energy and takes heat away from the body.

Conversely, as molecular motion decreases and temperatures drop, less energy is present to break the hydrogen bonds between water molecules. These bonds remain intact and begin to form a rigid, lattice-like structure (e.g., ice) (Figure $2.1.2\mathbf{a}$). When frozen, ice is less dense than liquid water (the molecules are farther apart). This means that ice floats on the surface of a body of water (Figure $2.1.2\mathbf{b}$). In lakes, ponds, and oceans, ice will form on the surface of the water, creating an insulating barrier to protect the animal and plant life beneath from freezing in the water. If this did not happen, plants and animals living in water would freeze in a block of ice and could not move freely, making life in cold temperatures difficult or impossible.

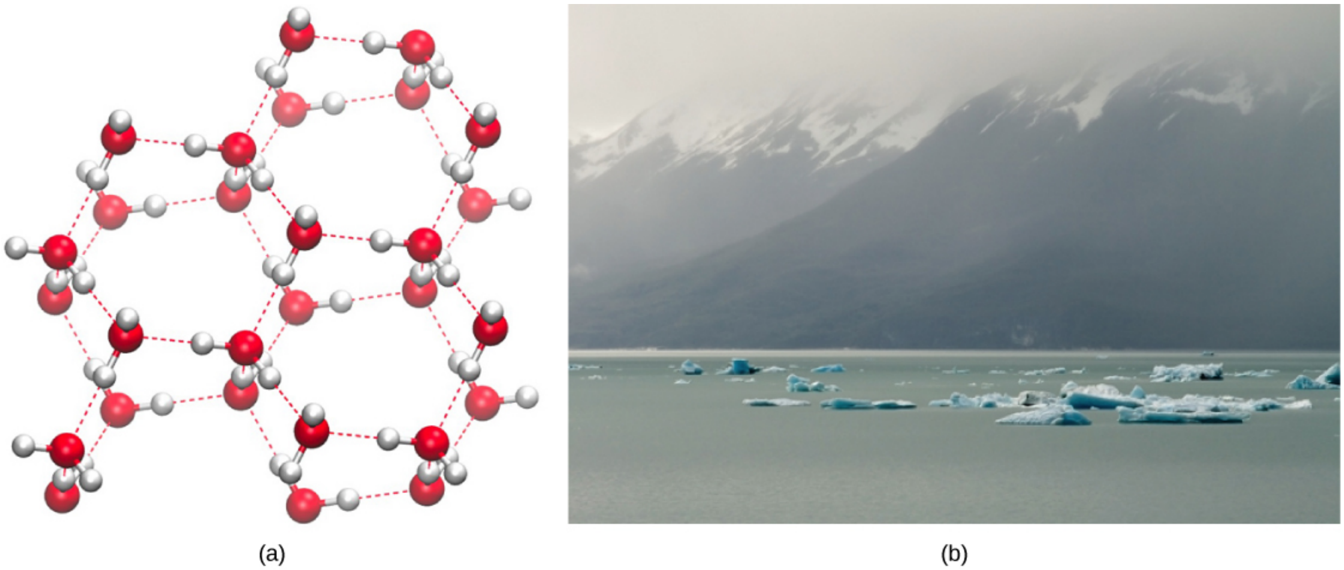


Figure 2.1.2 :
(a) The lattice structure of ice makes it less dense than the freely flowing molecules of liquid water. Ice's lower density enables it to (b) float on water (credit a: modification of work by Jane Whitney; credit b: modification of work by Carlos Ponte).

CONCEPT IN ACTION

Click here to see a 3-D animation of the structure of an ice lattice. (credit: image created by Jane Whitney using Visual Molecular Dynamics (VMD) software[1])

Water Is an Excellent Solvent

Because water is a polar molecule, with slight positive and negative charges, ionic compounds and polar molecules can readily dissolve in it. Water is, therefore, what is referred to as a solvent—a substance capable of dissolving another substance. The charged particles will form hydrogen bonds with a surrounding layer of water molecules. This is referred to as a sphere of hydration or hydration shells and serves to keep the particles separated or dispersed in the water. In the case of table salt (NaCl) mixed in water (Figure 2.1.3), the sodium and chloride ions separate, or dissociate, in the water, and spheres of hydration are formed around the ions. A positively charged sodium ion is surrounded by the partially negative charges of oxygen atoms in water molecules. A negatively charged chloride ion is surrounded by the partially positive charges of hydrogen atoms in water molecules. The polarity of the water molecule makes it an effective solvent and is important in its many roles in living systems (i.e. cell transport, secretion of waste products, nutrient absorbtion).

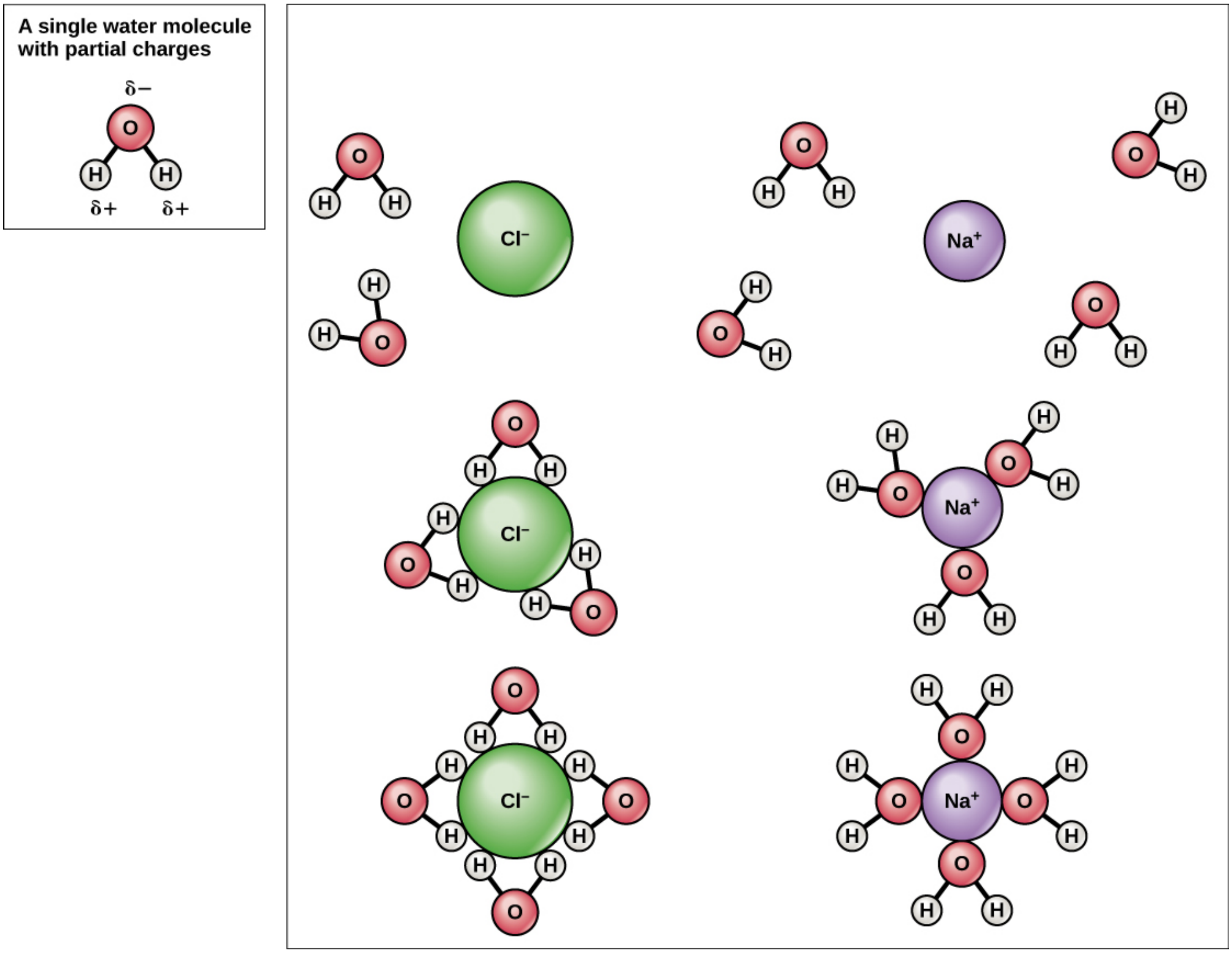


Figure 2.1.3: When table salt (NaCl) is mixed in water, spheres of hydration form around the ions.

Water Is Cohesive

Have you ever filled up a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water actually forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-air (gas) interface. Cohesion gives rise to surface tension, the capacity of a substance to withstand rupture when placed under tension or stress. When you drop a small scrap of paper onto a droplet of water, the paper floats on top of the water droplet, although the object is denser (heavier) than the water. This occurs because of the surface tension that is created by the water molecules. Cohesion and surface tension keep the water molecules intact and the item floating on the top. It is even possible to "float" a steel needle on top of a glass of water if you place it gently, without breaking the surface tension (Figure 2.1.4).

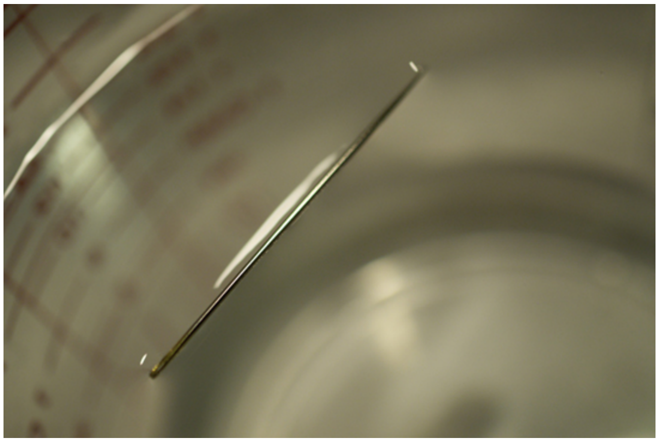


Figure 2.1.4: The weight of a needle on top of water pulls the surface tension downward; at the same time, the surface tension of the water is pulling it up, suspending the needle on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle (credit: Cory Zanker).

These cohesive forces are also related to the water's property of adhesion, or the attraction between water molecules and other molecules. This is observed when water "climbs" up a straw placed in a glass of water. You will notice that the water appears to be higher on the sides of the straw than in the middle. This is because the water molecules are attracted to the straw and therefore adhere to it.

Cohesive and adhesive forces are important for sustaining life. For example, because of these forces, water can flow up from the roots to the tops of plants for use in photosynthesis. Many aquatic organisms such as water striders or snails can travel along the surface of the water because of surface tension created by cohesive forces.

CONCEPT IN ACTION

To learn more about water, visit the U.S. Geological Survey Water Science for Schools: All About Water! website.

pH, Acids, Bases, and Buffers

The pH of a solution is a measure of its acidity or alkalinity. You have probably used litmus paper, paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid or base (alkalinity) exists in a solution. You might have even used some to make sure the water in an outdoor swimming pool is properly treated. In both cases, this pH test measures the amount of hydrogen ions that exists in a given solution. High concentrations of hydrogen ions yield a low pH (or acidic), whereas low levels of hydrogen ions result in a high pH (or alkaline/basic). The overall concentration of hydrogen ions is inversely related to its pH and can be measured on the pH scale (Figure 2.1.5). Therefore, the more hydrogen ions present, the lower the pH; conversely, the fewer hydrogen ions, the higher the pH.

The pH scale ranges from 0 to 14. A change of one unit on the pH scale represents a change in the concentration of hydrogen ions by a factor of 10, a change in two units represents a change in the concentration of hydrogen ions by a factor of 100. Thus, small changes in pH represent large changes in the concentrations of hydrogen ions. Pure water is neutral. It is neither acidic nor alkaline, and has a pH of 7.0. Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. The blood in your veins is slightly alkaline (pH = 7.4). The environment in your stomach is highly acidic (pH = 1 to 2). Orange juice is mildly acidic (pH = approximately 3.5), whereas baking soda is basic (pH = 9.0).

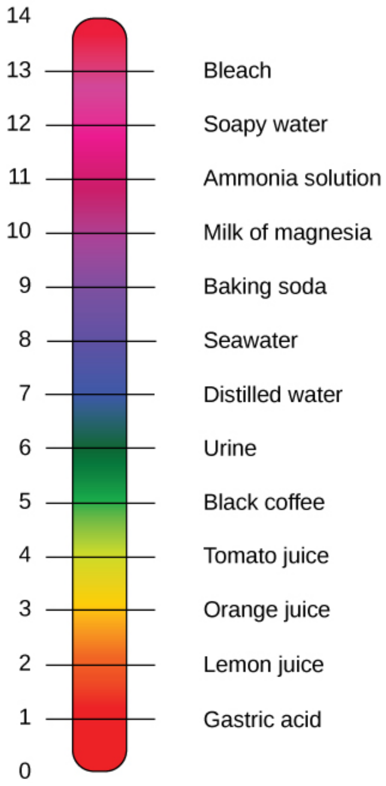


Figure 2.1.5: The pH scale measures the amount of hydrogen ions (H^+) in a substance (credit: modification of work by Edward Stevens).

Acids are substances that provide hydrogen ions (H^+) and lower pH, whereas bases provide hydroxide ions ($OH^–$) and raise pH. The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid and lemon juice are very acidic and readily give up H^+ when added to water. Conversely, bases are those substances that readily donate $OH^–$. The $OH^–$ ions combine with H^+ to produce water, which raises a substance's pH. Sodium hydroxide and many household cleaners are very alkaline and give up $OH^–$ rapidly when placed in water, thereby raising the pH.

Most cells in our bodies operate within a very narrow window of the pH scale, typically ranging only from 7.2 to 7.6. If the pH of the body is outside of this range, the respiratory system malfunctions, as do other organs in the body. Cells no longer function properly, and proteins will break down. Deviation outside of the pH range can induce coma or even cause death.

So how is it that we can ingest or inhale acidic or basic substances and not die? Buffers are the key. Buffers readily absorb excess H^+ or $OH^–$, keeping the pH of the body carefully maintained in the aforementioned narrow range. Carbon dioxide is part of a prominent buffer system in the human body; it keeps the pH within the proper range. This buffer system involves carbonic acid (H_2CO_3) and bicarbonate ($HCO_3^–$) anion. If too much H^+ enters the body, bicarbonate will combine with the H^+ to create carbonic acid and limit the decrease in pH. Likewise, if too much $OH^–$ is introduced into the system, carbonic acid will rapidly dissociate into bicarbonate and H^+ ions. The H^+ ions can combine with the $OH^–$ ions, limiting the increase in pH. While carbonic acid is an important product in this reaction, its presence is fleeting because the carbonic acid is released from the body as carbon dioxide gas each time we breathe. Without this buffer system, the pH in our bodies would fluctuate too much and we would fail to survive.

The same buffer system also works in the ocean where CO_2 reacts with seawater to form carbonic acid (H_2CO_3), which dissociates into bicarbonate ($HCO_3^–$) and carbonate (CO_3^{2-}) ions:

$$CO_2 + H_2O \Leftrightarrow H_2CO_3 \Leftrightarrow HCO_3^- + H^+ \Leftrightarrow CO_3^{2-} + 2H^+ \tag{2.1.1}$$

The sum of these three carbon species is called dissolved inorganic carbon ($DIC = CO_2 + HCO_3^- + CO_3^{2-}$) or total carbon. The equilibrium between the species depends on the pH. In the current ocean, pH is about 8.1, which leads to about 86.5 % of DIC being in the form of bicarbonate ions, 13.0 % in the form of carbonate ions, and only 0.5 % in the form of aqueous CO_2 (Fig. \(\PageIndex{6}; Zeebe and Wolf-Gladrow, 2001).

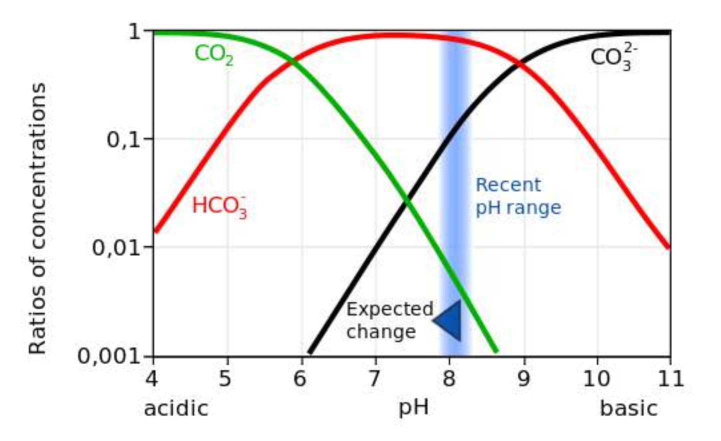


Figure 2.1.6: Ratios of carbonate species concentrations as a function of the pH. Currently average seawater has a pH of about 8.1. Therefore most carbon in the ocean is in the form of bicarbonate. Addition of anthropogenic CO_2 decreases the pH. "Bjerrum Plot" is available in the public domain.

Dissociation of carbonic acid into bicarbonate (baking soda) produces a hydrogen ion H^+, which increases the pH of the water. Most hydrogen ions, however, re-combine with carbonate ions to form additional bicarbonate ions. Nevertheless, adding CO_2 to seawater increases its hydrogen ion concentration (decreases its pH) and decreases the carbonate ion concentration. This process is called ocean acidification.

Summary

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds, which allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules give water the ability to hold heat better than many other substances. As the temperature rises, the hydrogen bonds between water continually break and reform, allowing for the overall temperature to remain stable, although increased energy is added to the system. Water's cohesive forces allow for the property of surface tension. All of these unique properties of water are important in the chemistry and physics of living organisms.

The pH of a solution is a measure of the concentration of hydrogen ions in the solution. A solution with a high number of hydrogen ions is acidic and has a low pH value. A solution with a high number of hydroxide ions is basic and has a high pH value. The pH scale ranges from 0 to 14, with a pH of 7 being neutral. Buffers are solutions that moderate pH changes when an acid or base is added to the buffer system. Buffers are important in biological systems because of their ability to maintain constant pH conditions.

Sources

1. 1 Humphrey, W., Dalke, A. and Schulten, K., "VMD—Visual Molecular Dynamics", *J. Molec. Graphics*, 1996, vol. 14, pp. 33-38. http://www.ks.uiuc.edu/Research/vmd/
2. Zeebe, R. E., and D. A. Wolf-Gladrow (2001), CO_2 in Seawater: Equilibrium, Kinetics, Isotopes, Elsevier, Amsterdam.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) from the following sources:

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

- 2.1: The Building Blocks of Molecules https://bio.libretexts.org/Bookshelv...fig-ch02_01_06
- **1.4: Carbon** by Andreas Schmittner is licensed CC BY-NC 4.0.

2.2: Water (Hydrologic) Cycle

Water is essential for all living processes. The human body is more than one-half water and human cells are more than 70 percent water. Water is also the only substance that occurs naturally on earth in three forms: solid, liquid and gas. Of the stores of water on Earth, 97.5% is salt water (Figure 2.2.1). Of the remaining water, 99% is locked as underground water or ice. Ice caps and glaciers are the largest reservoirs of fresh water but this water is inconveniently located, mostly in Antarctica and Greenland. Shallow groundwater is the largest reservoir of usable fresh water. Less than one percent of fresh water is present in lakes and rivers, the most heavily used water resource.

Many organisms are dependent on this small amount of surface fresh water supply, a lack of which can have important effects on ecosystem dynamics. If all of world's water was shrunk to the size of 1 gallon, then the total amount of fresh water would be about 1/3 cup, and the amount of readily usable fresh water would be 2 tablespoons.

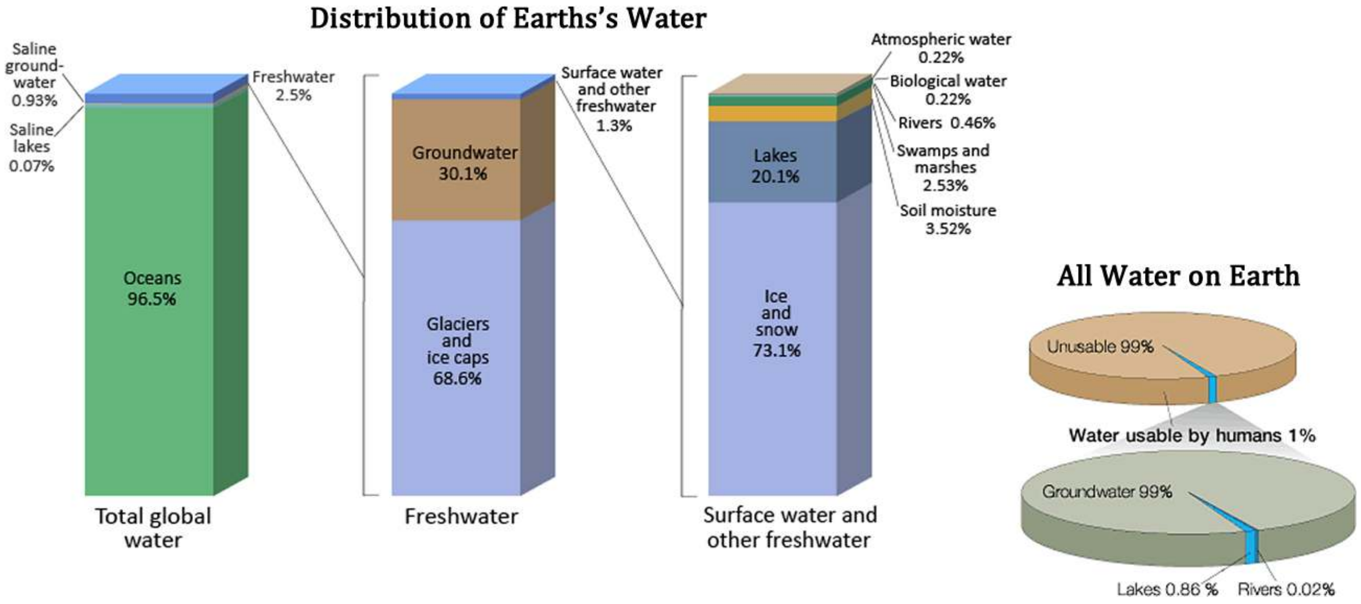


Figure 2.2.1: Earth's Water Reservoirs -- Bar chart Distribution of Earth's water including total global water, fresh water, and surface water and other fresh water and Pie chart Water usable by humans and sources of usable water. *Source: United States Geographical Survey Igor Skiklomanov's chapter "World fresh water resources" in Peter H. Gleick (editor), 1993, Water in Crisis: A Guide to the World's Fresh Water Resources.*

Water Reservoirs

The **hydrosphere** is the area of Earth where water movement and water storage occurs. **Water reservoirs** are the locations where water is stored. (Note that this term can also refer to artificial lakes created by dams.) Water is found as a liquid on the surface (rivers, lakes, oceans) and beneath the surface (groundwater), as ice (polar ice caps and glaciers), and as water vapor in the atmosphere. Figure 2.2.2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir.

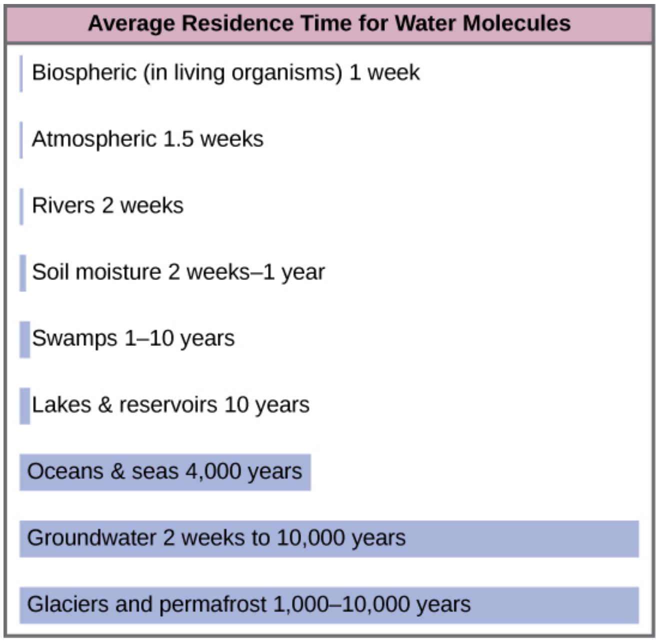


Figure 2.2.2: Average residence time that water remains in each reservoir. Image from OpenStax is licensed under CC-BY.

The Water Cycle

The various processes that occur during the cycling of water are illustrated in Figure 2.2.3. The processes include the following:

- evaporation and sublimation
- transpiration
- condensation and precipitation
- infiltration and subsurface water flow (groundwater discharge)
- surface runoff and snowmelt
- streamflow

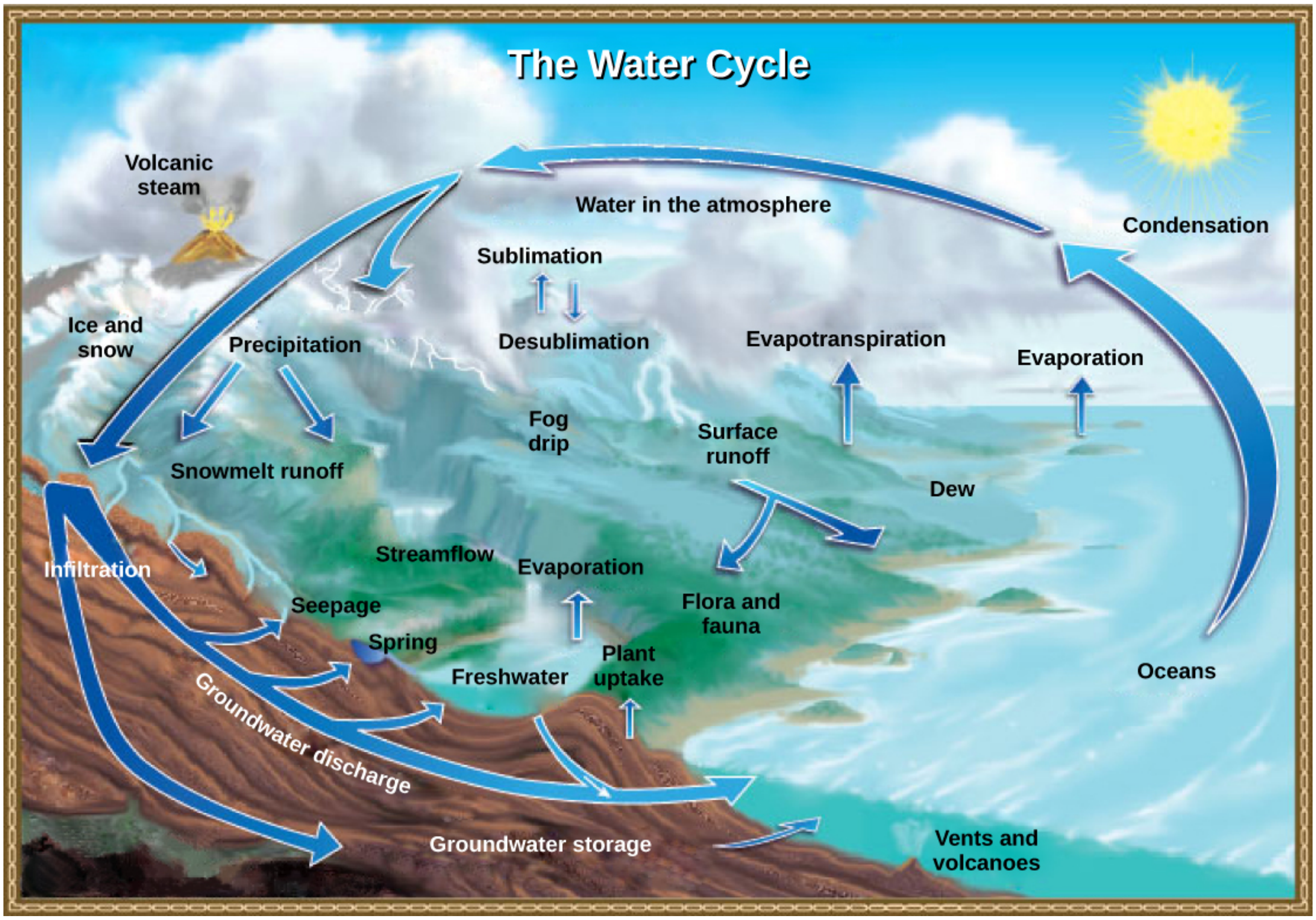


Figure 2.2.3: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean (credit: modification of work by John M. Evans and Howard Perlman, USGS).

The water cycle is driven by the Sun's energy as it warms the oceans and other surface waters. This leads to evaporation (water to water vapor) of liquid surface water and sublimation (ice to water vapor) of frozen water, thus moving large amounts of water into the atmosphere as water vapor. As the water vapor rises in the atmosphere, it cools and condenses. **Condensation** is the process in which water vapor changes to tiny droplets of liquid water. Over time, this water vapor condenses into clouds as liquid or frozen droplets and eventually leads to precipitation (rain or snow), which returns water to Earth's surface. Most precipitation falls into the ocean. Some frozen precipitation becomes part of ice caps and glaciers. These masses of ice can store frozen water for hundreds of years or longer. Rain reaching Earth's surface may evaporate again, flow over the surface, or percolate into the ground. Most easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

In most natural terrestrial environments rain encounters vegetation before it reaches the soil surface. A significant percentage of water evaporates immediately from the surfaces of plants. What is left reaches the soil and begins to move down. Surface runoff will occur only if the soil becomes saturated with water in a heavy rainfall. **Infiltration** is the process through which water sinks into the ground and is determined by the soil or rock type through which water moves. Soil texture (particle size) is an important control on water movement. Most water in the soil will be taken up by plant roots. Water enters the vascular system of the plant through the roots and evaporates, or transpires, through the stomata of the leaves. The plant will use some of this water for its own metabolism, and some of that will find its way into animals that eat the plants, but much of it will be lost back to the atmosphere through a process known as **evapotranspiration**. Water in the soil that is not taken up by a plant and that does not evaporate is able to percolate into the subsoil and bedrock. Here it forms groundwater.

Groundwater is a significant reservoir of fresh water. It exists in the pore spaces between particles in sand and gravel, or in the fissures in rocks. Shallow groundwater flows slowly through these pore spaces and fissures and eventually finds its way to a stream or lake where it becomes a part of the surface water again. Streams do not flow because they are replenished from rainwater directly; they flow because there is a constant inflow from groundwater below. Some groundwater is found very deep in the bedrock and can persist there for millennia. Most groundwater reservoirs, or **aquifers**, are the source of drinking or irrigation water drawn up through wells. In many cases these aquifers are being depleted faster than they are being replenished by water percolating down from above.

An important part of the water cycle is how water varies in salinity, which is the abundance of dissolved ions in water. Freshwater (such as lakes, rivers, and near-surface groundwater) has a relatively low salinity. The saltwater in the oceans is highly saline, with about 35,000 mg of dissolved ions per liter of seawater. Evaporation is a distillation process that produces nearly pure water with almost no dissolved ions. As water vaporizes, it leaves the dissolved ions in the original liquid phase. Eventually, condensation forms clouds and sometimes precipitation. After rainwater falls onto land, it dissolves minerals in rock and soil, which increases its salinity. Rain and surface runoff are major ways in which minerals, including phosphorus and sulfur, are cycled from land to water.

Precipitation Patterns

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. More precipitation falls near the equator, and landmasses there are characterized by a tropical rainforest climate (Figure 2.2.4). Less precipitation tends to fall near 20–30° north and south latitude, where the world's largest deserts are located. These rainfall and climate patterns are related to global wind circulation cells. The intense sunlight at the equator heats air, causing it to rise and cool, which decreases the ability of the air mass to hold water vapor and results in frequent rainstorms. Around 30° north and south latitude, descending air conditions produce warmer air, which increases its ability to hold water vapor and results in dry conditions. Both the dry air conditions and the warm temperatures of these latitude belts favor evaporation. Global precipitation and climate patterns are also affected by the size of continents, major ocean currents, and mountains.

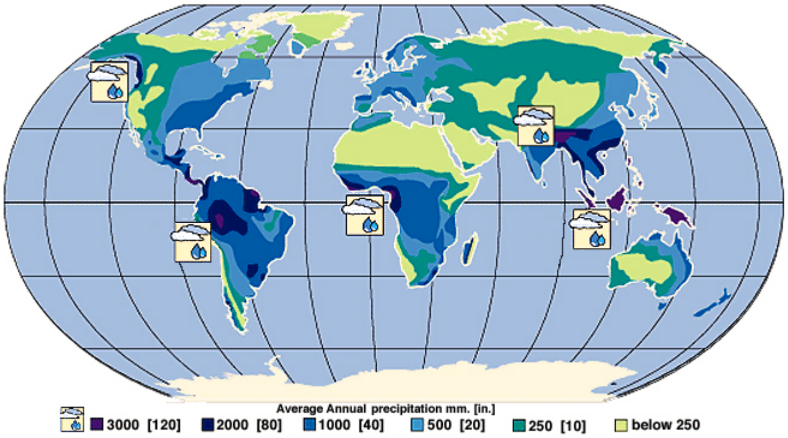


Figure 2.2.4: World Rainfall Map -- The false-color map above shows the amount of rain that falls around the world. Areas of high rainfall include Central and South America, western Africa, and Southeast Asia. Since these areas receive so much rainfall, they are where most of the world's rainforests grow. Areas with very little rainfall usually turn into deserts. The desert areas include North Africa, the Middle East, western North America, and Central Asia. *Source: United States Geological Survey Earth Forum, Houston Museum Natural Science.*

In the United States, the 100th Meridian roughly marks the boundary between the humid and arid parts of the country (figure 2.2.5). Irrigation is required to grow crops west of the 100th Meridian. In the West, surface water is stored in reservoirs (artificial lakes) and mountain snowpacks and strategically released through a system of canals during times of high use.

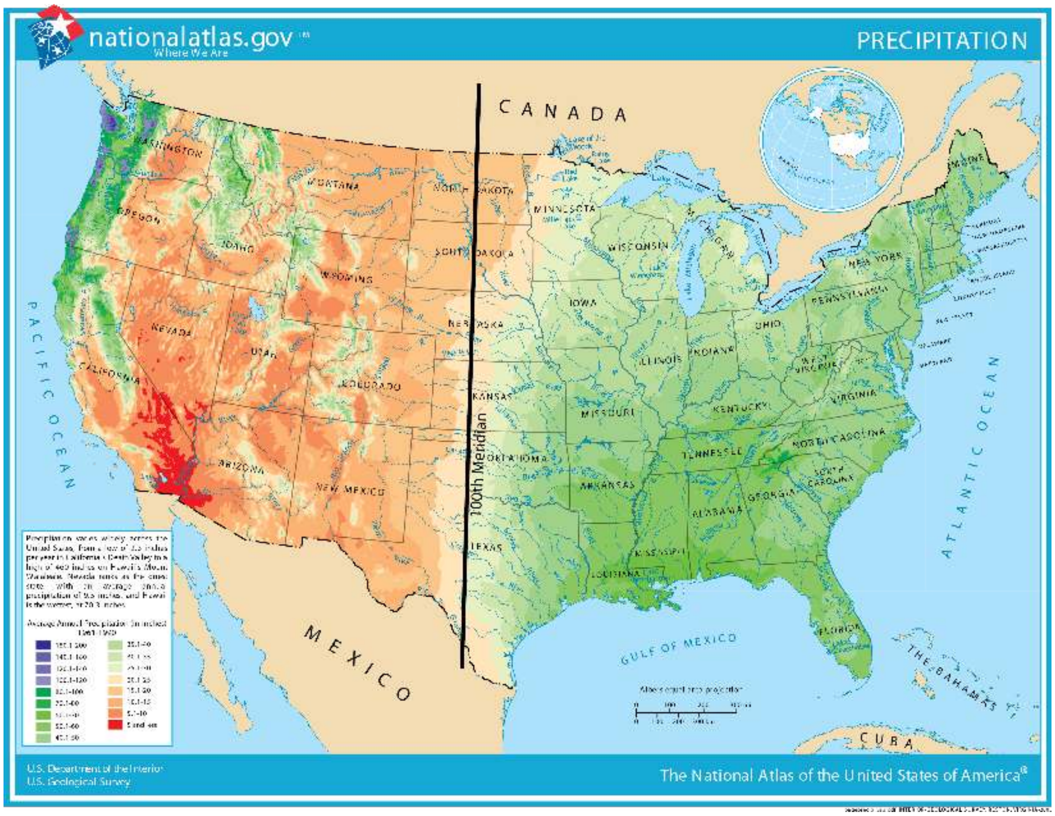
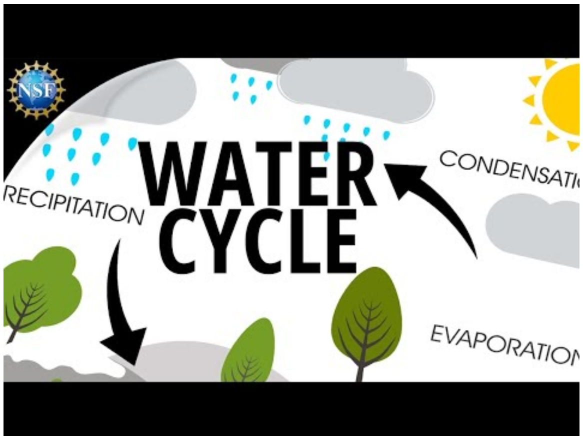


Figure 2.2.5: Distribution of precipitation in the United States. The 100th Meridian is approximately where the average precipitation transitions from relatively wet to dry. Eastern states are mostly green, indicating greater precipitation than most western states, which are mainly orange or red (indicating low precipitation). *Source: U.S. Geological Survey.*

Further "Reading"

The steps of the water cycle are also explained in the video below.



For more information on the water cycle you might want to watch this water cycle video from USGS.

Contributors and Attributions

Modified by Kyle Whittinghill and Melissa Ha from the following sources

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY from *Biology 2e* by OpenStax (CC-BY). Access for free at openstax.org.
- **6.6: Water Cycle** by CK-12: Biology Concepts, is licensed CC BY-NC
- Biogeochemical Cycles and the Flow of Energy in the Earth System and Water Cycle and Fresh Water Supply from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Water Cycle and Fresh Water Supply, Water Supply Problems and Solutions, and Biogeochemical Cycles from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- The Water Cycle, Water Use and Distribution, and Groundwater from *An Introduction to Geology* by Chris Johnson et al. (licensed under CC-BY-NC-SA)
- Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0.

2.3: Soils

Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition and texture of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Soil develops very slowly over long periods of time, and its formation results from natural and environmental forces acting on mineral, rock, and organic compounds. Soils can be divided into two groups: organic soils are those that are formed from sedimentation and primarily composed of organic matter, while those that are formed from the weathering of rocks and are primarily composed of inorganic material are called mineral soils. Mineral soils are predominant in terrestrial ecosystems, where soils may be covered by water for part of the year or exposed to the atmosphere.

Soil is Important

Soil is important to our society primarily because it provides the foundation of agriculture and forestry. Soil plays a key role in plant growth. Beneficial aspects to plants include providing physical support, water, heat, nutrients, and oxygen. Mineral nutrients from the soil can dissolve in water and then become available to plants. Soil plays a role in nearly all biogeochemical cycles on the Earth's surface. Global cycling of key elements such as carbon (C), nitrogen (N), phosphorous (P), and sulfur (S) all pass through soil. In the hydrologic (water) cycle, soil helps to mediate **infiltration** (percolating) from the surface into the groundwater. Microorganisms living in soil can also be important components of biogeochemical cycles through the action of decomposition and other processes such as nitrogen fixation.

Through their roots, plants absorb water and minerals (e.g., nitrates, phosphates, potassium, copper, zinc). Of the mineral nutrients absorbed from the soil, **macronutrients**, including nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), sulfur (S), and silicon (Si) are needed by plants in significant quantities. **Micronutrients** are essential elements that are needed only in small quantities, but can still be limiting to plant growth since these nutrients are not so abundant in nature. Micronutrients include chlorine (Cl), iron (Fe), boron (B), manganese (Mn), sodium (Na), zinc (Zn), copper (Cu), nickel (Ni), and molybdenum (Mo). There are some other elements that tend to aid plant growth but are not absolutely essential.

Micronutrients and macronutrients are desirable in particular concentrations and can be detrimental to plant growth when concentrations in soil solution are either too low (limiting) or too high (toxicity). Mineral nutrients are useful to plants only if they are in an extractable form in soil solutions, such as a dissolved ion rather than in solid mineral. Many nutrients move through the soil and into the root system as a result of concentration gradients, moving by diffusion from high to low concentrations across semi-permeable membranes in root cells (passive transport). However, some nutrients are selectively absorbed by active transport across the root membranes, enabling concentrations to become higher inside the plant than in the soil.

Although many aspects of soil are beneficial to plants, excessively high levels of trace metals (either naturally occurring or added by humans) or applied herbicides can be toxic to some plants (Figure $2.3.1$).

Figure 2.3.1: These native plants are affected by herbicides that were used to kill nearby weeds. Image by Matt Lavin is available under CC-BY-SA 2.0.

An important factor affecting soil fertility is soil **pH** (the negative log of the hydrogen ion concentration). Soil pH is a measure of the acidity or alkalinity of the soil solution. On the pH scale (0 to 14) a value of seven represents a neutral solution; a value less than seven represents an **acidic** solution and a value greater than seven represents an **alkaline** solution. Soil pH affects the health of microorganisms in the soil and controls the availability of nutrients in the soil solution. Strongly acidic soils (less than 5.5) hinder the growth of bacteria that decompose organic matter in the soil. This results in a buildup of organic matter that has yet to be decomposed, which leaves important nutrients such as nitrogen in forms that are unusable by plants. Soil pH also affects the solubility of nutrient-bearing minerals. This is important because the nutrients must be dissolved in solution for plants to assimilate them through their roots. Most minerals are more soluble in slightly acidic soils than in neutral or slightly alkaline soils. Strongly acid soils (pH four to five), though, can result in high concentrations of aluminum, iron and manganese in the soil solution, which may inhibit the growth of some plants.

Several factors determine soil pH. Organic material in soil decreases pH to an extent, but it also acts as a **buffer**, limiting changes in pH. Climate is also important, with high amounts of rainfall lowering pH and increasing leaching (draining of nutrients and other dissolved ions with percolating water). Some types of parent material, such as those high in silicon, decrease pH, while others, such as limestone increase pH.

Soil Composition

Soil consists of organic matter (about 5%), inorganic mineral matter (40-45% of soil volume), water (about 25%) and air (about 25%) (Figure 2.3.2). The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil.

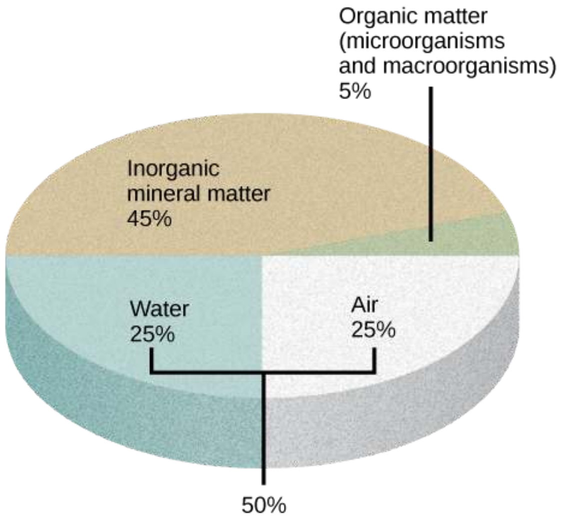


Figure 2.3.2: The four major components of soil are shown: inorganic minerals, organic matter, water, and air. Image is from OERTX and is available in the public domain.

The organic material consists of dead organisms in various stages of decomposition. It is dark-colored because it contains **humus**, partially decayed matter containing organic acids. Humus enriches the soil with nutrients, gives the soil a loose texture that holds water, and allows air to diffuse through it. Oxygen is important for plant roots and many inhabitants of the soil. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 100 μm to 2 mm in diameter are **sand**. (A **micrometer**, μm, 10^{-6} m, or a millionth of a meter.) Soil particles between 2 and 100 μm are called **silt**, and even smaller particles, less than 2 μm in diameter, are called **clay**.

Soil should ideally contain 50 percent solid material and 50 percent pore space (Figure 2.3.3). **Pore space** refers to the gaps in between soil particles. The larger the soil particles, the larger the pore spaces. Water can quickly pass through large pore spaces, so soils high in sand drain easily. Smaller soil particles have more surface area relative to volume and produce narrow pore spaces. Water clings to these surfaces, and soils high in clay thus retain water. (Clay is also negatively charged, which attracts water.) About one-half of the pore space should contain water, and the other half should contain air.

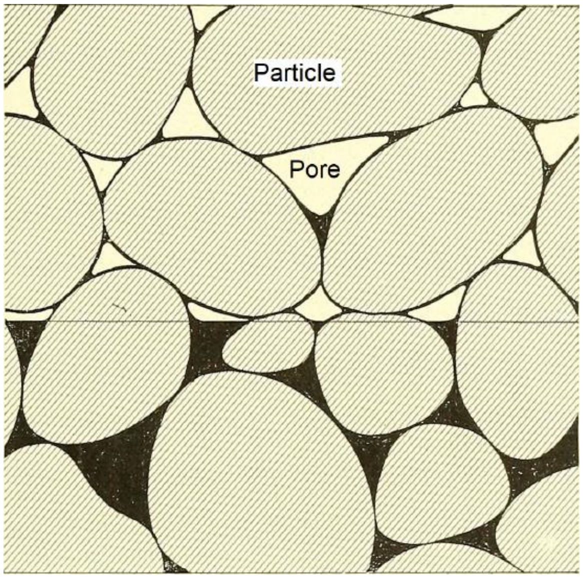


Figure 2.3.3: Soil particles and the pore spaces in between them. The black shading represents water, which fills the pore spaces in the lower portion of the soil and clings to narrow portions of pore space in the top portion of the soil. Image from "Forest physiography; physiography of the United States and principles of soils in relation to forestry" is available in the public domain.

Soil texture is based on percentages of sand, silt, and clay (Figure 2.3.4). Soils that have a high percentage of one particle size are named after that particle (a clay soil has a high percentage of clay). Other soils have a mixture of two particle sizes and very little of the third size. For example, silty clay has roughly 50% clay and 50% silt while sandy clay has 50-60% sand and 35-50% clay. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus. These soils are called **loams**, and they are optimal for agriculture. A medium loam has roughly 40% sand, 40% silt, and 20% clay. Larger particles (sand) facilitate drainage, and small particles (clay) facilitate water retention, so loam soils both have good drainage and can remain moist. Soils that deviate slightly from a medium loam include loamy sand, sandy loam, sandy clay loam, clay loam, silty clay loam, and silty loam.

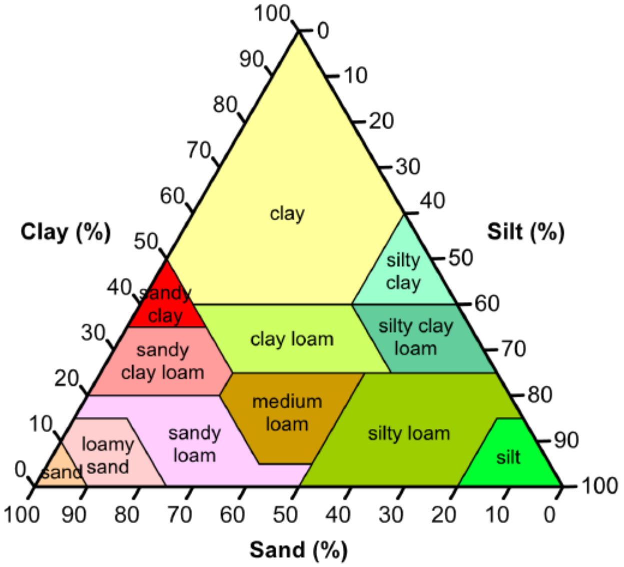


Figure 2.3.4: A soil texture triangle is used to determine the soil texture based on the percentages of sand, silt, and clay. The left axis represents the percentage of clay. The right axis represents the percentage of silt. The bottom axis represents the percentage of sand. Most soils that contain more than 40% of clay particles are classified as clays. Exceptions are silty clays, which contain 40-60% clay and 40-60% silt. Another exception are sandy clays, which contain 35-50% clay and 50-70% sand. Clay loams and silty clay loams contain 25-40% clay. Clay loams contain 20-60% silt, and silty clay loams contain 60-75% silt. Sandy clay loams contain 20-35% clay and 50-80% sand. Medium loams contain 5-25% clay, 20-50% silt, and 30-55% sand. Soils with more than 50% silt and no more than 25% clay are either silty loams or silts. Silts have 80-100% silt and no more than 15% clay. Sand have 90-100% sand. Loamy sands have 75-90% sand and no more than 15% clay. A soil with a composition that does not fit into the already described categories would be a sandy loam. To determine the soil texture, first find the percentage of clay and trace a line horizontally to the right. At the same time, find the percentage of silt and trace a line diagonally (down and to the left, parallel to the clay axis). The two lines will meet at the correct soil type. For example, traced lines from 20% clay and 40% silt intersect at the medium loam category. To confirm, trace a diagonal line (down and to the right, parallel to the sit axis) from this point to the sand axis. This line cross the axis at 40%. In summary, a line can be traced from each axis that is parallel to axis that is counterclockwise of it. "Soil Composition" by Richard Wheeler is available under CC-BY-SA 3.0.

Soils can be divided into two groups based on how they form. **Organic soils** are those that are formed from sedimentation and often contain more than 30% organic matter. They form when organic matter, such as leaf litter, is deposited more quickly than it can be decomposed (Figure 2.3.5). **Mineral soils** are formed from the weathering of rocks, typically contain no more than 30% organic matter, and are primarily composed of inorganic material. **Weathering** occurs when biological, physical, and chemical processes, such as erosion, leaching, or high temperatures, break down rocks.

Figure 2.3.5: Decomposition of organic material occurs very slowly in this acidic bog. The organic material accumulates, which is characteristic of organic soils. "Sphagnum Bog" by William L. Farr is available under CC-BY-SA 4.0.

Soil has Horizons

Soil distribution is not uniform because its formation results in the production of layers; together, the vertical section of a soil is called the **soil profile**. Within the soil profile, soil scientists define zones called horizons. A **horizon** is a soil layer with distinct physical and chemical properties that differ from those of other layers.

The soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon and 4) C horizon (Figure 2.3.6).

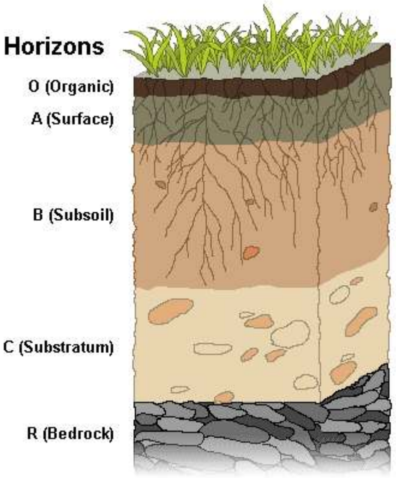


Figure 2.3.6: This image shows the different horizons, or layers, in soil. Vegetation grows at the surface. The top, deep brown layer is the O (organic) horizon. Below this is the gray A horizon (topsoil, or surface). Next is the light brown B horizon (subsoil). The C horizon (substratum, or soil base) is tan and includes larger pieces of rocks. The gray bedrock is the deepest layer. The E (eluviated) horizon that is sometimes found between the A and B horizons is absent here. "Graphic of Soil Profile" by Wilsonbiggs is licensed under CC BY-SA 4.0.

Upper horizons (labeled as the A and O horizons) are richer in organic material and so are important in plant growth, while deeper layers (such as the B and C horizons) retain more of the original features of the bedrock below. Some soils may have additional layers (like the E horizon, Figure 2.3.7), or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers.

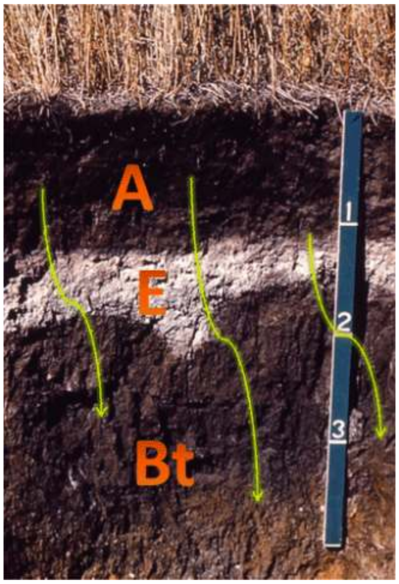


Figure 2.3.7): Photograph shows a soil profile from South Dakota revealing three horizons. The A horizon (topsoil) is dark brown and extend about 1 foot. Below it is the white E (eluviated) horizon, which is about 6 inches thick. The B horizon (subsoil, labeled Bt) is the medium brown and the lowest visible layer The yellow arrows symbolize translocation of fine clays to the B horizon. The scale is in feet. *Source: University of Idaho and modified by D. Grimley*.

O horizon

The very top of the **O horizon** consists of partially decayed organic debris like leaves (Figure 2.3.6). This horizon is usually dark in color because of humus.

A horizon

The **A horizon** (topsoil) consists of a mixture of organic material (from decomposition) with inorganic products of chemical weathering of rocks, and it is therefore the beginning of true mineral soil (Figure 2.3.7). In this area, rainwater percolates through the soil and carries materials from the surface. The A horizon may be only 5 cm (2 in.), or it may over a meter. For instance, river deltas like the Mississippi River delta have deep layers of topsoil. Microbial processes occur in the top soil, and this horizon supports plant growth. Many organisms, such as earthworms and insects live among the plant roots in this horizon.

B horizon

The **B horizon** (subsoil) consists of small particles that have moved downward, resulting in a dense layer in the soil (Figure 2.3.7). In some soils, the B horizon contains nodules or a layer of calcium carbonate. The subsoil is usually lighter in color than topsoil and often contains an accumulation of minerals.

C horizon

The **C horizon** (soil base), includes the **parent material**, the organic and inorganic substances from which soils form (Figure 2.3.6). Weathering parent material represents the first steps in the chemical breakdown of rock into soil. Often the weathered parent material is underlain by the parent material itself, although in some places it has been carried from another location by wind, water, or glaciers. Beneath the C horizon lies bedrock. The chemical nature of the parent material, whether granite, limestone, or sandstone, for example, has a great influence on the fertility of the soil derived from it.

Several Factors Affect Soil Formation and Composition

The fundamental factors that affect soil genesis can be categorized into five elements: climate, organisms, topography, parent material, and time. One could say that the relief, climate, and organisms dictate the local soil environment and act together to cause weathering and mixing of the soil parent material over time.

Climate

The role of climate in soil development includes aspects of temperature and precipitation. Soils in very cold areas with permafrost conditions (such as the arctic tundra) tend to be shallow and weakly developed due to the short growing season. In warm, tropical climates, soils tend to be thicker (but lacking in organic matter), with extensive leaching and mineral alteration. In such climates, organic matter decomposition and chemical weathering occur at an accelerated rate. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

Ancient soils, sometimes buried and preserved in the subsurface, are referred to as **paleosols** (Figure 2.3.8) and reflect past climatic and environmental conditions.

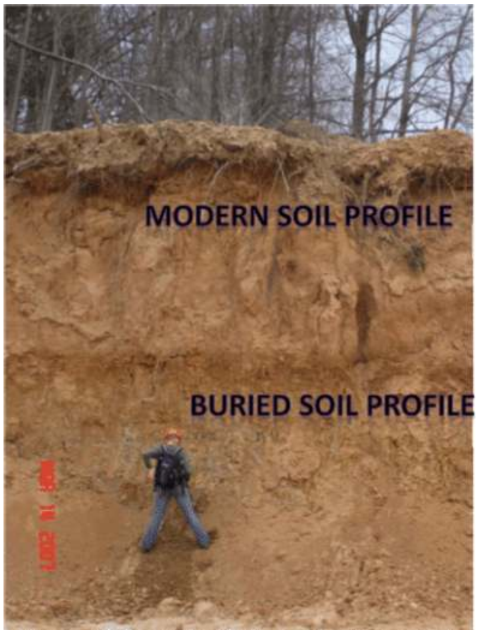


Figure 2.3.8: Modern versus Buried Soil Profiles: a buried soil profile, or paleosol (above geologist 's head), represents soil development during the last interglacial period, while a modern soil profile (Alfisol) occurs near the land surface. *Source: D. Grimley*.

Organisms

The presence of living organisms in the soil (**soil biota**) greatly affects soil formation and structure. A diversity of animals are found in the soil such as nematodes, spiders, insects, centipedes, millipedes, pillbugs, slugs, and earthworms (Figure 2.3.9). The soil also contains microorganisms like bacteria, archaea, fungi, and "protists". Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce more fragmentation. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition. Microorganisms not only decompose organic matter, but contribute to other processes in nutrient cycles, such as nitrogen fixation. Many soil animals also contribute decomposition either directly as detritivores or indirectly through the soil food web.

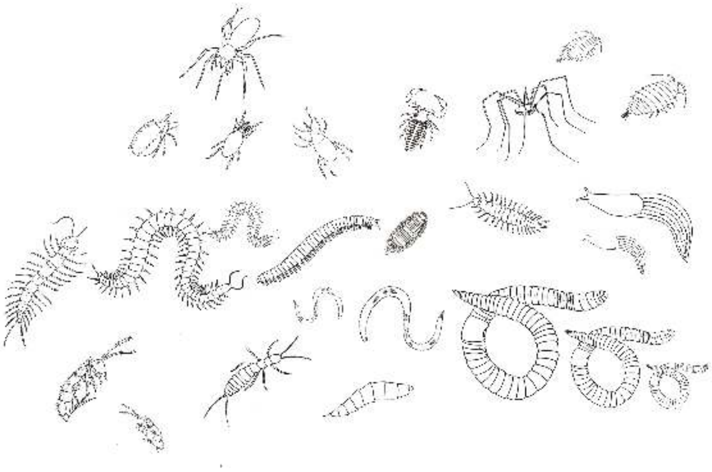


Figure 2.3.9: Illustration of animals commonly found in the soil. "Soil Fauna" by Arne Henriks is licensed under CC BY 2.0.

Parent Material

Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

The type of parent material may also affect the rapidity of soil development. Parent materials that are highly weatherable (such as volcanic ash) will transform more quickly into highly developed soils, whereas parent materials that are quartz-rich rocks (and more difficult to break down) will take longer to develop into soils. Parent materials also provide nutrients to plants and can affect soil internal drainage.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Soils on steep slopes are more prone to erosion and may be thinner than soils that are on relatively level ground. **Infiltration**, the percolating of water through the soil, is limited in steep soils.

The local topography can have important microclimatic effects. In the northern hemisphere, south-facing slopes are exposed to more direct sunlight angles and are thus warmer and drier than north-facing slopes. The cooler, moister north-facing slopes have a more dynamic plant community and thicker soils because extensive root systems stabilize the soil and reduce erosion (figure 2.3.10).

Figure 2.3.10: A north-facing slope (left) and south-facing slope (right) in the Mediterranean climate (chaparral) of the Santa Monica Mountains, California. Vegetation on the north-facing slope is denser due to cool, moist conditions relative to the south-facing slope. "Slope Effect" by Noah Elhardt is licensed under CC BY-SA 2.5.

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

In general, soil profiles tend to become thicker (deeper), more developed, and more altered over time. However, the rate of change is greater for soils in youthful stages of development. The degree of soil alteration and deepening slows with time and at some point, after tens or hundreds of thousands of years, may approach an equilibrium condition where erosion and deepening (removals and additions) become balanced. **Young soils** (< 10,000 years old) are strongly influenced by parent material and typically develop horizons and character rapidly. Over time, as weathering processes deepen, mix, and alter the soil, the parent material becomes less recognizable as chemical, physical, and biological processes take effect. **Moderate age soils** (roughly 10,000 to 500,000 years old) are slowing in profile development and deepening, and may begin to approach equilibrium conditions. **Old soils** (>500,000 years old) have generally reached their limit as far as soil horizonation and physical structure, but may continue to alter chemically or mineralogically.

Soil development is not always continual. Geologic events such as landslides, glacier advance, or the rising of shorelines can rapidly bury soils. Erosion in rivers and shorelines can cause removal or truncation of soils, and wind or flooding slowly deposit sediment that adds to the soil. Animals can mix the soil and sometimes cause **soil regression**, a reversal or "bump in the road" for the normal path of development, and this increases development over time.

Soil are Classified Into Groups

Soils are classified into one of 12 soil orders based on soil horizons, how they form, and their chemical compositions. For example, Mollisols (Figure 2.3.12), which are found in temperate grasslands, have a thick topsoil rich in organic content. Aridisols, on the other hand, are dry soils that contain calcium carbonate and are found in deserts. Each soil order is further divided into suborders. See USDA's The Twelve Orders of Soil Taxonomy and The Twelve Soil Orders from the University of Idaho for more details.

Contributiors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) and Melissa Ha from the following sources:

- The Soil from *General Biology* by OpenStax (CC-BY)
- Soil Profiles and Processes and Soil-Plant Interactions from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0.
- Soil from *Biology* by John W. Kimball (licensed under CC-BY)

2.4: The Atmosphere

The Atmosphere

The **atmosphere**, the gaseous layer that surrounds the earth, formed over four billion years ago and is held in place by the attractive forces of gravity. During the evolution of the solid earth, volcanic eruptions released gases into the developing atmosphere. Assuming the outgasing was similar to that of modern volcanoes, the gases released included: water vapor (H_2O), carbon monoxide (CO), carbon dioxide (CO_2), hydrochloric acid (HCl), methane (CH4), ammonia (NH_3), nitrogen (N_2) and sulfur gases. The atmosphere was reducing because there was no free oxygen. Most of the hydrogen and helium that outgassed would have eventually escaped into outer space due to the inability of the earth's gravity to hold on to their small masses. There may have also been significant contributions of volatiles from the massive meteoritic bombardments known to have occurred early in the earth's history.

Water vapor in the atmosphere condensed and rained down, eventually forming lakes and oceans. The oceans provided homes for the earliest organisms which were probably similar to cyanobacteria. Oxygen was released into the atmosphere by these early organisms, and carbon became sequestered in sedimentary rocks. This led to our current oxidizing atmosphere, which is mostly comprised of nitrogen (roughly 78 percent) and oxygen (roughly 21 percent) with 0.9% argon (Ar) and 0.04% carbon dioxide (CO_2). The atmosphere also contains highly variable concentrations of water vapor, which can range from only 0.01% in frigid winter air in the Arctic to 5% in warm, humid, tropical air. The atmosphere also contains several gases in trace amounts, such as helium, neon, methane and nitrous oxide. One very important trace gas is ozone (O_3), which absorbs harmful UV radiation from the sun.

The earth's atmosphere extends outward to about 1,000 kilometers where it transitions to interplanetary space. However, most of the mass of the atmosphere (greater than 99 percent) is located within the first 40 kilometers. On average, the total weight of the atmospheric mass exerts a pressure at sea level of around 1.0×10^5 pascals (Pa; or one atmosphere), which is equivalent to 1.0 kg per cm^2. The density of the atmospheric mass is much greater close to the surface and decreases rapidly with increasing altitude. The vertical temperature profile of the atmosphere is variable and depends upon the types of radiation that affect each atmospheric layer. This, in turn, depends upon the chemical composition of that layer (mostly involving trace gases). Based on these factors, the atmosphere can be divided into four distinct layers: the troposphere, stratosphere, mesosphere, and thermosphere (Figure 2.4.1). The boundaries of the layers are inexact because they may vary over time and space. Beyond the atmosphere is outer space, an immeasurably vast region where the Earth exerts no detectable chemical or thermal influences.

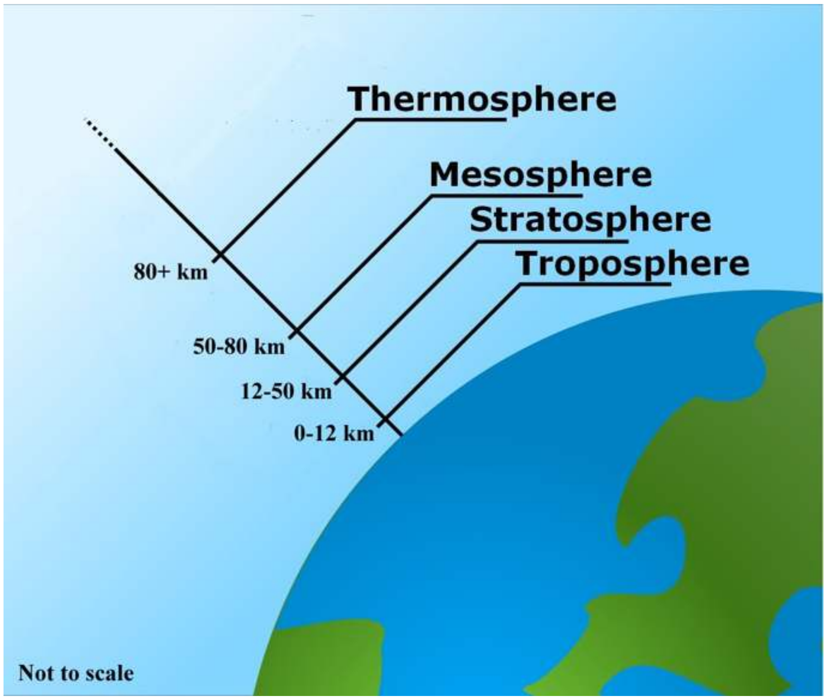


Figure 2.4.1: The layers of the atmosphere. the troposphere is the closest to the Earth's surface (0-12 km). Next, is the stratosphere (12-50 km), mesosphere (50-80 km), and thermosphere (80+ km). The outermost layer (the exosphere) is not shown. **Ground-level ozone** in the troposphere is a form of air pollution, but the **ozone layer** in the stratosphere helps filter UV rays. "Atmospheric Layers" by GFDL is licensed under CC BY-SA 3.0.

The **troposphere** (or lower atmosphere) contains 85-90% of the atmospheric mass and extends from the surface to an altitude of 8-20 km. It is thinner at high latitudes, and thicker at equatorial latitudes, but also varies seasonally, at any place being thicker during the summer than in the winter. Because convective air currents (winds) are common in the troposphere (the name troposphere means "region of mixing") it is sometimes referred to as the "weather layer." It also contains some 99 percent of the total water vapor of the atmosphere. The temperature of the troposphere is warm (roughly 17º C) near the surface of the earth. This is due to the absorption of infrared radiation from the surface by water vapor and other greenhouse gases (e.g. carbon dioxide, nitrous oxide and methane) in the troposphere. The concentration of these gases decreases with altitude, and therefore, the heating effect is greatest near the surface. The temperature in the troposphere decreases at a rate of roughly 6.5º C per kilometer of altitude. The temperature at its upper boundary is very cold (roughly -60º C). Water vapor evaporated from the earth's surface condenses in the cooler upper regions of the troposphere and falls back to the surface as rain. Dust and pollutants injected into the troposphere become well mixed in the layer, but are eventually washed out by rainfall. The troposphere is therefore self cleaning. A narrow zone at the top of the troposphere is called the **tropopause**. It effectively separates the underlying troposphere and the overlying stratosphere. The temperature in the tropopause is relatively constant. Strong eastward winds, known as the **jet stream**, also occur here.

The **stratosphere** extends from the troposphere to as high as about 50 km, depending on the season and latitude. Within the stratosphere there are few convective air currents. The temperature profile of the stratosphere is quite different from that of the troposphere. The temperature remains relatively constant up to roughly 25 kilometers and then gradually increases up to the upper boundary of the layer. The amount of water vapor in the stratosphere is very low, so it is not an important factor in the temperature regulation of the layer. Instead, it is ozone (O3) that causes the observed temperature inversion. Most of the ozone in the atmosphere is contained in a layer of the stratosphere from roughly 20 to 30 kilometers. This ozone layer absorbs solar energy in the form of ultraviolet radiation (UV), and the energy is ultimately dissipated as heat in the stratosphere. This heat leads to the rise in temperature. Stratospheric ozone is also very important for living organisms on the surface of the earth as it protects them by absorbing most of the harmful UV radiation from the sun. The upper boundary of the stratosphere is known as the **stratopause**, which is marked by a sudden decrease in temperature.

The third layer in the earth's atmosphere is called the **mesosphere**. It extends from the stratopause (about 50 kilometers) to roughly 85 kilometers above the earth's surface. Because the mesosphere has negligible amounts of water vapor and ozone for generating heat, the temperature drops across this layer. It is warmed from the bottom by the stratosphere. The air is very thin in this region with a density about 1/1000 that of the surface. With increasing altitude this layer becomes increasingly dominated by lighter gases, and in the outer reaches, the remaining gases become stratified by molecular weight.

The fourth layer, the **thermosphere**, extends outward from about 85 kilometers to about 600 kilometers. Its upper boundary is ill defined. The temperature in the thermosphere increases with altitude, up to 1500º C or more. The high temperatures are the result of absorption of intense solar radiation by the last remaining oxygen molecules. The temperature can vary substantially depending upon the level of solar activity. The lower region of the thermosphere (up to about 550 kilometers) is also known as the **ionosphere**. Because of the high temperatures in this region, gas particles become ionized. The ionosphere is important because it reflects radio waves from the earth's surface, allowing long-distance radio communication. The visual atmospheric phenomenon known as the northern lights also occurs in this region. The outer region of the atmosphere is known as the **exosphere**. The exosphere represents the final transition between the atmosphere and interplanetary space. It extends about 1000 kilometers and contains mainly helium and hydrogen. Most satellites operate in this region.

Climate and Weather both Happen in the Atmosphere

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather. Both long-term climate patterns and short-term weather patterns have to do with conditions in the atmosphere.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. Climate scientists often average over decades to determine climate in a given location. **Climate change** refers to any significant change in the measures of climate lasting for an extended period of time. In other words, climate change includes major changes in temperature, precipitation, or wind patterns, among other effects, that occur over several decades or longer. More details about climate can be found in the sections of this book on "Earth's Energy Balance," "What Makes the Climate Change?," and "Past Climate Change."

In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable. For more on how Atmospheric and Oceanic Circulation affect weather patterns across the globe, see the section of this book on "Atmospheric and Oceanic Circulation." We won't be covering short-term weather patterns in this text, but there are many good resources for learning more about meteorology including Roland Stull's book Practical Meteorology.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered “average” weather.

Contributors and Attributions

Modified by Kyle Whittinghill, Melissa Ha, and Rachel Schleiger from the following sources:

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- Kyle Whittinghill (University of Pittsburgh)
- Contributed by Melissa Ha and Rachel Schleiger Faculty (Biological Sciences) at Yuba College & Butte College
- Climate and the Effects of Global Climate Change from *General Biology* by OpenStax (licensed under CC-BY)
- Climate Change from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Carbon Cycle from *Biology* by John W. Kimball (licensed under CC-BY)
- The Physical World from *Environmental Science: A Canadian Perspective* by Bill Freedman
- Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0
- The Atmosphere from *AP Environmental Science* by University of California College Prep accessed through CNX.

2.5: Earth's Energy Balance

Earth’s Temperature is a Balancing Act

Earth’s temperature depends on the balance between energy entering and leaving the planet. When incoming energy from the sun is absorbed, Earth warms. When the sun’s energy is reflected back into space, Earth avoids warming. When energy is released from Earth into space, the planet cools. Many factors, both natural and human, can cause changes in Earth’s energy balance, including:

- Changes in the greenhouse effect, which affects the amount of heat retained by Earth’s atmosphere;
- Variations in the sun’s energy reaching Earth;
- Changes in the reflectivity of Earth’s atmosphere and surface.

The balance of incoming and outgoing heat on Earth is referred to as its **energy budget**. As with any budget, to maintain constant conditions the budget must be balanced so that the incoming heat equals the outgoing heat. The energy budget of Earth appears below (Figure 2.5.1).

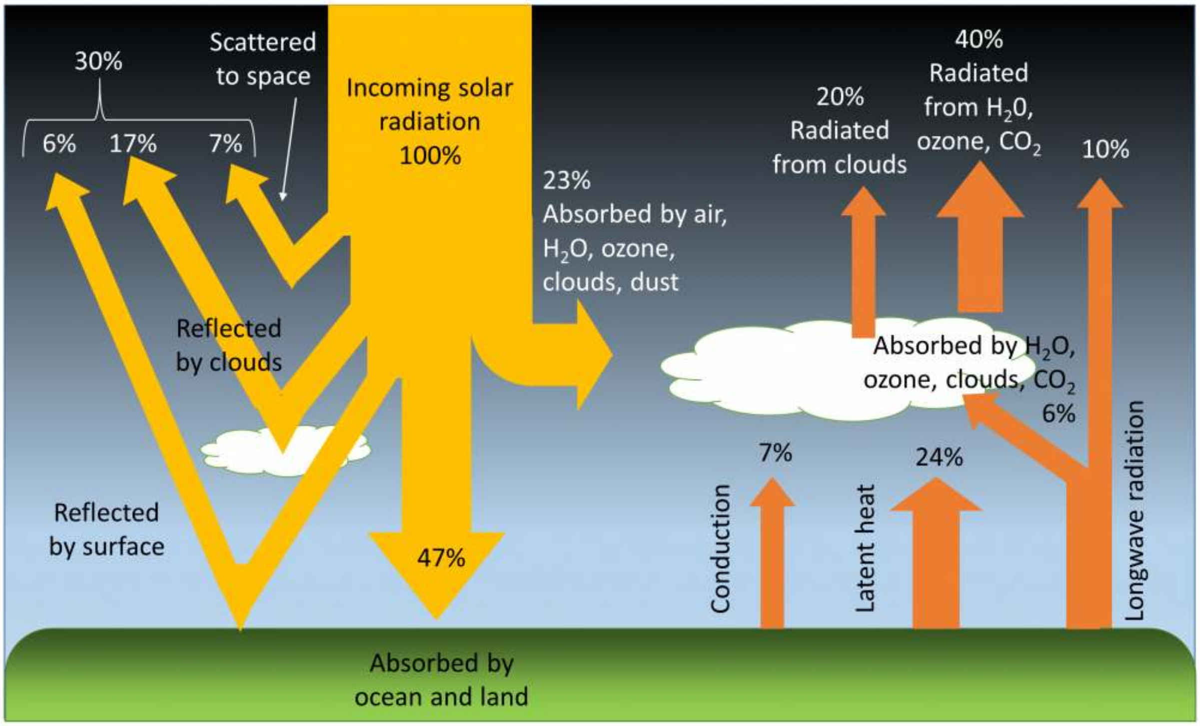


Figure 2.5.1 : Earth’s energy budget. Of all of the solar radiation reaching Earth, 30% is reflected back to space and 70% is absorbed by the Earth (47%) and atmosphere (23%). The heat absorbed by the land and oceans is exchanged with the atmosphere through conduction, radiation, and latent heat (phase change). The heat absorbed by the atmosphere is eventually radiated back into space. *Source: Paul Webb, Roger Williams University.*

Solar radiation from the sun is composed of mostly ultraviolet (UV), visible light, and infrared (IR) radiation (Figure 2.5.2). Components of solar radiation include parts with a shorter wavelength than visible light, like ultraviolet light, and parts of the spectrum with longer wavelengths, like IR and others (Figure 2.5.2). Of all of the solar energy reaching the Earth, about 30% is reflected back into space from the atmosphere, clouds, and surface of the Earth (Figure 2.5.1). Another 23% of the energy is absorbed by the water vapor, clouds, and dust in the atmosphere, where it is converted into heat.

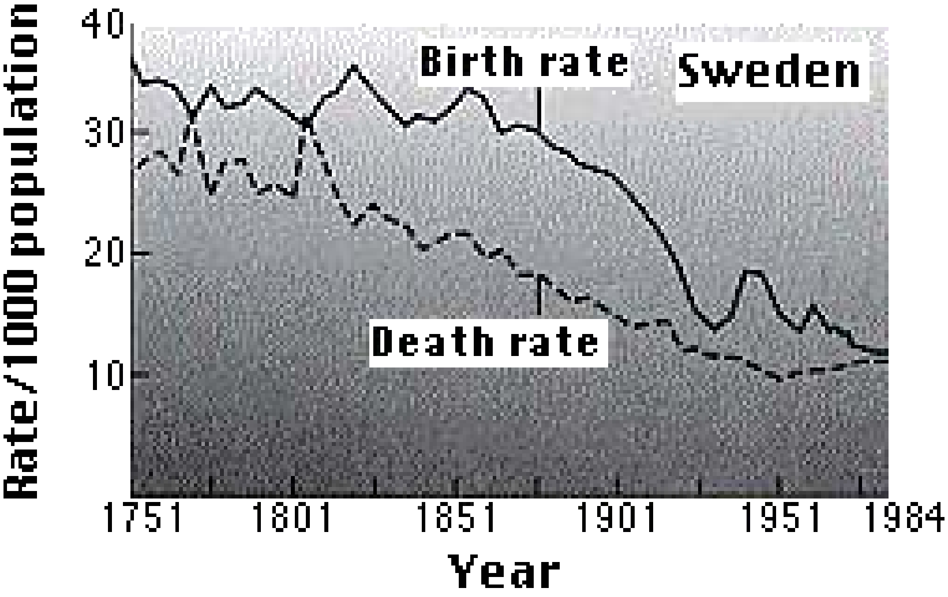


Figure 2.5.2: Incoming radiation absorbed, scattered, and reflected by atmospheric gases.

Just under half (47%) of the incoming solar radiation is absorbed by the land and ocean, and this energy heats up the Earth's surface. The energy absorbed by the Earth returns to the atmosphere through three processes; conduction, radiation, and latent heat (phase change) (Figure 2.5.1).

Conduction is the transfer of heat through direct contact between the surface and the atmosphere. Air is a relatively poor thermal conductor (which means it is a good insulator), so conduction represents only a small part of the energy transfer between the Earth and the atmosphere; equal to about 7% of the incoming solar energy.

All bodies with a temperature above absolute zero (-273^{o} C) radiate heat in the form of longwave, infrared **radiation** (Figure 2.5.2). The warmed Earth is no exception, and about 16% of the original solar energy is radiated from the Earth to the atmosphere (Figure 2.5.1). When sunlight warms a surface such as a paved surface, a patio, or deck, the warmer surface emits more thermal radiation, which is a type of IR radiation. So, there is a conversion from visible, UV, and IR to just thermal IR. This thermal IR is what we experience as heat. Some of this radiated energy will dissipate into space, but a significant amount of heat will be absorbed by the atmosphere. This is the basis for the **greenhouse effect** (Figure 2.5.3). In the greenhouse effect, shortwave solar radiation passes through the atmosphere and reaches the Earth's surface where it gets absorbed. When the radiation is re-emitted by the Earth, it is now in the form of long wavelength, infrared radiation, which does not easily pass through the atmosphere. Instead, this infrared radiation is absorbed by the atmosphere, particularly by the greenhouse gases such as CO_2, methane, and water vapor. As a result, the atmosphere heats up. Some of the infrared radiation absorbed by the atmosphere is also re-emitted back to the planet's surface, further increasing warming. Without the greenhouse effect, the average temperature on Earth would be about -18^{o} C, which is too cold for liquid water, and therefore life as we know it could not exist!

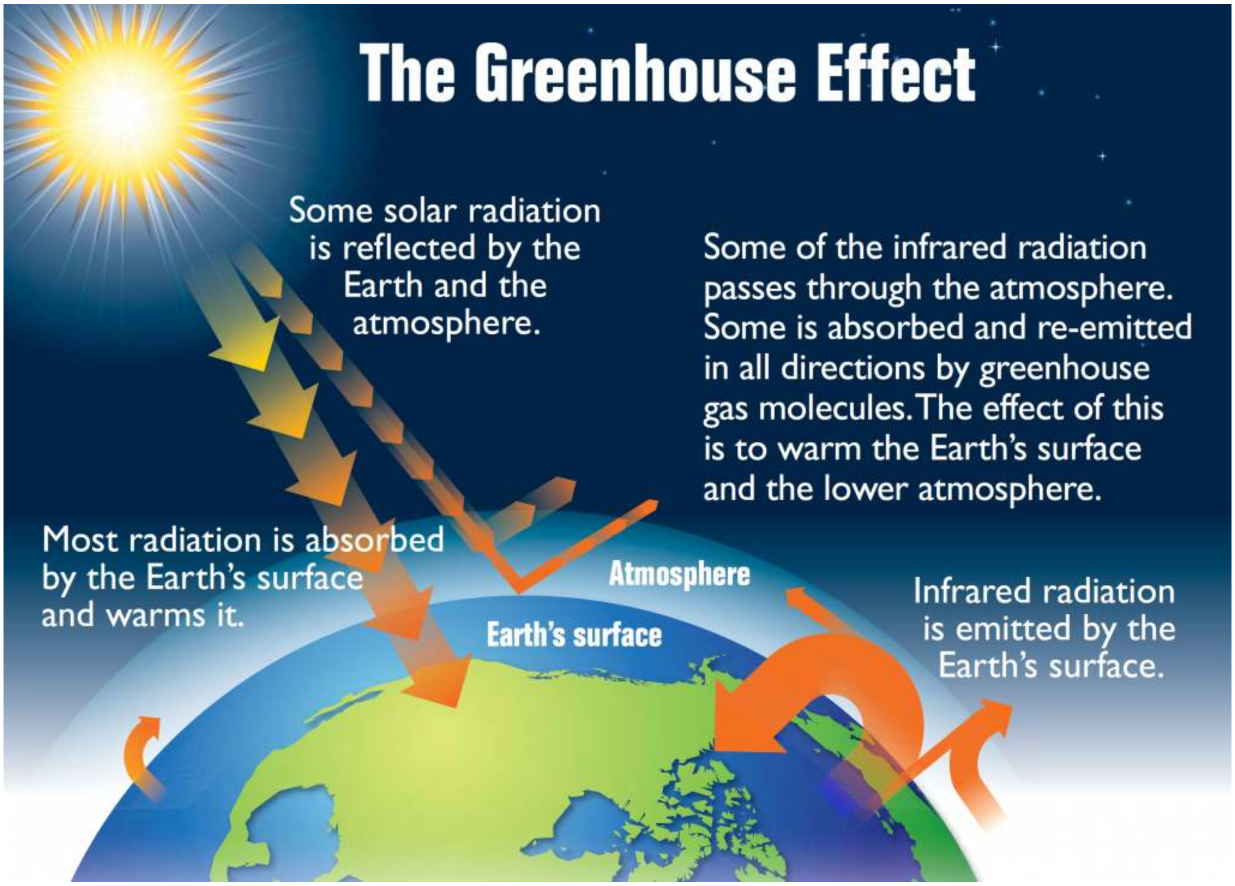


Figure 2.5.3: An explanation of the greenhouse effect. "Earth's Greenhouse Effect" by US EPA is available in the public domain.

The largest pathway for energy exchange between the land or oceans and the atmosphere is **latent heat** transferred through **phase changes**; heat released or absorbed when water moves between solid, liquid, and vapor forms. Heat must be added to liquid water to make it evaporate, and when water vapor is formed, that heat is removed from the ocean and transferred to the atmosphere along with the water vapor. When water vapor condenses into rain, that heat is then returned to the oceans. The same process happens with the formation and melting of ice. Heat is absorbed by ice when it melts, and heat is released when ice forms, and these phase changes transfer heat between the oceans and the atmosphere.

To complete the energy budget, the heat that is absorbed by the atmosphere either directly from solar radiation or as a result of conduction, radiation and latent heat, is eventually radiated back into space (Figure 2.5.1).

Greenhouse Gasses

Throughout this chapter we will be talking about the role of **greenhouse gases** (GHGs) in controlling the climate, so it is important to understand what greenhouse gases are and how they work. As you know, the dominant gases of the atmosphere are nitrogen (as N_2) and oxygen (as O_2). These gas molecules have only two atoms each and are not GHGs. Some of the other important gases of the atmosphere are water vapor (H_2O), carbon dioxide (CO_2), and methane (CH_4). All of these have more than two atoms, and they are GHGs. (For more information on the relative amounts of different gasses in the atmosphere, see Atmosphere). All molecules vibrate at various frequencies and in various ways, and some of those vibrations take place at frequencies within the range of the infrared (IR) radiation that is emitted by Earth's surface. Gases with two atoms, such as O_2, can only vibrate by stretching (back and forth), and those vibrations are much faster than the IR radiation (Figure 2.5.4). Gases with three or more atoms (such as CO_2) vibrate by stretching as well, but they can also vibrate in other ways, such as by bending (Figure 2.5.4). Those vibrations are slower and match IR radiation frequencies. When IR radiation interacts with CO_2 or with one of the other GHGs, the molecular vibrations are enhanced because there is a match between the wavelength of the IR light and the vibrational frequency of the molecule. This makes the molecule vibrate more vigorously, heating the surrounding air in the process. These molecules also emit IR radiation in all directions, some of which reaches Earth's surface. The heating caused by the more vigorous vibrations of GHGs is the **greenhouse effect**.

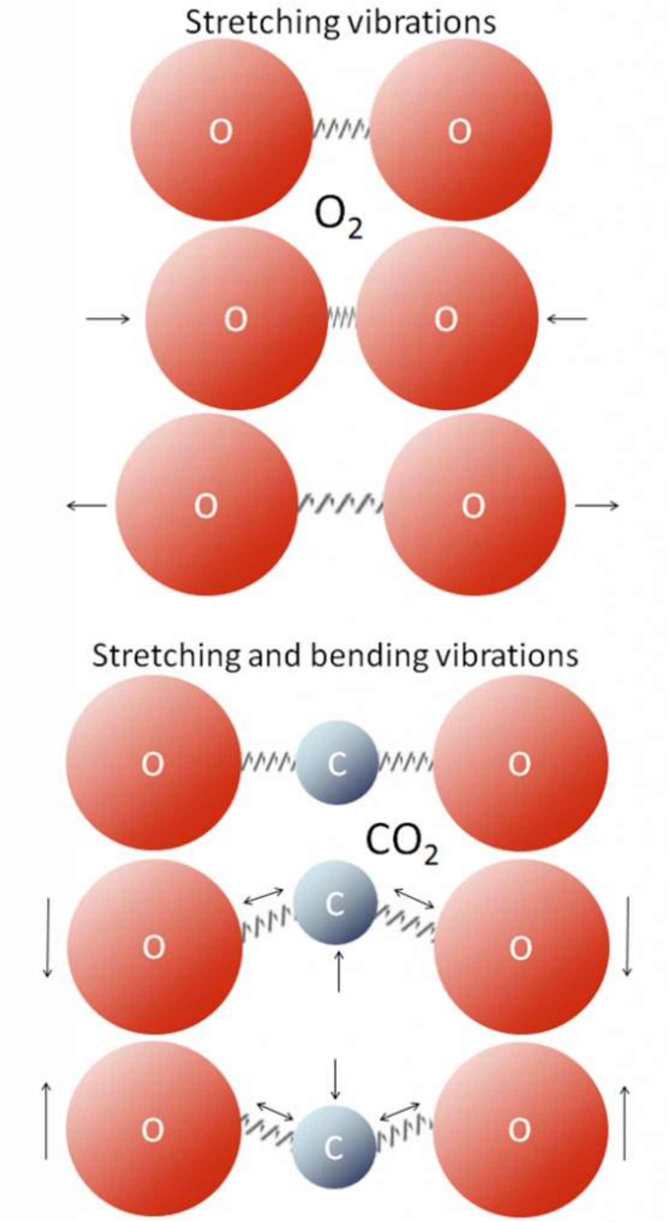


Figure 2.5.4: Stretching versus bending vibrations in atmospheric gases. Image by Steven Earle is licensed under CC BY.

Differential Heating of Earth’s Surface

If the Earth was a flat surface facing the sun, every part of that surface would receive the same amount of incoming solar radiation. However, because the Earth is a sphere, sunlight is not equally distributed over the Earth’s surface, so different regions of Earth will be heated to different degrees. This differential heating of Earth’s surface occurs for a number of reasons. First, because of the curvature of Earth, sunlight only falls perpendicularly to the surface at the center of the sphere (equatorial regions). At any other point on Earth, the angle between the surface and the incoming solar radiation is less than 90^o. Because of this, the same amount of incoming solar radiation will be concentrated in a smaller area at the equator, but will be spread over a much larger area at the poles (Figure 2.5.5). Thus the tropics receive more intense sunlight and a greater amount of heating per unit of area than the polar regions. The angle at which sunlight strikes the Earth contributes to differential heating of the surface in an additional way. At the poles, because of the angle at which the solar energy strikes the surface, more of the light will glance off of the surface and the atmosphere and be reflected back into space. At the equator, the direct angle with which light reaches the surface results in more of the energy being absorbed by the earth rather than being reflected (bouncing off the surface). Recall that the earth is also tilted, changing which part of the earth's surface is pointed directly at the sun during different seasons (see What Makes the Climate Change for more on Earth's Tilt).

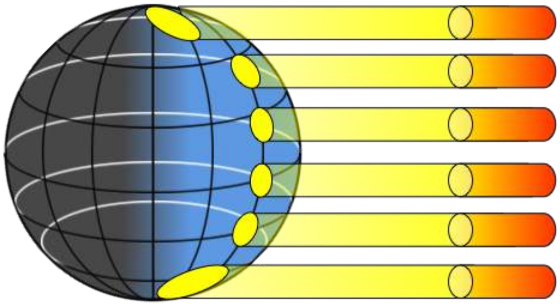


Figure 2.5.5: Because of the curvature of the Earth, the same amount of sunlight will be spread out over a larger area at the poles compared to the equator. The equator therefore receives more intense sunlight, and a greater amount of heat per unit of area. "Solar Angle of Incidence on Earth" by Thebiologyprimer is available in the public domain.

Finally, the poles reflect more solar energy than other parts of the Earth because the poles have a higher **albedo**. The albedo refers to reflectivity of a surface, expressed as the percentage of light that reflects off a given material. Lighter surfaces are more reflective than darker surfaces (which absorb more energy), and therefore have a higher albedo. Water in the oceans or on a lake is one of the darkest surfaces, reflecting less than 10% of the incident light, while clouds and snow or ice are among the brightest surfaces, reflecting 70% to 90% of the incident light (Figure 2.5.6).

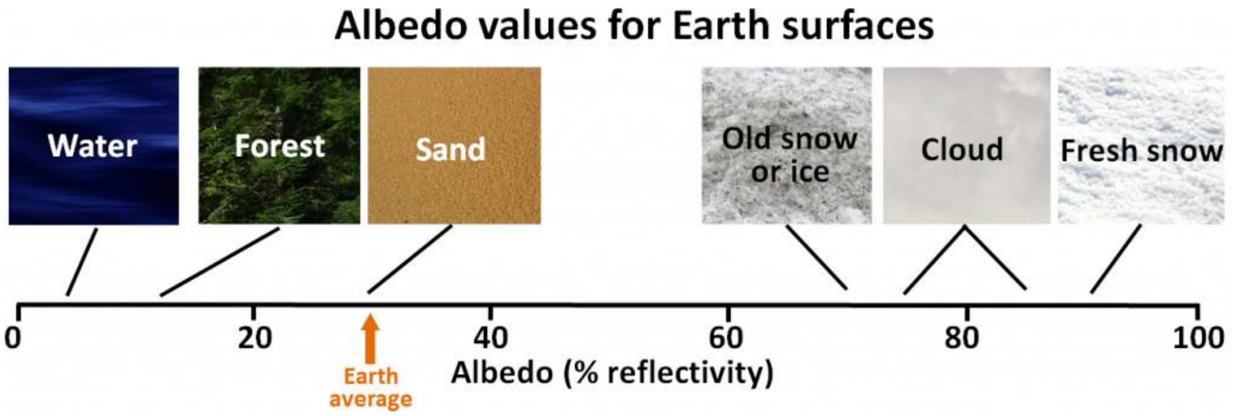


Figure 2.5.6: Typical albedo values for Earth surfaces. Image by Steven Earle is licensed under CC BY.

At the poles, the ice, snow and cloud cover create a much higher albedo, and the poles reflect more and absorb less solar energy than the lower latitudes (Figure 2.5.7). Through all of these mechanisms, the poles absorb much less solar radiation than equatorial regions, which is why the poles are cold and the tropics are very warm.

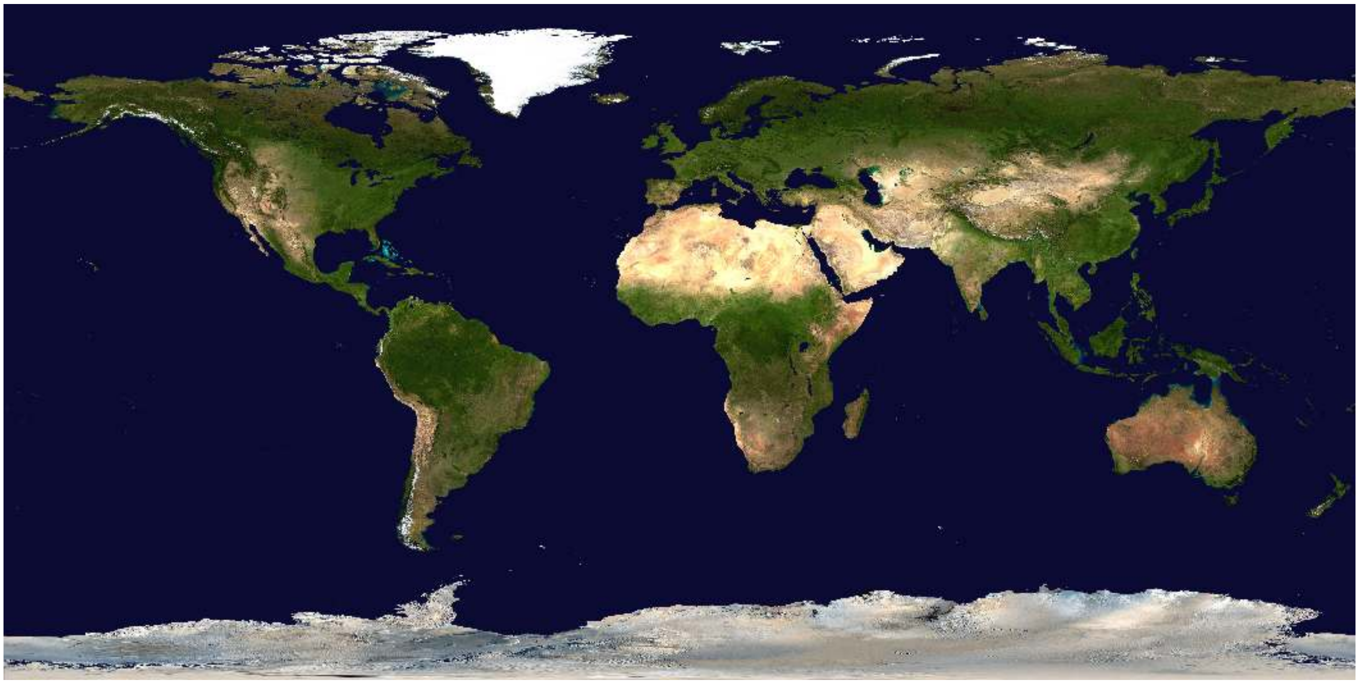


Figure 2.5.7: **Surface of Earth with Cloud Cover Removed** -- The surface of the Earth with cloud cover removed. The poles and deserts are much brighter than the oceans and forests. *Source: NASA Goddard Space Flight Center Image by Reto Stöckli. Courtesy of NASA's Earth Observatory.*

But there is an interesting twist to this global distribution of heat. The tropical regions actually receive more radiant heat than they emit, and the poles emit more heat than they receive (Figure 2.5.8). We should therefore expect that the tropics will be getting continually warmer, while the poles become increasingly cold. Yet this is not the case; so what is happening? Rather than the heat remaining isolated near the equator, about 20% of the heat from the tropics is transported to the poles before it is emitted. This large scale transport of energy moderates the climates at both extremes. The mechanisms for this heat transfer are ocean and atmospheric circulation.

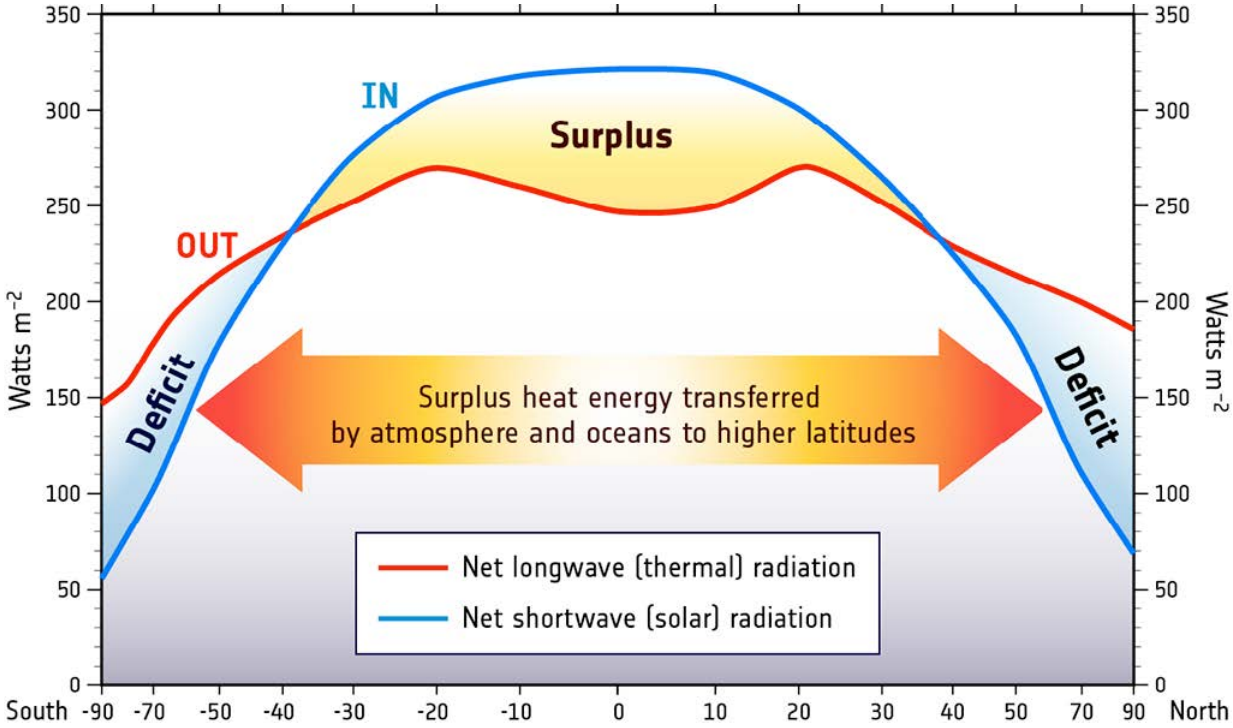


Figure 2.5.8: The balance between heat gain and heat loss as a function of latitude. Excess heat received near the equator is transferred towards the poles *Source: National Oceanography Centre (NOC).*

The Earth's Tilt causes Seasons

One of the fundamental facts of life at Earth's mid-latitudes, is that there are significant variations in the heat we receive from the Sun during the course of the year. The difference between seasons gets more pronounced the farther north or south from the equator we travel, and the seasons in the Southern Hemisphere are the opposite of what we find on the northern half of Earth. The seasons are actually caused by the 23.5° tilt of Earth's axis which continues to point the same direction in the sky throughout the year (figure 2.5.9). As Earth travels around the Sun, in June the Northern Hemisphere "leans into" the Sun and is more directly illuminated. In December, the situation is reversed: the Southern Hemisphere leans into the Sun, and the Northern Hemisphere leans away. In September and March, Earth leans "sideways"—neither into the Sun nor away from it—so the two hemispheres are equally favored with sunshine. When we lean into the Sun, sunlight hits us at a more direct angle and is more effective at heating Earth's surface (figure 2.5.10). During the summer season, the sun also spends more time above the horizon, resulting in more energy hitting the surface of the Earth.

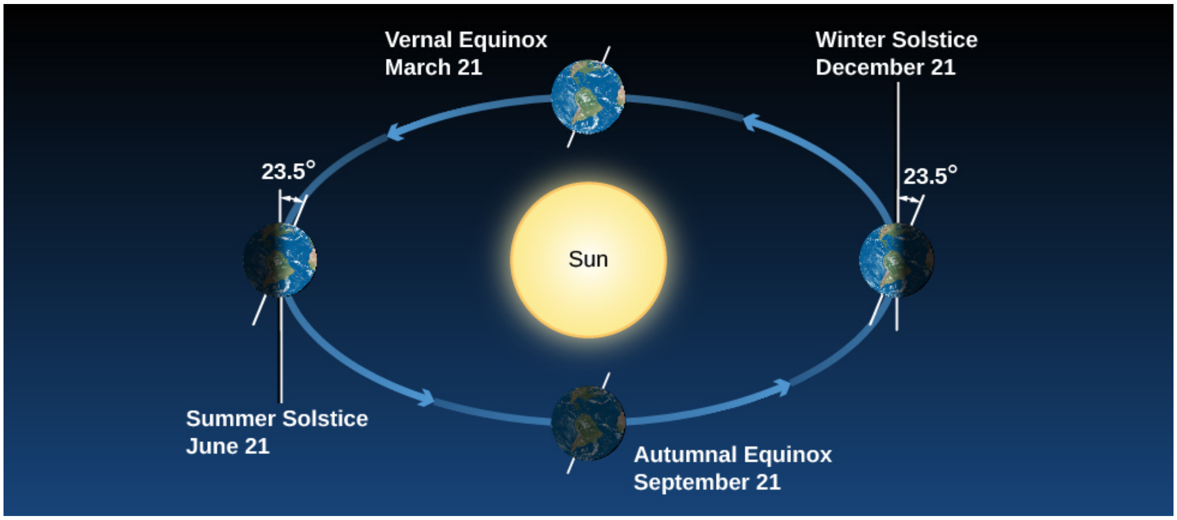


Figure 2.5.9: We see Earth at different seasons as it circles the Sun. In June, the Northern Hemisphere "leans into" the Sun, and those in the North experience summer and have longer days. In December, during winter in the Northern Hemisphere, the Southern Hemisphere "leans into" the Sun and is illuminated more directly. In spring and autumn, the two hemispheres receive more equal shares of sunlight. *Source: [4.2: The Seasons](#).*

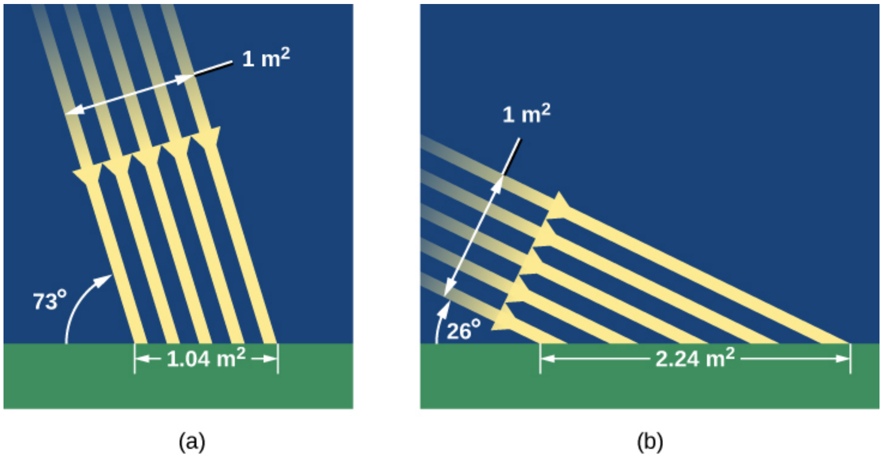


Figure 2.5.10: The Sun's Rays in Summer and Winter. (a) In summer, the Sun appears high in the sky and its rays hit Earth more directly, spreading out less. (b) In winter, the Sun is low in the sky and its rays spread out over a much wider area, becoming less effective at heating the ground. *Source: [4.2: The Seasons](#).*

Further Reading

The National Aeronautical and Space Administration (NASA) Earth Observatory website has an array of climate resources. For a more in-depth discussion of Earth's energy budget, go to http://earthobservatory.nasa.gov/Features/EnergyBalance/

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Pittsburgh)

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

- Contributed by Melissa Ha and Rachel Schleiger Faculty (Biological Sciences) at Yuba College & Butte College
- Contributed by Paul Webb Professor (Biology) at Rodger Williams University
- Contributed by Chris Johnson, Matthew D. Affolter, Paul Inkenbrandt, & Cam Mosher Faculty (Geology) at Salt Lake Community College
- Contributed by Steven Earle Faculty (Geology) at Vancouver Island University
- 5.2 Climate Processes; External and Internal Controls from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin
- 19.1 What Makes Climate Change from *Physical Geology* by Steven Earle (licensed under CC-BY)
- Sourced from OpenGeology from *An Introduction to Geology* Section 15.2 Earth's Temperature
- 8.1 Earth's Heat Budget from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- Climate and the Effects of Global Climate Change from *General Biology* by OpenStax (licensed under CC-BY)
- Climate Change from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- 4.2: The Seasons from *Astronomy* by OpenStax (licensed under CC-BY)

2.6: Atmospheric and Oceanic Circulation

Atmospheric Circulation

Differential heating of the Earth's surface results in equatorial regions receiving more heat than the poles. As air is warmed at the equator it becomes less dense and rises, while at the poles the cold air is denser and sinks. If the Earth was non-rotating, the warm air rising at the equator would reach the upper atmosphere and begin moving horizontally towards the poles. As the air reached the poles it would cool and sink, and would move over the surface of Earth back towards the equator. This would result in one large atmospheric convection cell in each hemisphere (Figure $2.6.1$), with air rising at the equator and sinking at the poles, and the movement of air over the Earth's surface creating the winds. On this non-rotating Earth, the prevailing winds would thus blow from the poles towards the equator in both hemispheres (Figure $2.6.1$).

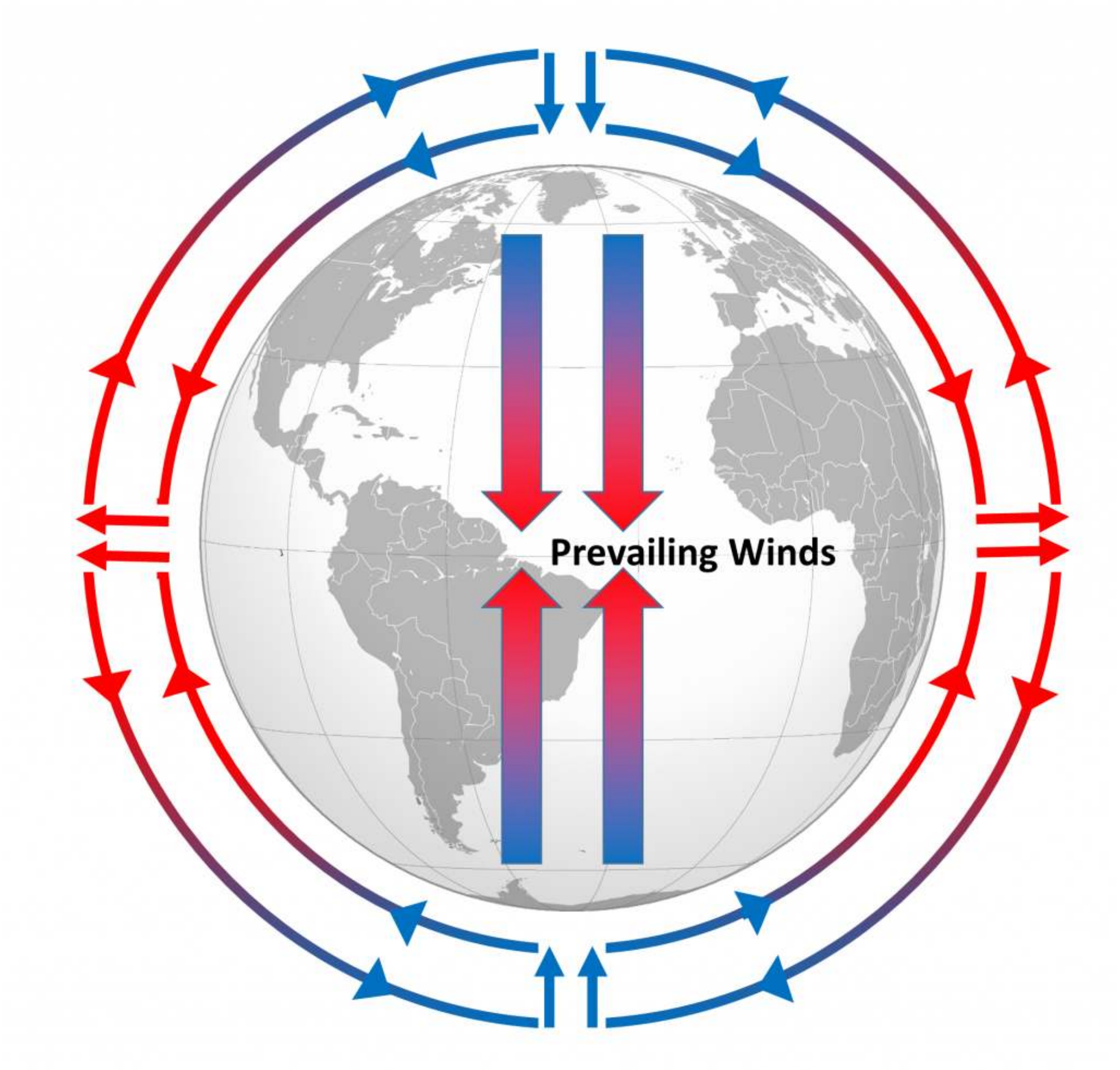


Figure $2.6.1$: Hypothetical atmospheric convection cells on a non-rotating Earth. Air rises at the equator and sinks at the poles, creating a single convection cell in each hemisphere. The prevailing winds moving over the Earth's surface blow from the poles towards the equator in both hemispheres (Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

The non-rotating situation in Figure (2.6.1) is of course only hypothetical, and in reality the Earth's rotation makes this atmospheric circulation a bit more complex. The paths of the winds on a rotating Earth are deflected by the **Coriolis Effect**. The Coriolis Effect is a result of the fact that different latitudes on Earth rotate at different speeds. This is because every point on Earth must make a complete rotation in 24 hours, but some points must travel farther, and therefore faster, to complete the rotation in the same amount of time. In 24 hours a point on the equator must complete a rotation distance equal to the circumference of the Earth, which is about 40,000 km. A point right on the poles covers no distance in that time; it just spins. So the speed of rotation at the equator is about 1600 km/hr, while at the poles the speed is 0 km/hr. Latitudes in between rotate at intermediate speeds; approximately 1400 km/hr at 30^o and 800 km/hr at 60^o. As objects move over the surface of the Earth they encounter regions of varying speed, which causes their path to be deflected by the Coriolis Effect.

To explain the Coriolis Effect, imagine a cannon positioned at the equator and facing north. Even though the cannon appears stationary to someone on Earth, it is in fact moving east at about 1600 km/hr due to Earth's rotation. When the cannon fires the projectile travels north towards its target; but it also continues to move to the east at 1600 km/hr, the speed it had while it was still in the cannon. As the shell moves over higher latitudes, its momentum carries it eastward faster than the speed at which the ground beneath it is rotating. For example, by 30^o latitude the shell is moving east at 1600 km/hr while the ground is moving east at only 1400 km/hr. Therefore, the shell gets "ahead" of its target, and will land to the east of its intended destination. From the point of view of the cannon, the path of the projectile appears to have been deflected to the right (red arrow, Figure 2.6.2). Similarly, a cannon located at 60^o and facing the equator will be moving east at 800 km/hr. When its shell is fired towards the equator, the shell will be moving east at 800 km/hr, but as it approaches the equator it will be moving over land that is traveling east *faster* than the projectile. So the projectile gets "behind" its target, and will land to the west of its destination. But from the point of view of the cannon facing the equator, the path of the shell still appears to have been deflected to the right (green arrow, Figure 2.6.2). Therefore, in the Northern Hemisphere, the apparent Coriolis deflection will *always* be to the **right**.

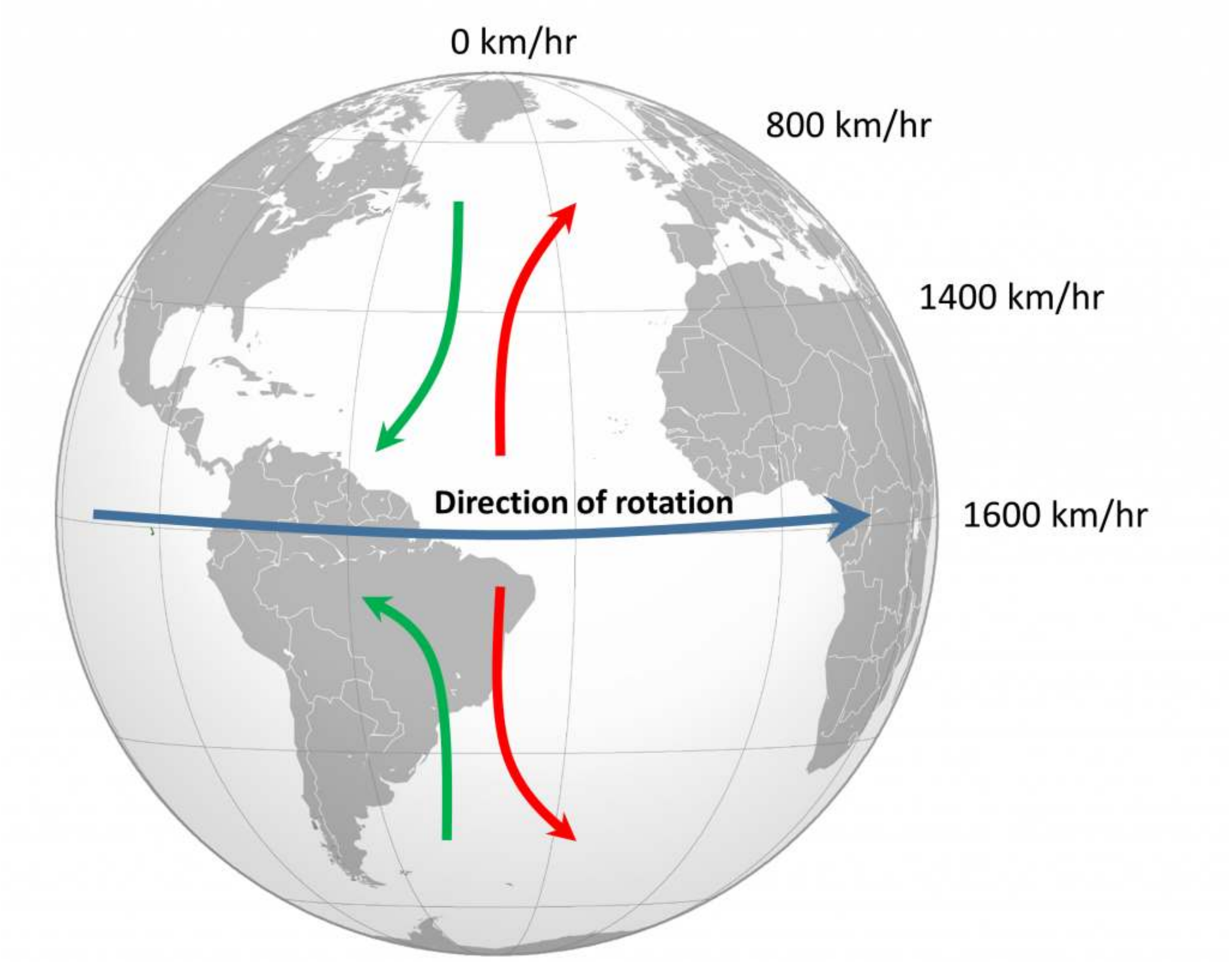


Figure 2.6.2: The Coriolis Effect. Objects moving from the equator towards the poles (red arrows) move into a region of slower rotational speed and their paths are deflected "ahead" of their point of origin. Movement from high latitudes to low latitudes (green arrows) goes from a region of low speed to a region of higher rotation speed, and there is deflection "behind" their point of origin. In the Northern Hemisphere this deflection is always to the right from the point of origin, and in the Southern Hemisphere the deflection is always to the left
(Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

In the Southern Hemisphere the situation is reversed (Figure 2.6.2). Objects moving towards the equator from the south pole are moving from low speed to high speed, so are left behind and their path is deflected to the left. Movement from the equator towards the south pole also leads to deflection to the left. In the Southern Hemisphere, the Coriolis deflection is always to the **left** from the point of origin.

The magnitude of the Coriolis deflection is related to the difference in rotation speed between the start and end points. Between the poles and 60^o latitude, the difference in rotation speed is 800 km/hr. Between the equator and 30^o latitude, the difference is only 200 km/hr (Figure 2.6.2). Therefore the strength of the Coriolis Effect is stronger near the poles, and weaker at the equator.

Because of the rotation of the Earth and the Coriolis Effect, rather than a single atmospheric convection cell in each hemisphere, there are three major cells per hemisphere. Warm air rising at the equator cools as it moves through the upper atmosphere, and it descends at around 30^o latitude. The convection cells created by rising air at the equator and sinking air at 30^o are referred to as **Hadley Cells**, of which there is one in each hemisphere. The cold air that descends at the poles moves over the Earth's surface towards the equator, and by about 60^o latitude it begins to rise, creating a **Polar Cell** between 60^o and 90^o. Between 30^o and 60^o lie the **Ferrel Cells**, composed of sinking air at 30^o and rising air at 60^o (Figure 2.6.3). With three convection cells in each hemisphere that rotate in alternate directions, the surface winds no longer always blow from the poles towards the equator as in the non-rotating

Earth in Figure 2.6.1. Instead, surface winds in both hemispheres blow towards the equator between 90° and 60° latitude, and between 0° and 30° latitude. Between 30° and 60° latitude, the surface winds blow towards the poles (Figure 2.6.3).

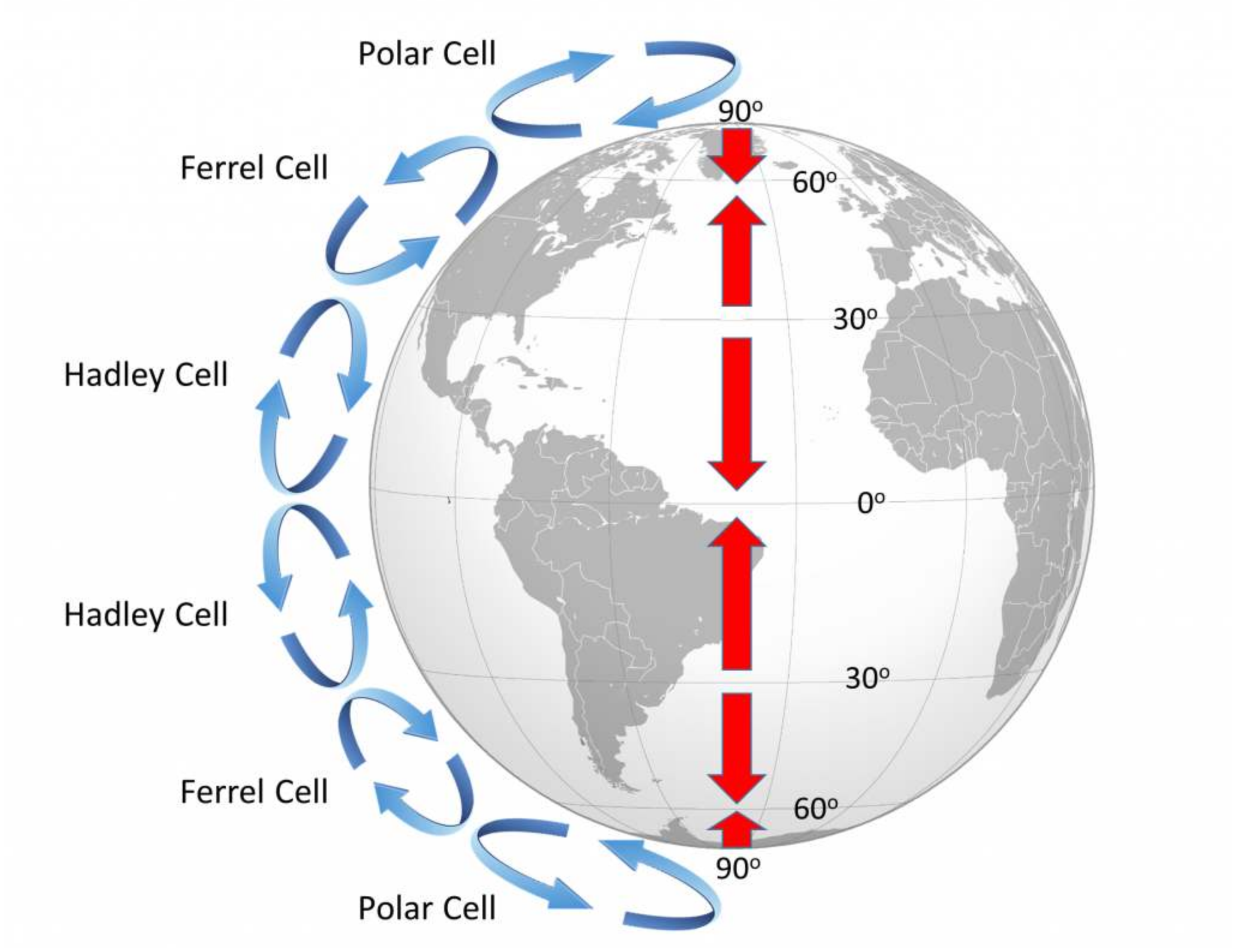


Figure 2.6.3: On a rotating Earth, there are three atmospheric convection cells in each hemisphere, leading to alternating bands of surface winds (red arrows)
(Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

The surface winds created by the atmospheric convection cells are also influenced by the Coriolis Effect as they change latitudes. The Coriolis Effect deflects the path of the winds to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Adding this deflection leads to the pattern of prevailing winds illustrated in Figure 2.6.4). Between the equator and 30° latitude are the **trade winds**; the northeast trade winds in the Northern Hemisphere and the southeast trade winds in the Southern Hemisphere (note that winds are named based on the direction from which they originate, not where they are going). The **westerlies** are the dominant winds between 30° and 60° in both hemispheres, and the **polar easterlies** are found between 60° and the poles.

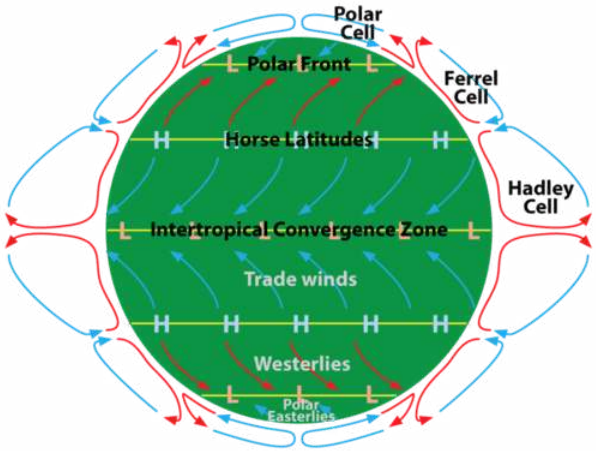


Figure 2.6.4: The atmospheric circulation cells, showing direction of winds at Earth's surface. The atmosphere is thicker at the equator than at the poles. *Created by Zachary Wilson for CK-12 Foundation CC BY-NC 3.0.*

In between these wind bands lie regions of high and low pressure. High pressure zones occur where air is descending, while low pressure zones indicate rising air. Along the equator the rising air creates a low pressure region called the **doldrums**, or the **Intertropical Convergence Zone** (**ITCZ**) (convergence zone because this is where the trade winds converge). The **doldrums** refer to regions of low pressure around the equator. In these areas, air is rising rather than moving horizontally, so these regions commonly encounter very light winds. The lack of wind could leave sailing ships becalmed for days or weeks at a time, which was not good for the morale of the ship's crew. At 30º latitude there are high pressure zones of descending air known as the **horse latitudes**, or the subtropical highs. Like the doldrums the **horse latitudes** are also areas with light winds, this time due to descending air, which could leave ships becalmed. The term **trade winds** may have originally derived from the terms for "track" or "path", but the term may have become more common during European exploration and commercialization of the New World. Mariners sailing from Europe to the New World could sail south until they reached the trade winds, which would then propel their ships across the Atlantic to the Caribbean. To return to Europe, ships could sail to the northeast until they entered the westerlies, which would then steer them back to Europe. Finally, at 60º lies another low pressure region called the **polar front**. It should be noted that these high and low pressure zones are not fixed in place; their latitude fluctuates depending on the season, and these fluctuations have important implications for regional climates.

In addition to their role in creating the surface winds, these high and low pressure systems also influence other climatic phenomena (Figure 2.6.5). Along the equator air is rising as it is warmed by solar radiation. Warm air contains more water vapor than cold air, which is why we experience humidity during the summer and not during the winter. The water content of air roughly doubles with every 10^{o} C increase in temperature. So the air rising at the equator is warm and full of water vapor; as it rises into the upper atmosphere it cools, and the cool air can no longer hold as much water vapor, so the water condenses and forms rain. Therefore, low pressure systems are associated with precipitation, and we see wet habitats like tropical rainforests near the equator (Figure 2.6.5). The ITCZ migrates slightly with the season, following the relative motion of sunlight between the Tropic of Cancer and Tropic of Capricorn. Because land areas heat more quickly than the oceans and there are more land areas in the Northern Hemisphere, during the Northern Hemisphere's summer, the ITCZ is approximately 5 degrees north of the equator, while in the winter, it shifts back and is approximately at the equator. As the ITCZ shifts, the dominant wind belts also shift slightly north in summer and south in winter, which causes the wet and dry seasons in this area.

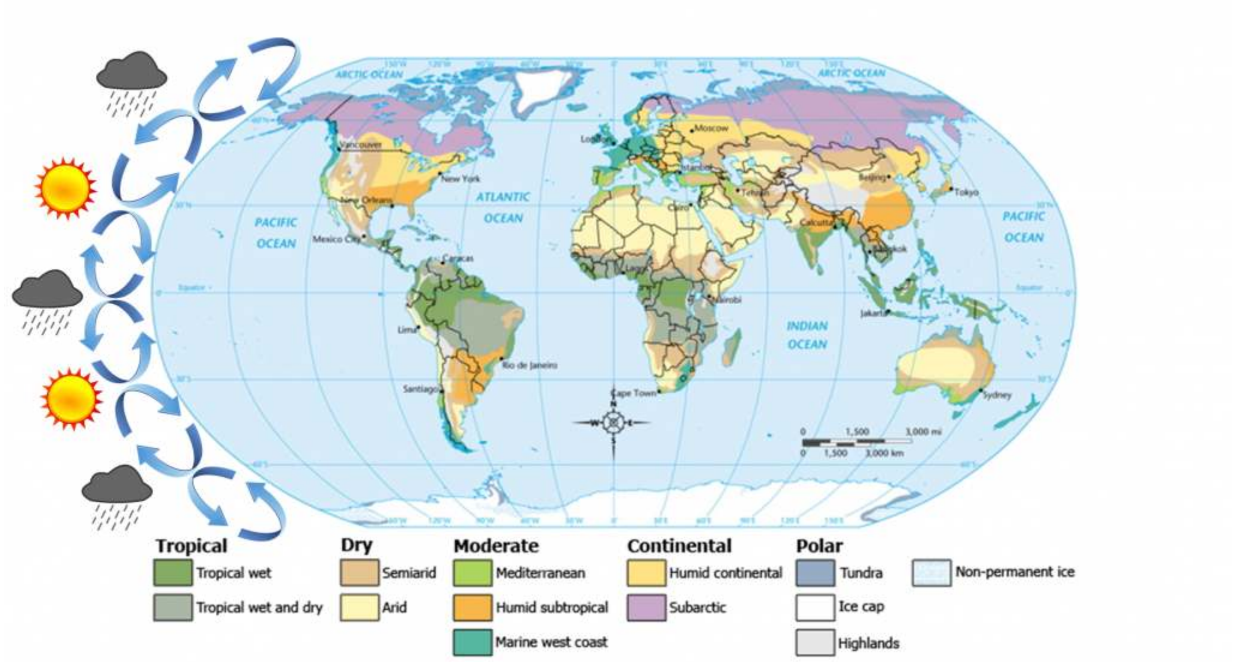


Figure 2.6.5: Major global climatic regions in relation to atmospheric convection cells. Rising air and low pressure creates rain and wet environments at 0^{o} and 60^{o} latitudes, while high pressure, sinking air creates drier conditions at 30^{o} and 90^{o} latitudes. (Modified by Paul Webb; Map by Waitak at en.Wikipedia Later version(s) were uploaded by Splette at en.Wikipedia; Sun by Inductiveload (Own work Based on File:Nuvola_apps_kweather.svg); Raincloud by Calusarul (Own work); all [CC BY-SA 3.0], via Wikimedia Commons).

After rising and producing rain near the equator, the air masses move towards 30^{o} latitude and sink back towards Earth as part of the Hadley convection cells. This air has lost most of its moisture after producing the equatorial rains, so the sinking air is dry, resulting in arid climates near 30^{o} latitude in both hemispheres. Many of the major desert regions on Earth are located near 30^{o} latitude, including much of Australia, the Middle East, and the Sahara Desert of Africa (Figure 2.6.5). The air also becomes compressed and heats up as it sinks, absorbing any moisture from the clouds and creating clear skies. Thus high pressure systems are associated with dry weather and clear skies. This cycle of high and low pressure regions continues with the Ferrel and Polar convection cells, leading to rain and the boreal forests at 60^{o} latitude in the Northern Hemisphere (there are no corresponding large land masses at these latitudes in the Southern Hemisphere). At the poles, descending, dry air produces little precipitation, leading to the polar desert climate.

The elevation of the land also plays a role in precipitation and climactic characteristics. As moist air moves over land and encounters mountains it rises, expands, and cools because of the declining pressure and temperature. The cool air holds less water vapor, so condensation occurs and rain falls on the windward side of the mountains (Figure 2.6.6). As the air passes over the mountains to the leeward side, it is now dry air, and as it sinks the pressure increases, it heats back up, any moisture revaporizes, and it creates dry, deserts regions behind the mountains (Figure 2.6.6). This phenomenon is referred to as a **rain shadow**, and can be found in areas such as the Tibetan Plateau and Gobi Desert behind the Himalayas, Death Valley behind the Sierra Nevada mountains, and the dry San Joaquin Valley in California.

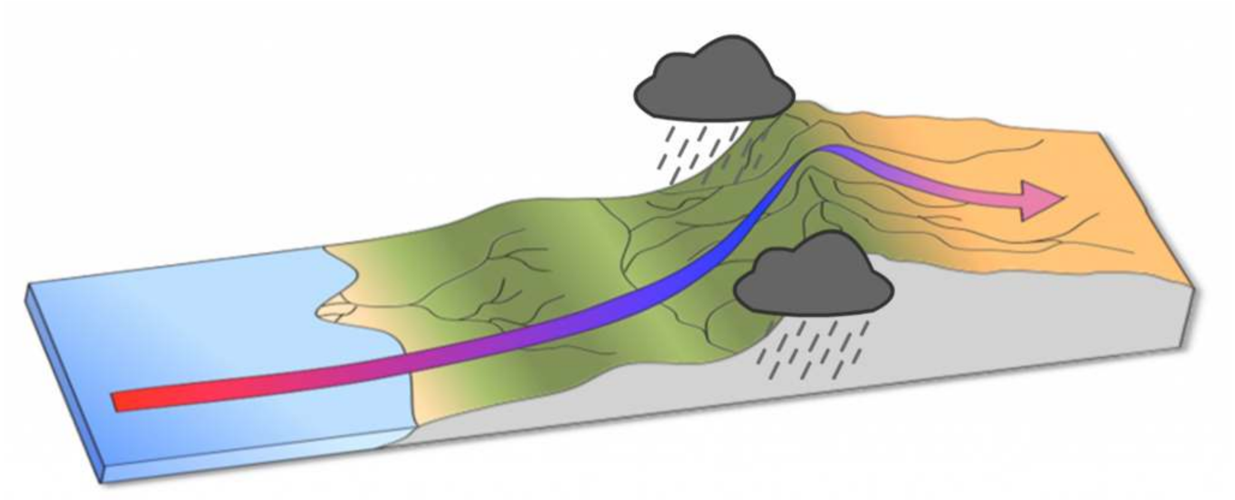


Figure 2.6.6: A rain shadow. Air rising over mountains cools and condenses and forms rain, leaving dry descending air and arid conditions on the other side of the mountain. *Modified by Paul Webb from Thebiologyprimer, public domain via Wikimedia Commons.*

Ocean Circulation

Not unexpectedly, the oceans are warmest near the equator—typically 25° to 30°C—and coldest near the poles—around 0°C (Figure 2.6.7). (Sea water will remain unfrozen down to about -2°C) Variations in sea-surface temperatures (SST) are related to redistribution of water by ocean currents, as we will see below. A good example of that is the plume of warm Gulf Stream water that extends across the northern Atlantic. St. John's, Newfoundland, and Brittany in France are at about the same latitude (47.5° N), but the average SST in St. John's is a frigid 3°C, while that in Brittany is a reasonably comfortable 15°C.

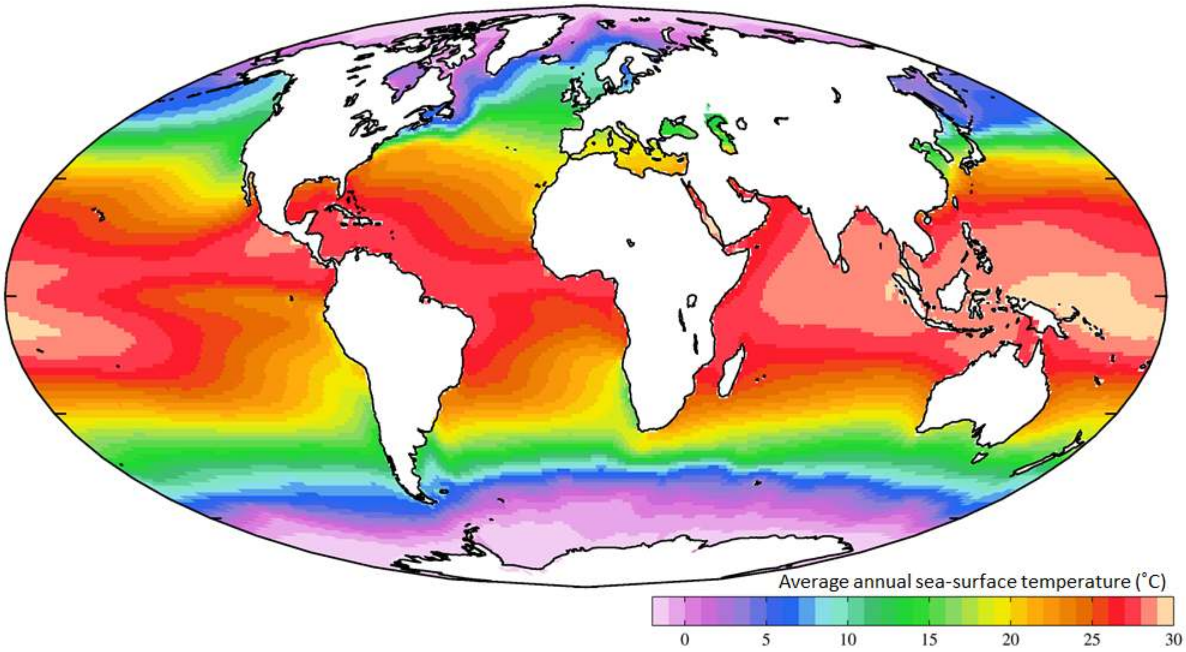


Figure 2.6.7: The global distribution of average annual sea-surface temperatures.
Source: Plumbago, licensed under CC BY-SA.

Currents in the open ocean are created by wind moving across the water and by density differences related to temperature and salinity. An overview of the main ocean currents is shown in Figure 2.6.8. As you can see, the northern hemisphere currents form circular patterns (**gyres**) that rotate clockwise, while the southern hemisphere gyres are counter-clockwise. This happens for the same reason that the water in your northern hemisphere sink rotates in a clockwise direction as it flows down the drain; this is caused by the **Coriolis effect**.

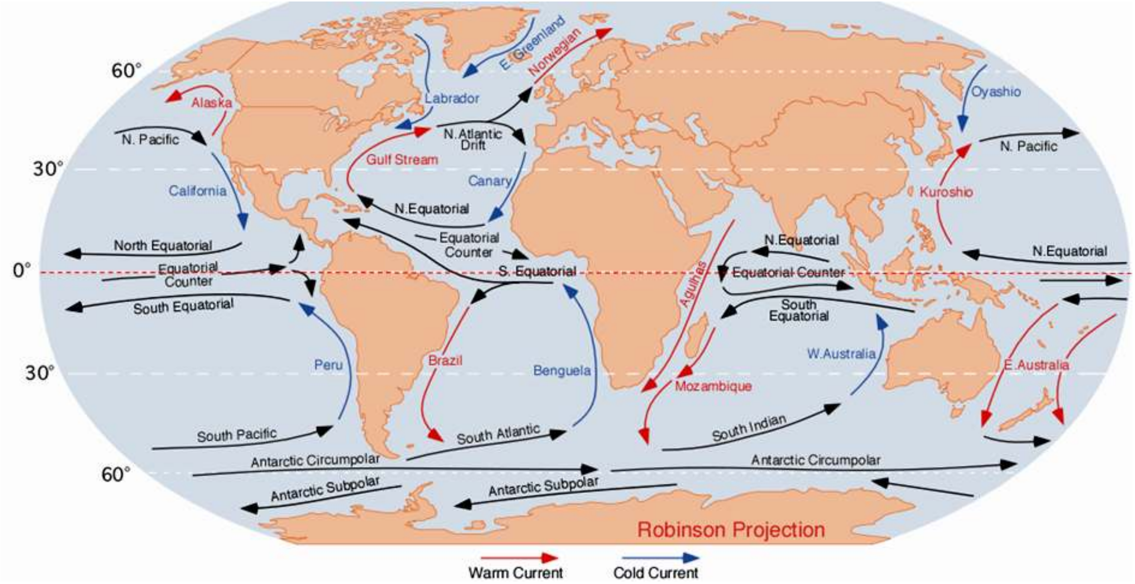


Figure 2.6.8: Overview of the main open-ocean currents. Red arrows represent warm water moving toward colder regions. Blue arrows represent cold water moving toward warmer regions. Black arrows represent currents that don't involve significant temperature changes.
Source: image "Corrientes Oceanicas" by Dr. Michael Pidwirny is available in the public domain.

Because the ocean basins are not like bathroom basins, not all ocean currents behave the way we would expect. In the North Pacific, for example, the main current flows clockwise, but there is a secondary current in the area adjacent to our coast—the Alaska Current—that flows counter-clockwise, bringing relatively warm water from California, past Oregon, Washington, and B.C. to Alaska. On Canada's eastern coast, the cold Labrador Current flows south past Newfoundland, bringing a stream of icebergs past the harbour at St. John's (Figure 2.6.9). This current helps to deflect the Gulf Stream toward the northeast, ensuring that Newfoundland stays cool, and western Europe stays warm.

Figure 2.6.9: An iceberg floating past Exploits Island on the Labrador Current.
Source: image "Newfoundland Iceberg" by Shawn is licensed under CC BY-SA 2.0.

The currents shown in Figure 2.6.8 are all surface currents, and they only involve the upper few hundred meters of the oceans. But there is much more going on underneath. The Gulf Stream, for example, which is warm and saline, flows past Britain and Iceland into the Norwegian Sea (where it becomes the Norwegian Current). As it cools down, it becomes denser, and because of its high salinity, which also contributes to its density, it starts to sink beneath the surrounding water (Figure 2.6.10). At this point, it is known as **North Atlantic Deep Water** (NADW), and it flows to significant depth in the Atlantic as it heads back south.

Meanwhile, at the southern extreme of the Atlantic, very cold water adjacent to Antarctica also sinks to the bottom to become **Antarctic Bottom Water** (AABW) which flows to the north, underneath the NADW.

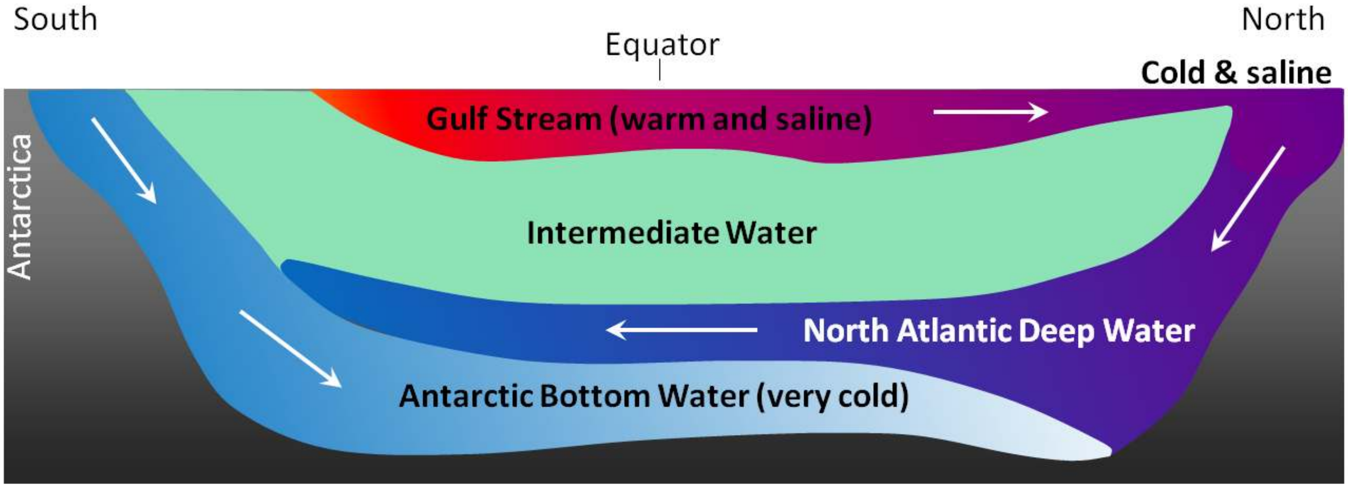


Figure 2.6.10: A depiction of the vertical movement of water along a north-south cross-section through the Atlantic basin. *Source: Steven Earle, licensed under CC BY.*

The descent of the dense NADW is just one part of a global system of seawater circulation, both at surface and at depth, as illustrated in Figure 2.6.11). The water that sinks in the areas of deep water formation in the Norwegian Sea and adjacent to Antarctica moves very slowly at depth. It eventually resurfaces in the Indian Ocean between Africa and India, and in the Pacific Ocean, north of the equator.

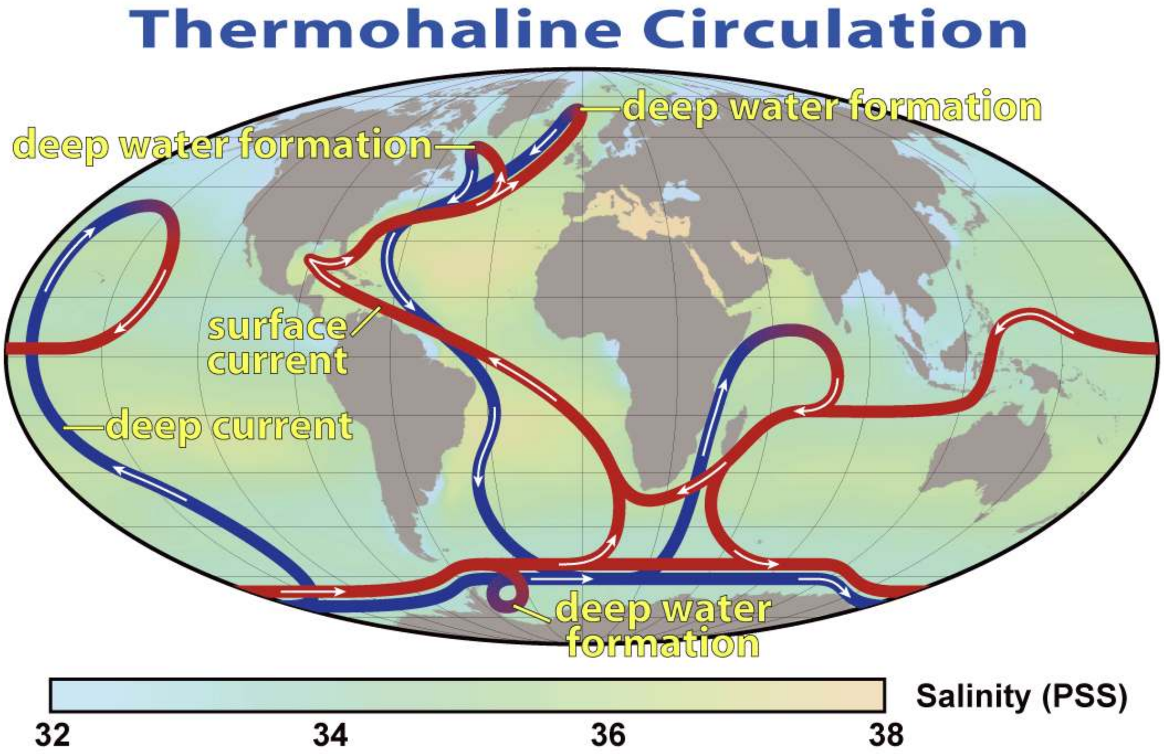


Figure 2.6.11: The thermohaline circulation system, also known as the Global Ocean Conveyor. *Source: image "A summary of the path of thermohaline circulation" by NASA is available in the public domain.*

The thermohaline circulation is critically important to the transfer of heat on Earth. It brings warm water from the tropics to the poles, and cold water from the poles to the tropics, thus keeping polar regions from getting too cold and tropical regions from getting too hot. A reduction in the rate of thermohaline circulation would lead to colder conditions and enhanced formation of sea ice at the poles. This would start a positive feedback process that could result in significant global cooling. There is compelling evidence to indicate that there were major changes in thermohaline circulation, corresponding with climate changes, during the Pleistocene Glaciation.

The movement of surface currents also plays a role in the vertical movements of deeper water, mixing the upper water column. **Upwelling** is the process that brings deeper water to the surface, and its major significance is that it brings nutrient-rich deep water to the nutrient-deprived surface, stimulating primary production (see section 7.3). **Downwelling** is where surface water is forced downwards, where it may deliver oxygen to deeper water. Downwelling leads to reduced productivity, as it extends the depth of the nutrient-limited layer. For more details on upwelling, downwelling, and ocean productivity see the section of Dr. Paul Webb's Oceanography book on Currents, Upwelling and Downwelling.

There are several interactions between ocean currents, ocean temperatures, and atmospheric circulation that cause cyclic global climate variability. The most well know of which is the **El Niño/Southern Oscillation** (**ENSO**) in the Pacific Ocean [also called **El Niño-La Niña Cycles**] associated with a band of warm ocean water that develops in the central and east-central equatorial Pacific. For more information on El Niño and La Niña, see the section of Dr. Paul Webb's Oceanography book on El Niño and La Niña. El Niño/Southern Oscillation (ENSO) is perhaps the most important ocean-atmosphere interaction phenomenon to cause cyclic global climate variability.

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Pittsburgh)

- Contributed by Paul Webb Professor (Biology) at Rodger Williams University
- Contributed by Steven Earle Faculty (Geology) at Vancover Island University
- 18.4 Ocean Water from *Physical Geology* by Steven Earle (licensed under CC-BY)
- 8.2 Winds and the Coriolis Effect from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- 8.3 Winds and Climate from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- 9.5: Currents, Upwelling and Downwelling from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- 9.6: El Niño and La Niña from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- 10.02: Controls of Climate from *Physical Geography and Natural Disasters* by Adam Dastrup (licensed under CC BY-NC-SA 4.0)

2.7: What Makes the Climate Change

There are two parts to climate change, the first one is known as **climate forcing**, which is when conditions change to give the climate a little nudge in one direction or the other. The second part of climate change, and the one that typically does most of the work, is what we call a **feedback**. When a climate forcing changes the climate a little, a whole series of environmental changes take place, many of which either exaggerate the initial change (**positive feedbacks**), or suppress the change (**negative feedbacks**). In this section we will be discussing primarily natural climate forcing. Natural climate forcing has been going on throughout geological time. A wide range of processes has been operating at widely different time scales, from a few years to billions of years.

An example of a climate-forcing mechanism is the increase in the amount of carbon dioxide (CO_2) in the atmosphere that results from our use of fossil fuels. CO_2 traps heat in the atmosphere and leads to climate warming. Warming changes vegetation patterns; contributes to the melting of snow, ice, and permafrost; causes sea level to rise; reduces the solubility of CO_2 in sea water; and has a number of other minor effects. Most of these changes contribute to more warming. Melting of permafrost, for example, is a strong positive feedback because frozen soil contains trapped organic matter that is converted to CO_2 and methane (CH_4) when the soil thaws. Both these gases accumulate in the atmosphere and add to the warming effect. On the other hand, if warming causes more vegetation growth, that vegetation should absorb CO_2, thus reducing the warming effect, which would be a negative feedback. Under our current conditions—a planet that still has lots of glacial ice and permafrost—most of the feedbacks that result from a warming climate are positive feedbacks and so the climate changes that we cause get naturally amplified by natural processes.

Natural Climate Forcing

Life Cycle of the Sun

The longest-term natural forcing variation is related to the evolution of the Sun. Like most other stars of a similar mass, our Sun is evolving. For the past 4.57 billion years, its rate of nuclear fusion has been increasing, and it is now emitting about 40% more energy (as light) than it did at the beginning of geological time (Figure 2.7.1). A difference of 40% is big, so it's a little surprising that the temperature on Earth has remained at a reasonable and habitable temperature for all of this time. The mechanism for that relative climate stability has been the evolution of our atmosphere from one that was dominated by CO_2, and also had significant levels of CH_4—both GHGs—to one with only a few hundred parts per million of CO_2 and just under 1 part per million of CH_4 because, over geological time, life and its metabolic processes have evolved and changed the atmosphere.

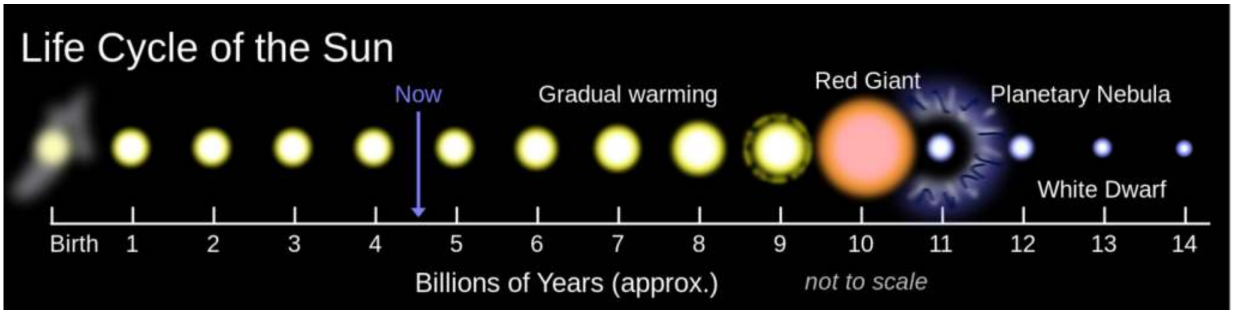


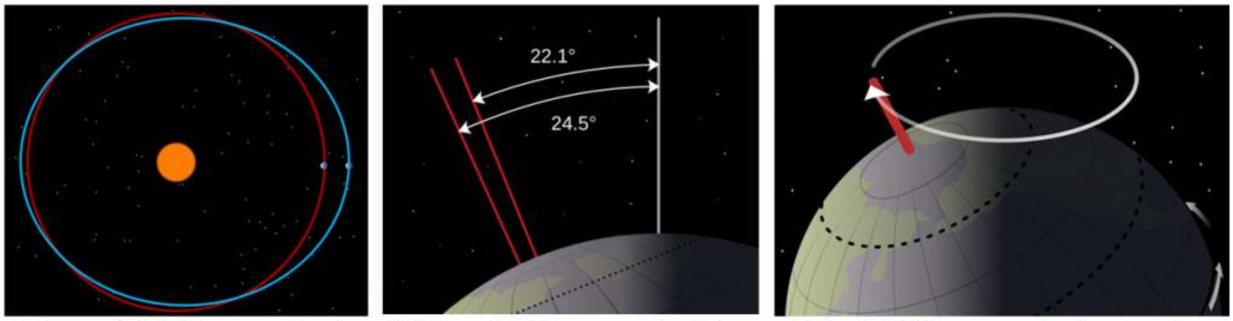
Figure 2.7.1: The life cycle of our Sun and of other similar stars. *Source: image "Solar Life Cycle" by Oliver Beatson is available in the public domain.*

Changes occurring in the sun itself can affect the intensity of the sunlight that reaches Earth's surface. The intensity of the sunlight can cause either warming (during periods of stronger solar intensity) or cooling (during periods of weaker solar intensity). The sun follows a natural 11-year cycle of small ups and downs in intensity, but the effect of these 11-year cycles on Earth's climate is small.

Milankovitch Cycles

Earth's orbit around the Sun is nearly circular, but like all physical systems, it has natural oscillations (Figure 2.7.2). The importance of changes in the **eccentricity** (shape) of the Earth's orbit, **tilt** of the Earth, and **precession** (where the Earth's axis points) to Earth's climate cycles (now known as **Milankovitch Cycles**) was first pointed out by Yugoslavian engineer and mathematician Milutin Milankovitch in the early 1900s. Milankovitch recognized that although the variations in the orbital cycles did not affect the total amount of **insolation** (light energy from the Sun) that Earth received, *it did affect where on Earth that* *energy was strongest*. Glaciations are most sensitive to the insolation received at latitudes of around 65°, and with the current configuration of continents, it would have to be 65° north (because there is almost no land at 65° south).

First, the shape of the orbit changes on a regular time scale — close to 100,000 years — from being close to circular to being very slightly elliptical. But the circularity of the orbit is not what matters; it is the fact that as the orbit becomes more elliptical, the position of the Sun within that ellipse becomes less central or more eccentric (Figure 2.7.2a). **Eccentricity** is important because when it is high, the Earth-Sun distance varies more from season to season than it does when eccentricity is low.



(a) The 100,000 year cycle of eccentricity of the Sun within the Earth's orbit. The blue orbit is more elliptical than the red one, and the Sun is offset from the centre of the ellipse

(b) The 41,000 year cycle of the angle of tilt (obliquity) of the Earth's axis (red lines) compared to a line perpendicular to the plane of the Earth's orbit (light blue line).

(c) the 20,000 year cycle of precession of the Earth's rotational axis

Figure 2.7.2: The cycles of Earth's orbit and rotation. These are also called the Milankovitch Cycles. *Source: Steven Earle, licensed under CC BY.*

Second, Earth rotates around an axis through the North and South Poles, and that axis is at an angle to the plane of Earth's orbit around the Sun (Figure 2.7.2b). The angle of tilt (also known as **obliquity**) varies on a time scale of 41,000 years. When the angle is at its maximum (24.5°), Earth's seasonal differences are accentuated. When the angle is at its minimum (22.1°), seasonal differences are minimized. The current hypothesis is that glaciation is favored at low seasonal differences as summers would be cooler and snow would be less likely to melt and more likely to accumulate from year to year.

Third, the direction in which Earth's rotational axis points also varies, on a time scale of about 20,000 years (Figure 2.7.2c). This variation, known as **precession**, means that although the North Pole is presently pointing to the star Polaris (the pole star), in 10,000 years it will point to the star Vega.

The most important aspects are whether the northern hemisphere is pointing toward the Sun at its closest or farthest approach, and how eccentric the Sun's position is in Earth's orbit. Two opposing situations are when the northern hemisphere is at its farthest distance from the Sun during summer, which means cooler summers, and when the northern hemisphere is at its closest distance to the Sun during summer, which means hotter summers. Cool summers—as opposed to cold winters—are the key factor in the accumulation of glacial ice, so the scenario where the northern hemisphere is at its farthest distance from the Sun during summer is the one that promotes glaciation. This factor is greatest when eccentricity is high (so the difference between the closest point to the Sun and furthest point from the Sun is larger). For a more detailed explanation on Mikankovich Cycles see Milankovitch.

As already stated, **climate feedbacks** are critically important in amplifying weak climate forcings into full-blown climate changes. When Milankovitch published his hypothesis in 1924, it was widely ignored, partly because it was evident to climate scientists that the forcing produced by the orbital variations was not strong enough to drive the significant climate changes of the glacial cycles. Those scientists did not recognize the power of positive feedbacks. It was not until 1973, 15 years after Milankovitch's death, that sufficiently high-resolution data were available to show that the Pleistocene glaciations were indeed driven by the orbital cycles, and it became evident that the orbital cycles were just the forcing that initiated a range of feedback mechanisms that made the climate change.

Data for tilt, eccentricity, and precession over the past 400,000 years have been used to determine the insolation levels at 65° north, as shown in Figure 2.7.4. Also shown in Figure 2.7.4 are Antarctic ice-core temperatures from the same time period. The correlation between the two is clear, and it shows up in the Antarctic record because when insolation changes lead to growth of glaciers in the northern hemisphere, southern-hemisphere temperatures are also affected.

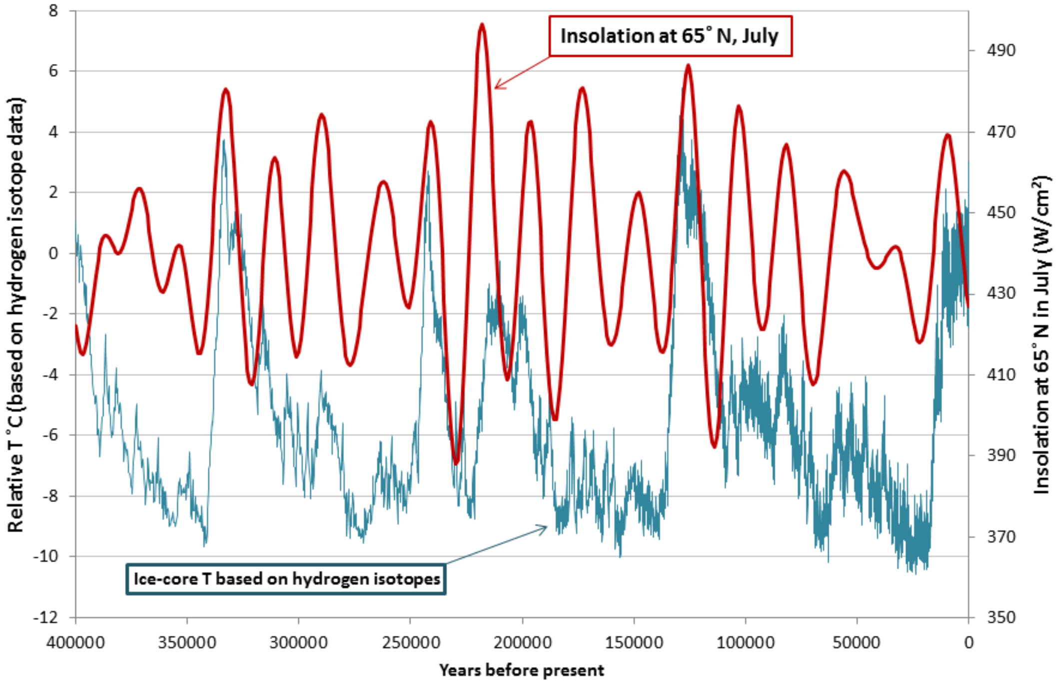


Figure 2.7.4: Insolation at 65° N in July compared with Antarctic ice-core temperatures.

Source: Steven Earle, licensed under CC BY. Based on data from Valerie Masson-Delmotte, "EPICA Dome C Ice Core 800KYr Deuterium Data and Temperature Estimates," WDCA Contribution Series Number : 2007 -091, NOAA/NCDC Paleoclimatology Program, Boulder CO, USA. Retrieved from: NOAA and from Berger, A. and Loutre, M.F. (1991). Insolation values for the climate of the last 10 million years. Quaternary Science Reviews, 10, 297-317.

Plate Tectonic Processes

Plate tectonic processes contribute to climate forcing in several different ways, and on time scales ranging from tens of millions to hundreds of millions of years. One mechanism is related to continental position. For example, we know that Gondwana (South America + Africa + Antarctica + Australia) was positioned over the South Pole between about 450 and 250 Ma, during which time there were two major glaciations (Andean-Saharan and Karoo) affecting the South polar regions and cooling the rest of the planet at the same time. Another mechanism is related to continental collisions. For example, the collision between India and Asia, which started at around 50 Ma, resulted in massive tectonic uplift. The consequent accelerated weathering of this rugged terrain consumed CO_2 from the atmosphere and contributed to gradual cooling over the remainder of the Cenozoic. Changes in continental position can also lead to changes in ocean circulation, and therefore the distribution of energy from equator to the poles. For example, the opening of the Drake Passage — due to plate-tectonic separation of South America from Antarctica — led to the development of the Antarctic Circumpolar Current, which isolated Antarctica from the warmer water in the rest of the ocean and thus contributed to Antarctic glaciation starting at around 35 Ma.

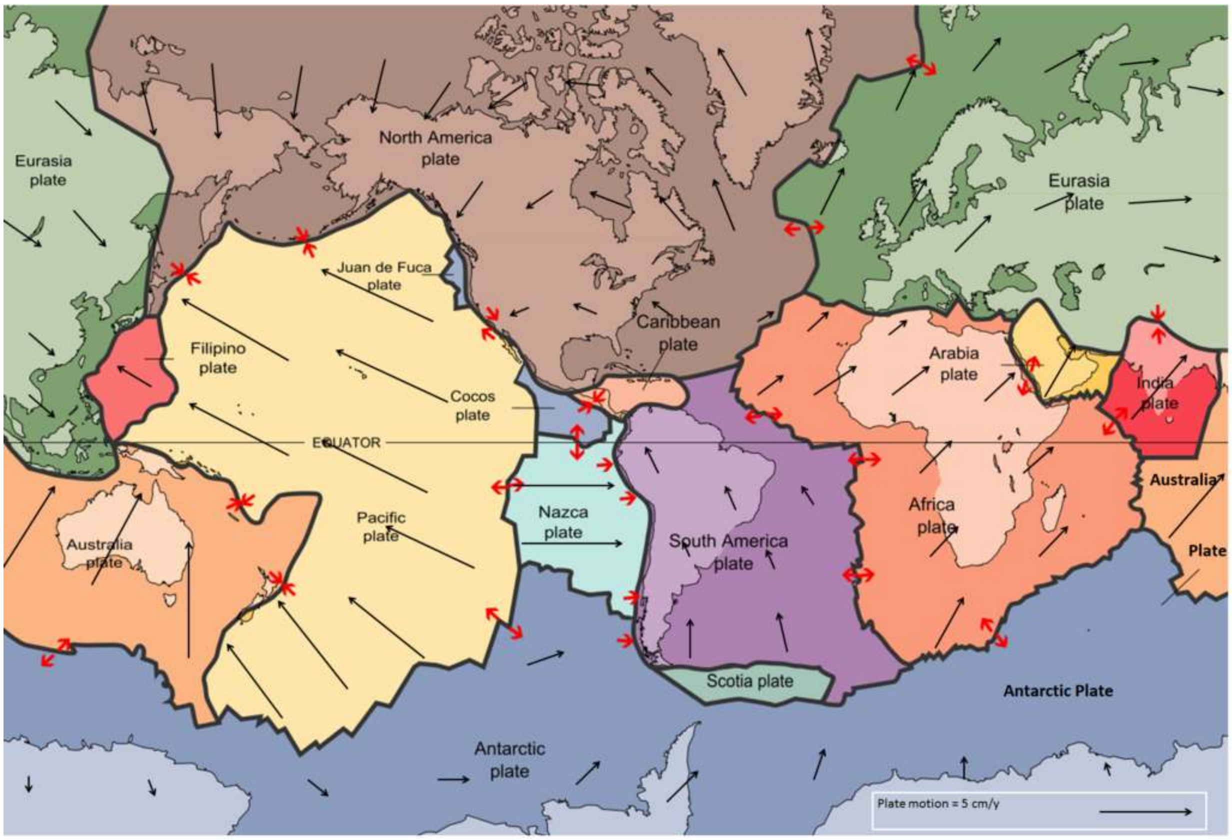


Figure 2.7.5: A map showing 15 of the Earth's tectonic plates and the approximate rates and directions of plate motions. *Source: image "Tectonic Plates" by USGS is available in the public domain and was adapted by Steven Earle.*

Volcanic eruptions don't just involve lava flows and exploding rock fragments; various particulates and gases are also released, including carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. Generally, volcanic eruptions cool the climate. Sulphur dioxide is an aerosol that reflects incoming solar radiation and has a net cooling effect that is short-lived (a few years in most cases, as the particulates settle out of the atmosphere within a couple of years), and doesn't typically contribute to longer-term climate change. This occurred in 1783 when volcanoes in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784. Volcanic CO_2 emissions can contribute to climate warming but only if a greater-than-average level of volcanism is sustained over a long time (at least tens of thousands of years). It is widely believed that the catastrophic end-Permian extinction (at 250 Ma) resulted from warming initiated by the eruption of the massive Siberian Traps over a period of at least a million years.

Greenhouse Gas Concentrations

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 2.7.6a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0 °C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure 2.7.6b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure 2.7.6b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

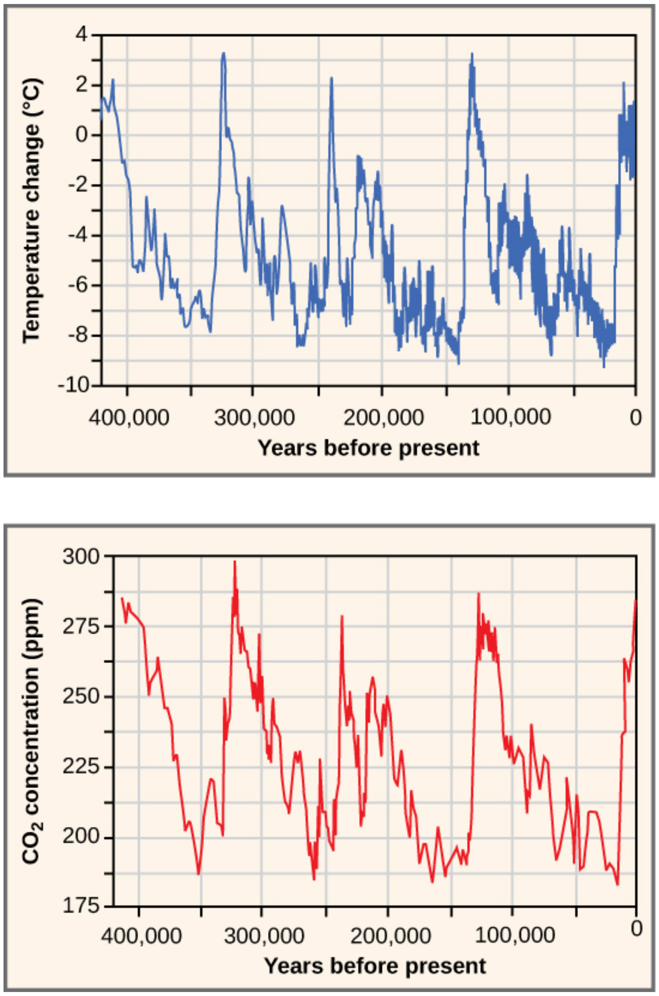


Figure 2.7.6: Ice at the Russian Vostok station in East Antarctica was laid down over the course 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Changes in Ocean Currents

Ocean currents are important to climate, and currents also have a tendency to oscillate. Glacial ice cores show clear evidence of changes in the Gulf Stream (and other parts of the thermohaline circulation system) that affected global climate on a time scale of about 1,500 years during the last glaciation.

The east-west changes in sea-surface temperature and surface pressure in the equatorial Pacific Ocean—known as the El Niño Southern Oscillation or ENSO—varies on a much shorter time scale of between two and seven years. These variations tend to garner the attention of the public because they have significant climate implications in many parts of the world. The past 65 years of ENSO index values are shown in Figure 2.7.7. The strongest **El Niños** in recent decades were in 1983 and 1998, and those were both very warm years from a global perspective. During a strong El Niño, the equatorial Pacific sea-surface temperatures are warmer than normal and heat the atmosphere above the ocean, which leads to warmer-than-average global temperatures.

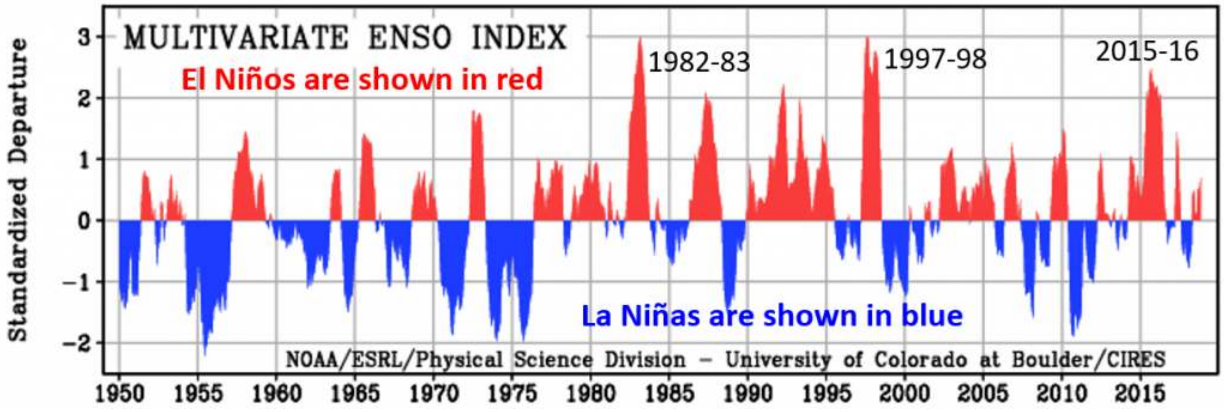


Figure 2.7.7: Variations in the ENSO index from 1950 to early-2019. *Source: Steven Earle with NOAA ("Multivariate ENSO Index (MEI)."*

For more information on El Niño and La Niña, see the section of Dr. Paul Webb's Oceanography book on El Niño and La Niña.

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Pittsburgh).

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- Contributed by Melissa Ha and Rachel Schleiger Faculty (Biological Sciences) at Yuba College & Butte College
- Contributed by Paul Webb Professor (Biology) at Rodger Williams University
- Contributed by Chris Johnson, Matthew D. Affolter, Paul Inkenbrandt, & Cam Mosher Faculty (Geology) at Salt Lake Community College
- Contributed by Steven Earle Faculty (Geology) at Vancover Island University
- 19.1 What Makes Climate Change from *Physical Geology* by Steven Earle (licensed under CC-BY)
- Sourced from OpenGeology from *An Introduction to Geology* Section 15.2 Earth's Temperature
- 8.1 Earth's Heat Budget from *Introduction to Oceanography* by Paul Webb (licensed under CC-BY)
- Climate and the Effects of Global Climate Change from *General Biology* by OpenStax (licensed under CC-BY)
- Climate Change from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Fundamentals of Plate Tectonics from *Physical Geology* by Steven Earle (licensed under a Creative Commons Attribution 4.0 International License)

2.8: Past Climate Change

Over Earth's history, the climate has changed a lot. For example, during the Mesozoic Era, the Age of Dinosaurs, the climate was much warmer and carbon dioxide was abundant in the atmosphere. However, throughout the Cenozoic Era (65 Million years ago to today), the climate has been gradually cooling. This section summarizes some of these major past climate changes.

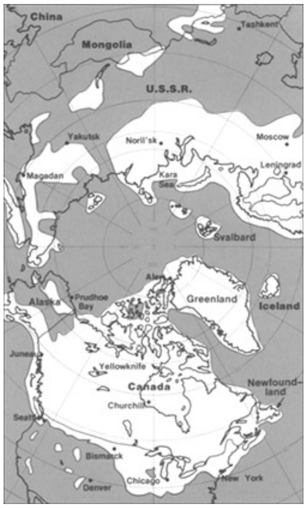


Figure 2.8.1: Maximum extent of Laurentide Ice Sheet.

Past Glaciations

Through geologic history, the climate has changed slowly over millions of years. Before the most recent Pliocene-Quaternary glaciation (Figure 2.8.1), there were three other major glaciations [20]. The oldest, known as the Huronian, occurred toward the end of the Archean-early Proterozoic (~2.5 billion years ago). The major event of that time, the great oxygenation event, is most commonly associated with the cause of that glaciation. The increased oxygen is thought to have reacted with the potent greenhouse gas methane, causing cooling [21].

The end of the Proterozoic (about 700 million years ago) had another glaciation, known as the **Snowball Earth hypothesis** [22]. Glacial evidence has been interpreted in widespread rock sequences globally and even has been linked to low-latitude glaciation [23]. Limestone rock (usually formed in tropical marine environments) and glacial deposits (usually formed in cold climates) are often found together from this time in regions all around the world. In Utah, Antelope Island in the Great Salt Lake has interbedded limestone and glacial deposits (diamictites) interpreted to be formed by continental glaciation [24]. The idea of the controversial Snowball Earth hypothesis is that a runaway albedo effect (ice and snow reflecting solar radiation) might cause the complete freezing of land and ocean surfaces and a collapse of biological activity. The ice-covered earth would only melt when carbon dioxide from volcanoes reached high concentrations, due to the inability for carbon dioxide to enter the then-frozen ocean. Some studies estimated carbon dioxide was 350 times higher than today's concentrations [22]. The complete freezing [25] and the extent of the freezing [26] has come into question.

Glaciation also occurred in the Paleozoic, most notably with the Karoo Glaciation of the Pennsylvanian (323 to 300 million years ago). This also was caused by an increase of oxygen and a subsequent drop in carbon dioxide, most likely produced by the evolution and rise of land plants [27].

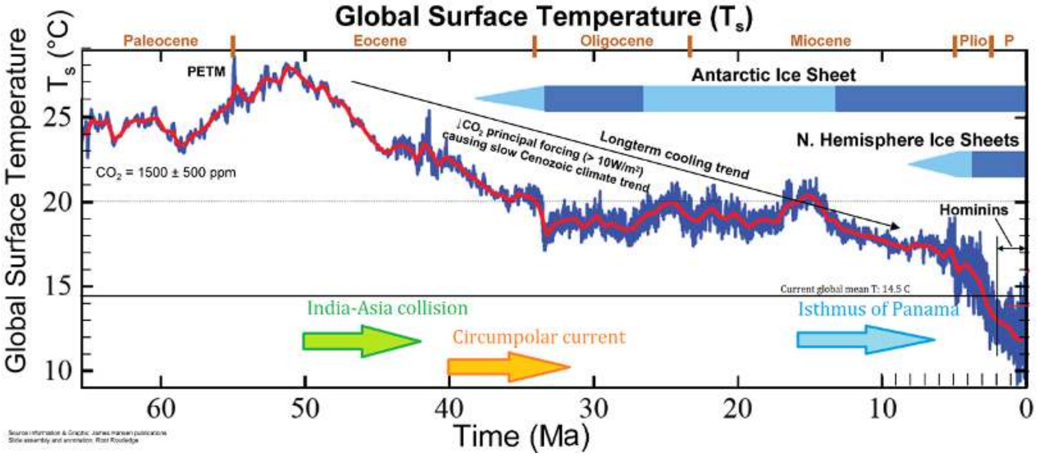


Figure 2.8.2: Global average surface temperature over the past 70 million years.

During the Cenozoic Era (the last 65 million years), the climate started out warm and gradually cooled to today. This warm time is called the **Paleocene-Eocene Thermal Maximum** and Antarctica and Greenland were ice-free during this time (Figure 2.8.2). Since the Eocene, tectonic events during the Cenozoic caused persistent and significant planetary cooling. For example, the collision of the Indian Plate with the Asian Plate created the Himalaya Mountains increasing weathering and erosion rates. An increased rate of weathering of silicate minerals, especially feldspar, consumes carbon dioxide from the atmosphere and therefore reduces the greenhouse effect, resulting in long-term cooling [28].

At about 40 Ma, the narrow gap between the South American Plate and the Antarctica Plate widened, resulting in the opening of the Drake Passage. This allowed for the unrestricted west-to-east flow of water around Antarctica, the Antarctic Circumpolar Current, which effectively isolated the southern ocean from the warmer waters of the Pacific, Atlantic, and Indian Oceans (Figure 2.8.3). The region cooled significantly, and by 35-million-year ago (Oligocene) glaciers had started to form on Antarctica [29].

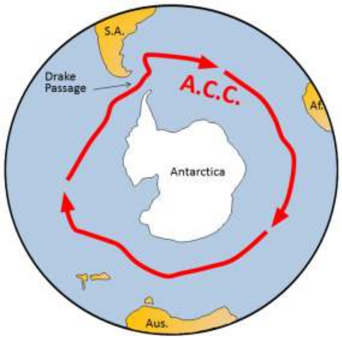
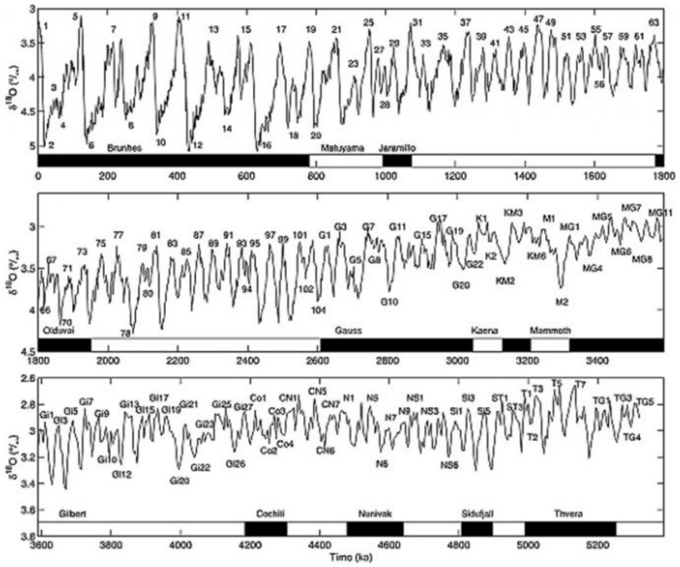


Figure 2.8.3: The Antarctic Circumpolar Current.

At around 15 Ma, subduction-related volcanism between Central and South America created the Isthmus of Panama that connected North and South America. This prevented water from flowing between the Pacific and Atlantic Oceans and reduced heat transfer from the tropics to the poles. This created a cooler Antarctica and larger Antarctic glaciers. The expansion of that ice sheet (on land and water) increased Earth's reflectivity (albedo), a positive feedback loop of further cooling: more reflective glacial ice, more cooling, more ice, and so on [30; 31].

By 5 million years ago (Pliocene Epoch), ice sheets had started to grow in North America and northern Europe. The most intense part of the current glaciation is the last 1 million years of the Pleistocene Epoch. The Pleistocene has significant temperature variations (through a range of almost 10°C) on time scales of 40,000 to 100,000 years, and corresponding expansion and contraction of ice sheets. These variations are attributed to subtle changes in Earth's orbital parameters called **Milankovitch cycles** [32; 33], which are explained in more detail in the section on natural climate forcings. Over the past million years, the glaciation cycles have been approximately every 100,000 years [34] with many glacial advances in the last 2 million years (Figure 2.8.4) (Lisiecki and Raymo, 2005) [35].

A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records



Source: Lisiecki, L. E., & Raymo, M. E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography*, *20*(1).

Figure 2.8.4: A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. X-axis is time in thousands of years (ka) so 200 is actually 200,000. *Source: Lisiecki and Raymo, 2005.*

Warmer portions of climate within an ice age are called **interglacials**, with brief versions called **interstadials**. These warming upticks are related to variations in Earth's climate like Milankovitch cycles. In the last 500,000 years, there have been 5 or 6 interglacials, with the most recent belonging to our current time, the Holocene (Figure 2.8.4).

Two of the more recent climate swings demonstrate the complexity of the changes: the Younger Dryas and the Holocene Climatic Optimum. These events are more recent and yet have conflicting information. The Younger Dryas cooling is widely recognized in the Northern Hemisphere [36], though the timing of the event (about 12,000 years ago) does not appear to be equal everywhere [37]. It also is difficult to find in the Southern Hemisphere [38]. The Holocene Climatic Optimum is the warming around 6,000 years ago [39], though it was not universally warmer, and probably not as warm as current warming [40], and not at the same time everywhere [41].

Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland. The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

Proxy Indicators of Past Climates

How do we know about past climates? Scientists use proxy indicators to understand past climate. A **proxy indicator** is a biological, chemical, or physical signature preserved in the rock, sediment, or ice record that acts like a "fingerprint" of something in the past [42]. Thus they are an indirect indicator of something like climate. For ancient glaciations from the Proterozoic and Paleozoic, there are rock formations of glacial sediments such as the diamictite (or tillite) of the Mineral Fork Formation in Utah. This dark rock has many fine-grained components plus some large out-sized clasts like a modern glacial till [43; 44].

For climate changes during the Cenozoic Era (the last 65 Ma), there is a detailed chemical record from the coring of deep-sea sediments as part of the Ocean Drilling Program (Figure 2.8.5). Studies of deep-sea sediment use stable carbon and oxygen isotopes obtained from the shells of deep-sea benthic foraminifera that have settled on the ocean floor over millions of years. Oxygen isotopes are a proxy indicator of deep-sea temperatures and continental ice volume [45].

Sediment Cores – Stable Oxygen Isotope

Figure 2.8.5: Sediment core from the Greenland continental slope. *Source: Hannes Grobe.*

Oxygen isotopes are an indicator of past climate. The two main stable oxygen isotopes are ^{16}O and ^{18}O. They both occur in water (H_2O) and in the calcium carbonate ($CaCO_3$) shells of foraminifera as the oxygen component of both of those molecules. The most abundant and lighter isotope is ^{16}O. Since it is lighter, it evaporates more easily from the ocean's surface as water vapor, which later turns to clouds and precipitation on the ocean and land.

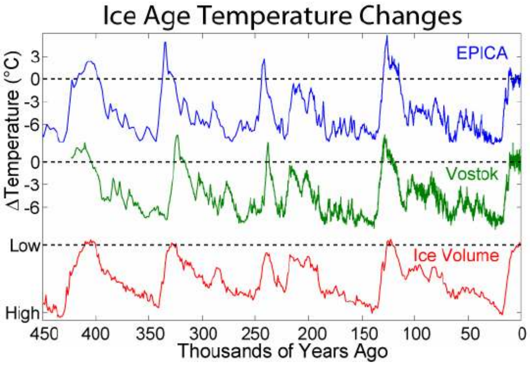


Figure 2.8.6: Antarctic temperature changes during the last few glaciations compared to global ice volume. The first two curves are based on the deuterium (heavy hydrogen) record from ice cores (EPICA Community Members 2004, Petit et al. 1999). The bottom line is ice volume based on oxygen isotopes from a composite of deep-sea sediment cores (Lisiecki and Raymo 2005).

During geologic times when the climate is cooler, more of this precipitation is locked onto land in the form of glacial ice. Consider the giant ice sheets, more than a mile thick, that covered a large part of North America during the last ice age only 14,000 years ago. During glaciation, the glaciers effectively lock away more ^{16}O, thus the ocean water and foraminifera shells become enriched in ^{18}O. Therefore, a ratio of ^{18}O to ^{16}O in calcium carbonate shells of foraminifera is an indicator of past climate. The sediment cores from the Ocean Drilling Program record a continuous accumulation of sediment (Figure 2.8.6).

Sediment Cores – Boron Isotopes and Acidity

Boron-isotope ratios in ancient planktonic foraminifera shells in deep-sea sediment cores have been used to estimate the pH (acidity) of the ocean over the past 60 million years. Ocean acidity is a proxy for past atmospheric CO^2 concentrations. In the early Cenozoic, around 60 million years ago, CO^2 concentrations were over 2,000 ppm and started falling around 55 to 40 million years ago possibly due to reduced CO^2 outgassing from ocean ridges, volcanoes, and metamorphic belts and increased carbon burial due to uplift of the Himalaya Mountains. By the Miocene (about 24 million years ago), CO^2 levels were below 500 ppm [46] and by 800,000 years ago CO^2 levels didn't exceed 300 ppm [47].

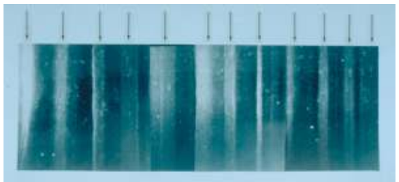


Figure 2.8.7: 19 cm long section of ice core showing 11 annual layers with summer layers (arrowed) sandwiched between darker winter layers. *Source: US Army Corps of Engineers.*

For the more recent Pleistocene climate, there is a more detailed and direct chemical record from coring into the Antarctic and Greenland ice sheets (Figure 2.8.7). Snow accumulates on these ice sheets and creates yearly layers. Ice cores have been extracted from ice sheets covering the last 800,000 years. Oxygen isotopes are collected from these annual layers and the ratio of ^{18}O to ^{16}O is used to determine temperature as discussed above. In addition, the ice traps small atmospheric gas bubbles as the snow turns to ice.

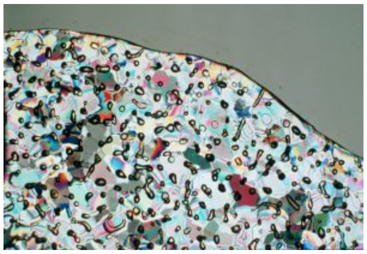


Figure 2.8.8: Antarctic ice showing hundreds of tiny trapped air bubbles from the atmosphere thousands of years ago. *Source: CSIRO.*

Small pieces of this ice are crushed and the ancient air extracted into a mass spectrometer that can detect the chemistry of the ancient atmosphere. Carbon dioxide levels are recreated from these measurements. Over the last 800,000 years, the maximum carbon dioxide concentration during warm times was about 300 ppm and the minimum during cold stretches was about 170 ppm [46; 47; 48] (Figure 2.8.9). The carbon dioxide content of earth's atmosphere is currently over 400 ppm.

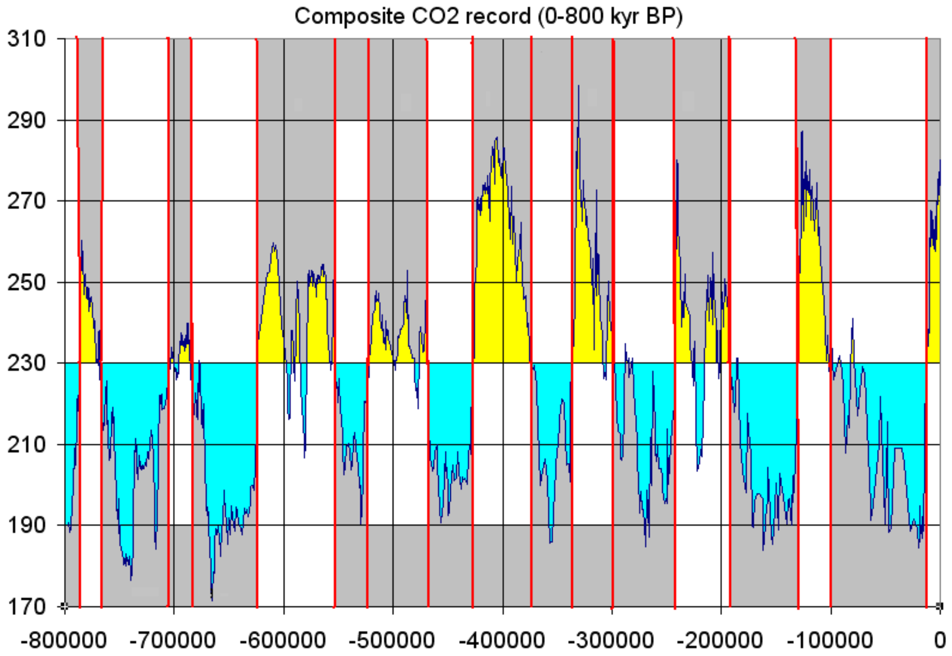


Figure 2.8.9: Composite carbon dioxide record from the last 800,000 years based on ice core data from EPICA Dome C Ice Core.

Oceanic Microfossils

Microfossils, like foraminifera, diatoms, and radiolarians, can be used to interpret past climate records. In sediment cores, different species of microfossils are found in different layers. Groups of these microfossils are called assemblages. One assemblage consists of species that lived in cooler ocean water (in glacial times) and another assemblage found at a different level in the same sediment core is made of warmer water species [49].

Tree Rings

Every year a tree will grow one ring with a light section and dark section (Figure 2.8.10). The rings vary in width. Since trees need a lot of water to survive, narrower rings indicate colder and drier climates. Since some trees can be several thousands years old, we can use their rings for regional paleoclimatic reconstructions. Further, dead trees such as those used in Puebloan ruins can be used to extend this proxy indicator, which showed long term droughts in the region and why their villages were abandoned (Figure 2.8.11).

Figure 2.8.10: Tree rings form every year. Rings that are farther apart are from wetter years and rings that are closer together are from dryer years.

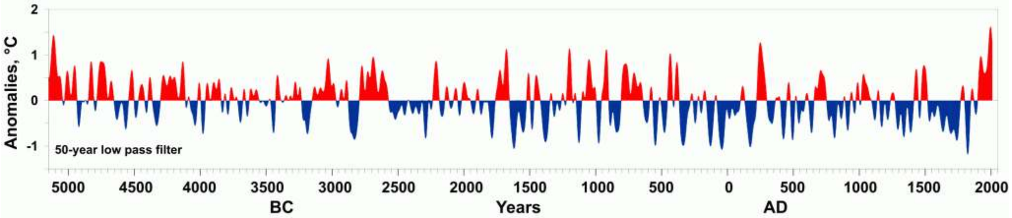


Figure 2.8.11: Summer temperature anomalies for the past 7000 years. *Source: R.M.Hantemirov.*

Pollen

Flowering plants produce pollen grains. Pollen is distinctive when viewed under a microscope (Figure 2.8.12). Sometimes pollen can be preserved in lake sediments that accumulate every year. Coring of lake sediments can reveal ancient pollen. Fossil pollen assemblages are groups of pollen from multiple species such as spruce, pine, and oak. Through time (via the sediment cores and radiometric age-dating techniques), the pollen assemblage will change revealing the plants that lived in the area at the time. Thus the pollen assemblages are an indicator of past climate since different plants will prefer different climates [50]. For example, in the Pacific Northwest east of the Cascades, a region close to the border of grasslands and forest, a study tracked pollen over the last 125,000 years covering the last two glaciations. As shown in the figure (Fig. 2 from reference Whitlock and Bartlein 1997 [51]), pollen assemblages with more pine tree pollen are found during glaciations and pollen assemblages with less pine tree pollen are found during interglacial times [51].

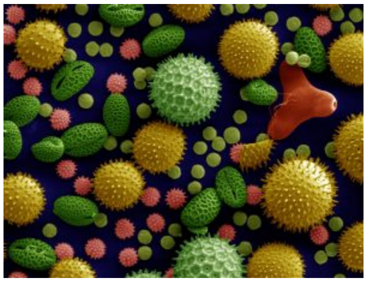


Figure 2.8.12: Scanning electron microscope image of modern pollen with false color added to distinguish plant species. *Source: Dartmouth Electron Microscope Facility, Dartmouth College.*

Other Proxy Indicators

Paleoclimatologists study many other phenomena to understand past climates such as human historical accounts, human instrument record from the recent past, lake sediments, cave deposits of calcium carbonates, and corals (both oxygen isotopes and growth rings).

Sources

20. Deynoux, M., Miller, J. M. G. & Domack, E. W. *Earth's Glacial Record*. (Cambridge University Press, 2004).

21. Kopp, R. E., Kirschvink, J. L., Hilburn, I. A. & Nash, C. Z. The Paleoproterozoic snowball Earth: a climate disaster triggered by the evolution of oxygenic photosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 11131–11136 (2005).

22. Hoffman, P. F., Kaufman, A. J., Halverson, G. P. & Schrag, D. P. A neoproterozoic snowball earth. *Science* **281**, 1342–1346 (1998).

23. Schopf, J. W. & Klein, C. Late Proterozoic Low-Latitude Global Glaciation: the Snowball Earth. in *The Proterozoic biosphere : a multidisciplinary study* (eds. Schopf, J. W. & Klein, C.) 51–52 (Cambridge University Press, 1992).

24. Doelling, H. H. *et al.* Geology of Antelope Island. *Davis County, Utah: Utah Geological and Mineral Survey Open-File Release* **144**, 82 (1988).

25. Allen, P. A. & Etienne, J. L. Sedimentary challenge to Snowball Earth. *Nat. Geosci.* **1**, 817–825 (2008).

26. Eyles, N. & Januszczak, N. 'Zipper-rift': a tectonic model for Neoproterozoic glaciations during the breakup of Rodinia after 750 Ma. *Earth-Sci. Rev.* (2004).

27. Berner, R. A. The carbon cycle and carbon dioxide over Phanerozoic time: the role of land plants. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **353**, 75–82 (1998).

28. Kump, L. R., Brantley, S. L. & Arthur, M. A. Chemical Weathering, Atmospheric CO2, and Climate. *Annu. Rev. Earth Planet. Sci.* **28**, 611–667 (2000).

29. Lagabrielle, Y., Goddéris, Y., Donnadieu, Y., Malavieille, J. & Suarez, M. The tectonic history of Drake Passage and its possible impacts on global climate. *Earth Planet. Sci. Lett.* **279**, 197–211 (2009).

30. Kuipers Munneke, P. *et al.* A new albedo parameterization for use in climate models over the Antarctic ice sheet. *J. Geophys. Res.* **116**, D05114 (2011).

31. Curry, J. A., Schramm, J. L. & Ebert, E. E. Sea Ice-Albedo Climate Feedback Mechanism. *J. Clim.* **8**, 240–247 (1995).

32. Milankovitch, M. Mathematische klimalehre und astronomische theorie der klimaschwankungen. (1930).

33. Roe, G. In defense of Milankovitch. *Geophys. Res. Lett.* **33**, L24703 (2006).

34. Abe-Ouchi, A. *et al.* Insolation-driven 100,000-year glacial cycles and hysteresis of ice-sheet volume. *Nature* **500**, 190–193 (2013).

35. Lisiecki, L. E. & Raymo, M. E. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography* **20**, (2005).

36. Carlson, A. E. The younger Dryas climate event. (2013).

37. Fairbanks, R. G. The age and origin of the "Younger Dryas climate event" in Greenland ice cores. *Paleoceanography* **5**, 937–948 (1990).

38. Kaplan, M. R. *et al.* Glacier retreat in New Zealand during the Younger Dryas stadial. *Nature* **467**, 194–197 (2010).

39. Ganopolski, A., Kubatzki, C., Claussen, M., Brovkin, V., V. & Petoukhov, V., V. The influence of vegetation-atmosphere-ocean interaction on climate during the mid-holocene. *Science* **280**, 1916–1919 (1998).

40. Hewitt, C. D. & Mitchell, J. F. B. A fully coupled GCM simulation of the climate of the mid-Holocene. *Geophys. Res. Lett.* **25**, 361–364 (1998).

41. He, Y. *et al.* Asynchronous Holocene climatic change across China. *Quat. Res.* **61**, 52–63 (2004).

42. Weissert, H. Deciphering methane's fingerprint. *Nature* **406**, 356–357 (2000).

43. Ojakangas, R. W. & Matsch, C. L. Upper Precambrian (Eocambrian) Mineral Fork Tillite of Utah: A continental glacial and glaciomarine sequence. *GSA Bulletin* **91**, 495–501 (1980).

44. Christie-Blick, N., Ojakangas, R. W. & Matsch, C. L. Upper Precambrian (Eocambrian) Mineral Fork Tillite of Utah: A Continental Glacial and Glaciomarine Sequence: Discussion and Reply. *The Geological Society of America Bulletin* **93**, 184–187 (1982).

45. Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693 (2001).

46. Pearson, P. N. & Palmer, M. R. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* **406**, 695–699 (2000).

47. Lüthi, D. *et al.* High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* **453**, 379–382 (2008).

48. Oak Ridge National Laboratory. 800,000-year Ice-Core Records of Atmospheric Carbon Dioxide (CO2). (2008). Available at: http://cdiac.ornl.gov/trends/co2/ice_core_co2.html. (Accessed: 14th September 2016)

49. Cunningham, W. L., Leventer, A., Andrews, J. T., Jennings, A. E. & Licht, K. J. Late Pleistocene–Holocene marine conditions in the Ross Sea, Antarctica: evidence from the diatom record. *The Holocene* **9**, 129–139 (1999).

50. Webb, T. & Thompson, W. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* **67**, 75–91 (1986).

51. Whitlock, C. & Bartlein, P. J. Vegetation and climate change in northwest America during the past 125 kyr. *Nature* **388**, 57–61 (1997).

Contributors and Attributions

Modified by Kyle Whittinghill (University of Vermont) from the following sources:

- Contributed by Chris Johnson, Matthew D. Affolter, Paul Inkenbrandt, & Cam Mosher Faculty (Geology) at Salt Lake Community College
- Sourced from OpenGeology from *An Introduction to Geology* Section 15.2 Prehistoric Climate Change

CHAPTER OVERVIEW

3: Introduction to Evolution

Learning Objectives

- Define evolution and explain its central role in biology.
- Introduce the different mechanisms of evolution, including natural selection, population bottlenecks, and genetic drift.
- Outline key patterns and processes of adaptive evolution.
- Explain the issues with common misconceptions about evolution, particularly natural selection.

Summary

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. Its power is that it provides direction for predictions about living things that are borne out in experiment after experiment. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that “nothing makes sense in biology except in the light of evolution". He meant that the tenet that all life has evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology.

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

3.1: Evolution

All species of living organisms, from bacteria to baboons to blueberries, evolved at some point from a different species. Although it may seem that living things today stay much the same, that is not the case—evolution is an ongoing process.

Figure 3.1.1: All organisms are products of evolution adapted to their environment. (a) Saguaro (*Carnegiea gigantea*) can soak up 750 liters of water in a single rain storm, enabling these cacti to survive the dry conditions of the Sonora desert in Mexico and the Southwestern United States. (b) The Andean semiaquatic lizard (*Potamites montanicola*) discovered in Peru in 2010 lives between 1,570 to 2,100 meters in elevation, and, unlike most lizards, is nocturnal and swims. Scientists still do no know how these ectotherms (cold-blooded animals) are able to move in the cold (10 to 15°C) temperatures of the Andean night (credit a: modification of work by Gentry George, U.S. Fish and Wildlife Service; credit b: modification of work by Germán Chávez and Diego Vásquez, ZooKeys).

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. Its power is that it provides direction for predictions about living things that are borne out in experiment after experiment. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that “nothing makes sense in biology except in the light of evolution.”[1] He meant that the tenet that all life has evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology.

Sources

1. 1 Dobzhansky, T. (1964). Biology, molecular and organismic. *American Zoologist, 4*(4), pp. 449. https://www.jstor.org/stable/3881145?origin=JSTOR-pdf.

Contributors and Attributions

Modified from the following sources:

- **18.0: Evolution** by OpenStax is licensed CC BY 4.0.
- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

3.2: Understanding Evolution

Skills to Develop

- Describe how the present-day theory of evolution was developed
- Define adaptation
- Explain convergent and divergent evolution
- Describe homologous and vestigial structures
- Discuss misconceptions about the theory of evolution

Evolution by natural selection describes a mechanism for how species change over time. That species change had been suggested and debated well before Darwin began to explore this idea. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed evolutionary ideas. In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there were extinct species.

During this time, James Hutton, a Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes operating like they are today over long periods of time. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was popularized in the nineteenth century by the geologist Charles Lyell who became a friend to Darwin. Lyell's ideas were influential on Darwin's thinking: Lyell's notion of the greater age of Earth gave more time for gradual change in species, and the process of change provided an analogy for gradual change in species. In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics by which modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and thus bring about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on evolutionary thought.

Charles Darwin and Natural Selection

In the mid-nineteenth century, the actual mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, including stops in South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape (Figure $3.2.1$). The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be species modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, and insect-eating finches had spear-like beaks for stabbing their prey.

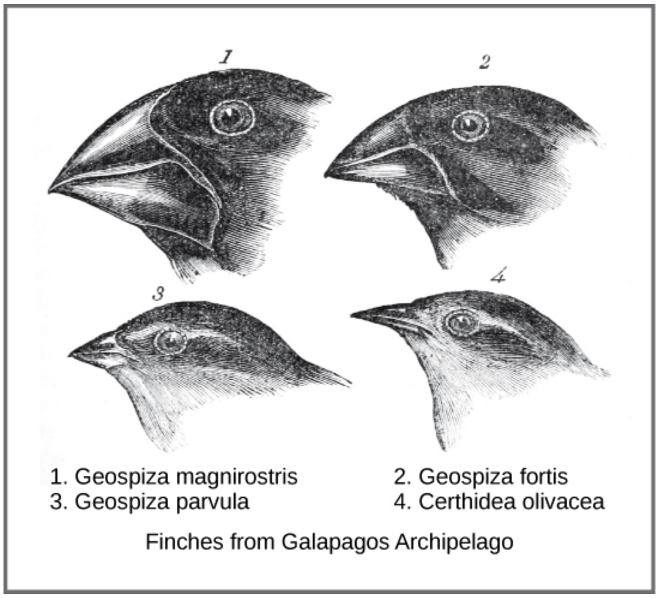


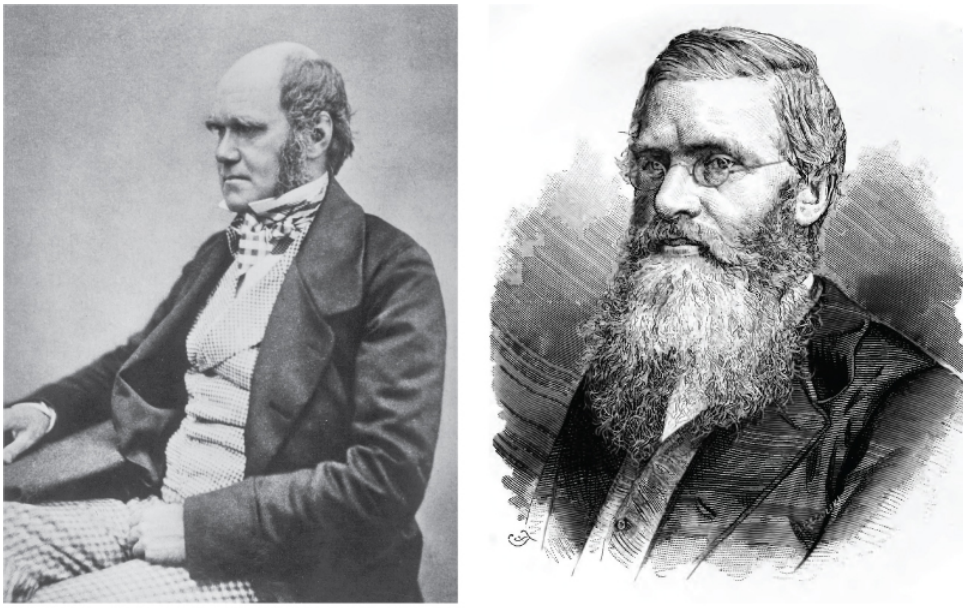
Figure $3.2.1$: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. Image is available on the public domain.

Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, also known as “survival of the fittest,” is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits; this leads to evolutionary change.

For example, a population of giant tortoises found in the Galapagos Archipelago was observed by Darwin to have longer necks than those that lived on other islands with dry lowlands. These tortoises were “selected” because they could reach more leaves and access more food than those with short necks. In times of drought when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that couldn’t reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring. Although no one, including Darwin and Wallace, knew how this happened at the time, it was a common understanding. Second, more offspring are produced than are able to survive, so resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace’s understanding of this principle came from reading an essay by the economist Thomas Malthus who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and Wallace reasoned that offspring with inherited characteristics which allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace (Figure $3.2.2$) presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year Darwin’s book, *On the Origin of Species,* was published. His book outlined in considerable detail his arguments for evolution by natural selection.



(a)

(b)

Figure 3.2.2: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection are time consuming and difficult to obtain. One of the best examples has been demonstrated in the very birds that helped to inspire Darwin’s theory: the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of natural selection. The Grants found changes from one generation to the next in the distribution of beak shapes with the medium ground finch on the Galápagos island of Daphne Major. The birds have inherited variation in the bill shape with some birds having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, the large hard seeds that large-billed birds ate were reduced in number; however, there was an abundance of the small soft seeds which the small-billed birds ate. Therefore, survival and reproduction were much better in the following years for the small-billed birds. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the size of bills had evolved to be smaller. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

Career Connection: Field Biologist

Many people hike, explore caves, scuba dive, or climb mountains for recreation. People often participate in these activities hoping to see wildlife. Experiencing the outdoors can be incredibly enjoyable and invigorating. What if your job was to be outside in the wilderness? Field biologists by definition work outdoors in the “field.” The term field in this case refers to any location outdoors, even under water. A field biologist typically focuses research on a certain species, group of organisms, or a single habitat (Figure 3.2.3).

Figure 3.2.3:
A field biologist tranquilizes a polar bear for study. *Source: Karen Rhode.*

One objective of many field biologists includes discovering new species that have never been recorded. Not only do such findings expand our understanding of the natural world, but they also lead to important innovations in fields such as medicine and agriculture. Plant and microbial species, in particular, can reveal new medicinal and nutritive knowledge. Other organisms can play key roles in ecosystems or be considered rare and in need of protection. When discovered, these important species can be used as evidence for environmental regulations and laws.

Processes and Patterns of Evolution

Natural selection can only take place if there is variation, or differences, among individuals **in a population**. Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity **in a population** comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes on the phenotype. A mutation affects the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival or fewer offspring. A mutation may produce a phenotype with a beneficial effect on fitness. And, many mutations will also have no effect on the fitness of the phenotype; these are called neutral mutations. Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Mutations can occur during both asexual and sexual reproduction.

Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring. Sexual reproduction does not create new alleles, but new combinations of alleles which means more genetic diversity in the population.

A heritable trait that helps the survival and reproduction of an organism in its present environment is called an adaptation. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the "fit" of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards' thick fur is an adaptation for living in the cold. The cheetahs' fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed, and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators (Figure $3.2.4$).

Figure $3.2.4$: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (*Liatrus spicata*) and the (b) purple coneflower (*Echinacea purpurea*) vary in appearance, yet both share a similar basic morphology (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker).

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years. For example, scientists have recovered highly detailed records showing the evolution of humans and horses (Figure $3.2.5$). The whale flipper shares a similar morphology to appendages of birds and mammals (Figure $3.2.6$) indicating that these species share a common ancestor.

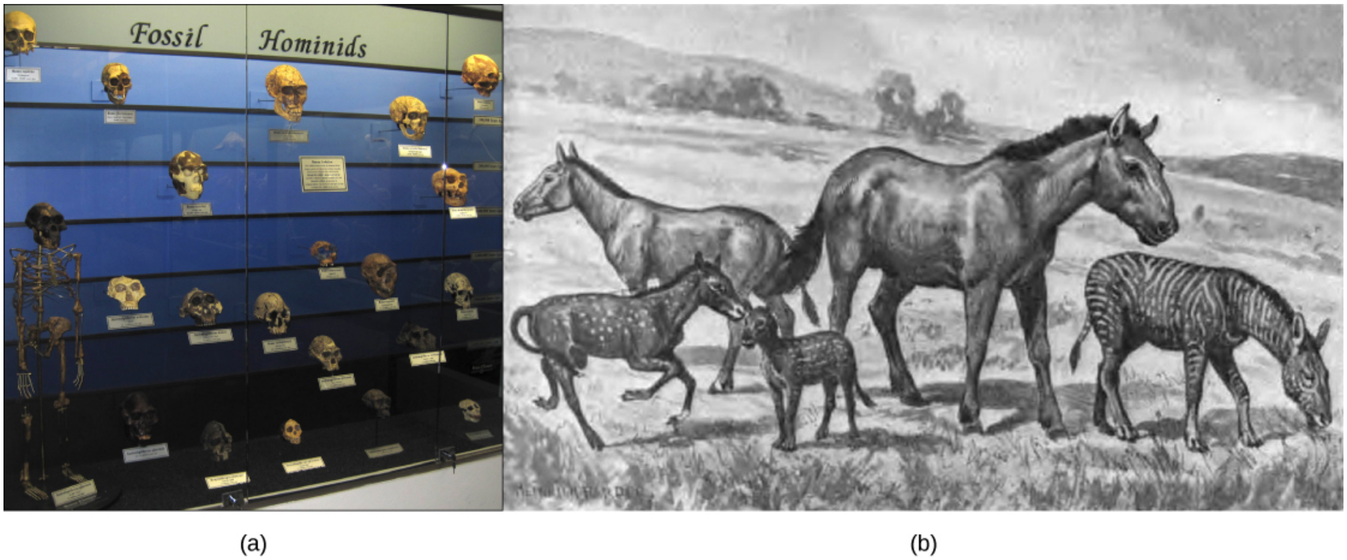


Figure 3.2.5: In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus *Equus* reveals that these ancient species resembled the modern horse (*Equus ferus*) but varied in size.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure 3.2.6) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

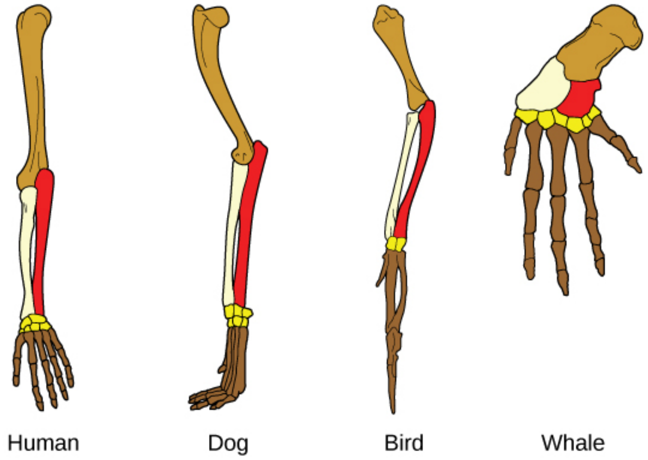


Figure 3.2.6: The similar construction of these appendages indicates that these organisms share a common ancestor.

Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called vestigial structures. Some examples of vestigial structures are wings on flightless birds, leaves on some cacti, and hind leg bones in whales.

Link to Learning

Visit this interactive site to guess which bones structures are homologous and which are analogous, and see examples of evolutionary adaptations to illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes during winter to blend with the snow and ice (Figure $3.2.7$). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.

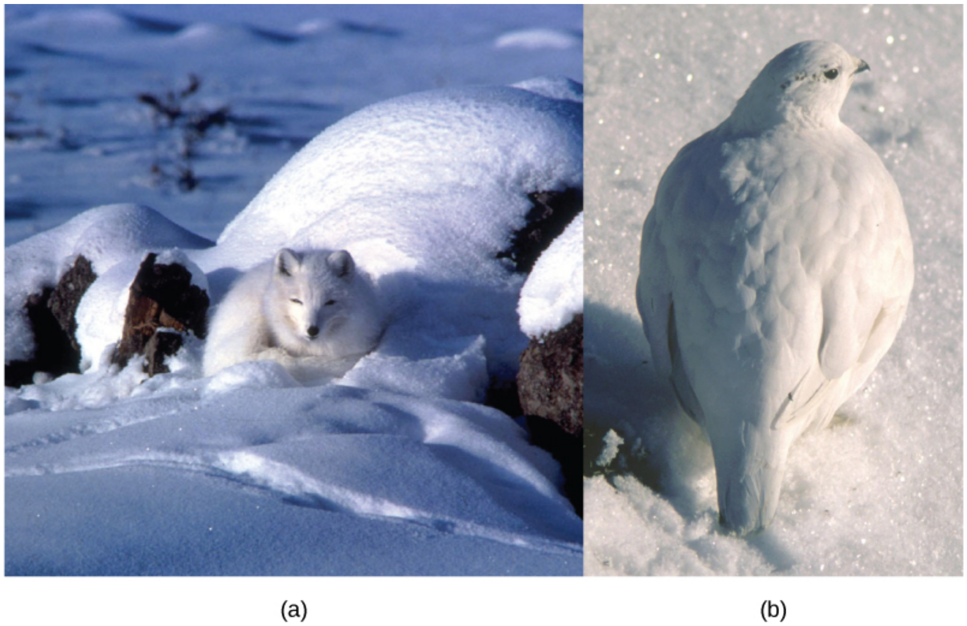


Figure $3.2.7$: The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments (credit a: modification of work by Keith Morehouse).

Embryology, the study of the development of the anatomy of an organism to its adult form, also provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best by their presence prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species to migrate. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and in the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the second copy continues to produce a functional protein.

Summary

Evolution is the process of adaptation through mutation which allows more desirable characteristics to be passed to the next generation. Over time, organisms evolve more characteristics that are beneficial to their survival. For living organisms to adapt and change to environmental pressures, genetic variation must be present. With genetic variation, individuals have differences in form and function that allow some to survive certain conditions better than others. These organisms pass their favorable traits to their offspring. Eventually, environments change, and what was once a desirable, advantageous trait may become an undesirable trait and organisms may further evolve. Evolution may be convergent with similar traits evolving in multiple species or divergent with diverse traits evolving in multiple species that came from a common ancestor. Evidence of evolution can be observed by means of DNA code and the fossil record, and also by the existence of homologous and vestigial structures.

Contributors and Attributions

Modified from the following sources:

- **18.1: Understanding Evolution** by OpenStax is licensed CC BY 4.0.
- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

3.3: Scientist Spotlight - Ynes Enriquetta Julietta Mexia

✓ Ynes Enriquetta Julietta Mexia 3.3.1

When retracing the history of ecology, it is easy to come to a full-stop at Charles Darwin's *On the Origin of Species*. His theory of evolution by natural selection shook the scientific community to its core, and observations used to synthesize this theory were collected on a five-year voyage around the world. However, Darwin was not the only one to achieve an expedition of such grandiose scale.

Motivated by a newfound interest in science, Ynes Enriquetta Mexia enrolled in classes at UC Berkeley in 1921. She was 51 years old at the time. By the age of 55, she was engaged in a series of botanical expeditions in remote Alaska and in South/Central America. Alongside a Stanford University botanist, Mexia collected 500 plant specimens on her first trip to Mexico. She went on to collect about 145,000 specimens over the next 13 years, 500 of which were new species. Charles Darwin collected a mere 500 specimens on his famed five-year voyage. In addition to the sheer number of Mexia's samples, she was a natural scientist whose research contributed immensely to the modern classification of plants in North America. Her "discoveries helped to clarify and complete botanical records."

Figure 3.3.1: Ynes Mexia. Source: https://en.wikipedia.org/wiki/Ynes_M...Ynes_Mexia.jpg

Despite her impressive fieldwork, Mexia never received recognition comparable to that of her male counterparts. However, of the 500 plant species she discovered, 50 were named after her, as well as the entire genus *Mexianthus*.

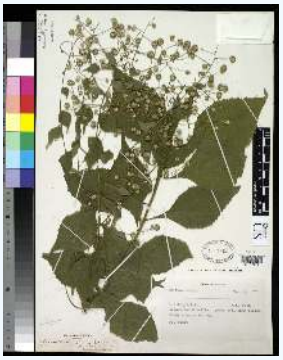


Figure 3.3.2: A *Mexianthus mexicanus* specimen collected by Ynes E.J. Mexia. *Source: Smithsonian Institution, available in the public domain.*

Sources

Spotlight inspiration from the Scientist Spotlights Initiative

Elias, Sarah. Ynes Enriquetta Julietta Mexia. <scientistspotlights.org/scientist/ynes-enriquetta-julietta-mexia/>. Accessed September 21, 2021.

> Smithsonian Institution. Mexianthus mexicanus B.L. Rob. <https://www.si.edu/object/mexianthus-mexicanus-bl-rob%3Anmnhbotany_2150513>. Accessed September 21, 2021.

3.4: Mechanisms of Evolution

Populations will not evolve unless factors such as natural selection, mutation, genetic drift, and migration (gene flow) change them. In fact, we know these factors are probably always affecting populations.

Natural Selection

Natural selection was discussed earlier in this chapter. Alleles are expressed in a phenotype. Depending on the environmental conditions, the phenotype confers an advantage or disadvantage to the individual with the phenotype relative to the other phenotypes in the population. If it is an advantage, then that individual will likely have more offspring than individuals with the other phenotypes, and this will mean that the allele behind the phenotype will have greater representation in the next generation. If conditions remain the same, those offspring, which are carrying the same allele, will also benefit. Over time, the allele will increase in frequency in the population.

Mutation

Mutation is a source of new alleles in a population. Mutation is a change in the DNA sequence of the gene. A mutation can change one allele into another, but the net effect is a change in frequency. The change in frequency resulting from mutation is small, so its effect on evolution is small unless it interacts with one of the other factors, such as selection. A mutation may produce an allele that is selected against, selected for, or selectively neutral. Harmful mutations are removed from the population by selection and will generally only be found in very low frequencies equal to the mutation rate. Beneficial mutations will spread through the population through selection, although that initial spread is slow. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. It should be noted that **mutation is the ultimate source of genetic variation in all populations**—new alleles, and, therefore, new genetic variations arise through mutation.

Genetic Drift

Another way a population's allele frequencies can change is genetic drift (Figure 3.4.1), which is simply the effect of chance. Genetic drift occurs because the alleles in an offspring generation are a random sample of the alleles in the parent generation. Alleles may or may not make it into the next generation due to chance events including mortality of an individual, events affecting finding a mate, and even the events affecting which gametes end up in fertilizations. Genetic drift is most important in small populations. If one individual in a population of ten individuals happens to die before it leaves any offspring to the next generation, all of its genes—a tenth of the population's gene pool—will be suddenly lost. In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much less impact on the population's genetic structure and is unlikely to remove all copies of even a relatively rare allele.

Imagine a population of ten individuals, half with allele *A* and half with allele *a* (the individuals are haploid). In a stable population, the next generation will also have ten individuals. Choose that generation randomly by flipping a coin ten times and let heads be *A* and tails be *a*. It is unlikely that the next generation will have exactly half of each allele. There might be six of one and four of the other, or some different set of frequencies. Thus, the allele frequencies have changed and evolution has occurred. A coin will no longer work to choose the next generation (because the odds are no longer one half for each allele). The frequency in each generation will drift up and down on what is known as a random walk until at one point either all *A* or all *a* are chosen and that allele is fixed from that point on. This could take a very long time for a large population. This simplification is not very biological, but it can be shown that real populations behave this way. The effect of drift on frequencies is greater the smaller a population is. Its effect is also greater on an allele with a frequency far from one half. Drift will influence every allele, even those that are being naturally selected.

ART CONNECTION

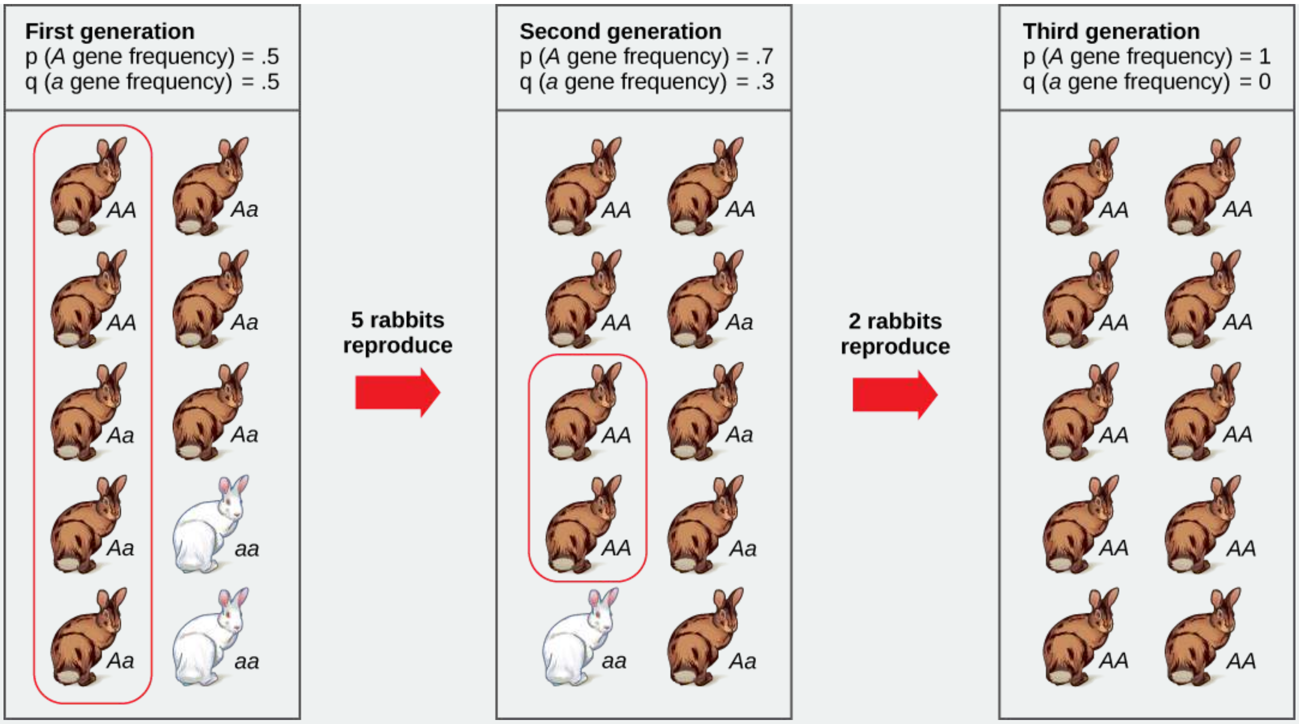


Figure 3.4.1: Genetic drift in a population can lead to the elimination of an allele from a population by chance. In each generation, a random set of individuals reproduces to produce the next generation. The frequency of alleles in the next generation is equal to the frequency of alleles among the individuals reproducing.

Exercise 3.4.1

Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island, where smaller populations are expected to occur.

Genetic drift can also be magnified by natural or human-caused events, such as a disaster that randomly kills a large portion of the population, which is known as the **bottleneck effect** that results in a large portion of the genome suddenly being wiped out (Figure 3.4.2). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population. The disaster must be one that kills for reasons unrelated to the organism’s traits, such as a hurricane or lava flow. A mass killing caused by unusually cold temperatures at night, is likely to affect individuals differently depending on the alleles they possess that confer cold hardiness.

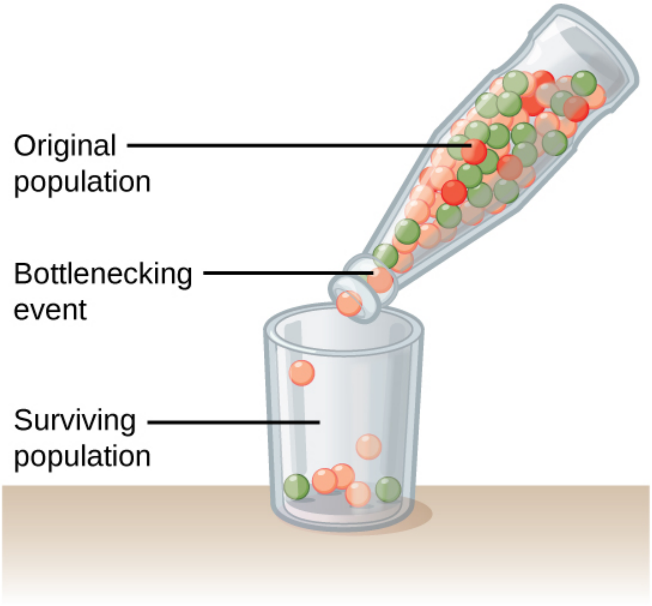


Figure 3.4.2:
A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location, or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population which results in the founder effect. The **founder effect** occurs when the genetic structure matches that of the new population's founding fathers and mothers.[1]

CONCEPT IN ACTION

Visit this site to learn more about genetic drift and to run simulations of allele changes caused by drift.

Gene Flow

Another important evolutionary force is gene flow, or the flow of alleles in and out of a population resulting from the migration of individuals or gametes (Figure 3.4.3). While some populations are fairly stable, others experience more flux. Many plants, for example, send their seeds far and wide, by wind or in the guts of animals; these seeds may introduce alleles common in the source population to a new population in which they are rare.

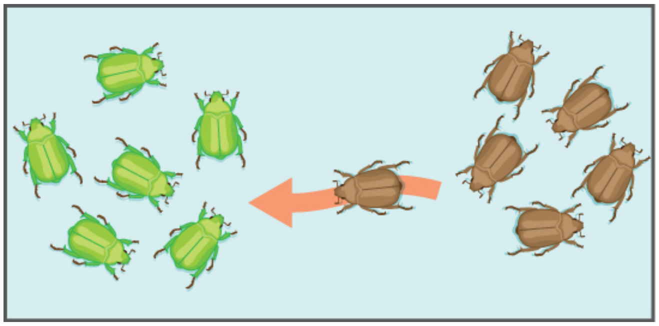


Figure 3.4.3: Gene flow can occur when an individual travels from one geographic location to another and joins a different population of the species. In the example shown here, the brown allele is introduced into the green population.

Summary

There are four factors that can change the allele frequencies of a population. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Mutations introduce new alleles into a population. Genetic drift stems from the chance occurrence that some individuals have more offspring than others and results in changes in allele frequencies that are random in direction. When individuals leave or join the population, allele frequencies can change as a result of gene flow.

Sources

1. 1 T. Pearson, et al. (2001). Molecular and genealogical evidence for a founder effect in Fanconi anemia families of the Afrikaner population of South Africa. *Proceedings of the National Academy of Sciences, 98* (10), pp. 5734-5739. DOI: 10.1073/pnas.091402398.

Contributors and Attributions

Modified from the following sources

- **11.2: Mechanisms of Evolution** by OpenStax is licensed CC BY 4.0.
- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

- **11.2: Mechanisms of Evolution** by OpenStax is licensed CC BY 4.0.

3.5: Adaptive Evolution

Skills to Develop

- Explain the different ways natural selection can shape populations
- Describe how these different forces can lead to different outcomes in terms of the population variation

Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency—a process known as adaptive evolution. Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual; it selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's evolutionary (Darwinian) fitness.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not the absolute fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called relative fitness, allows researchers to determine which individuals are contributing additional offspring to the next generation, and thus, how the population might evolve.

There are several ways selection can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes displayed can become more similar or more disparate.

Stabilizing Selection

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo stabilizing selection (Figure $3.5.1$). In a population of mice that live in the woods, for example, natural selection is likely to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most closely matched to that color will be most likely to survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them a bit lighter or a bit darker will stand out against the ground and be more likely to fall victim to predation. As a result of this selection, the population's genetic variance will decrease.

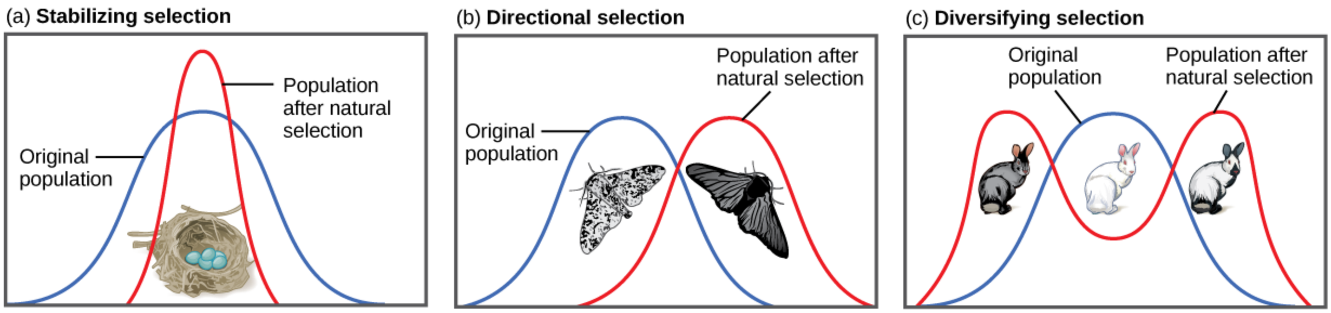
Directional Selection

When the environment changes, populations will often undergo directional selection (Figure $3.5.1$), which selects for phenotypes at one end of the spectrum of existing variation. A classic example of this type of selection is the evolution of the peppered moth in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. But as soot began spewing from factories, the trees became darkened, and the light-colored moths became easier for predatory birds to spot. Over time, the frequency of the melanic form of the moth increased because they had a higher survival rate in habitats affected by air pollution because their darker coloration blended with the sooty trees. Similarly, the hypothetical mouse population may evolve to take on a different coloration if something were to cause the forest floor where they live to change color. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.

Diversifying Selection

Sometimes two or more distinct phenotypes can each have their advantages and be selected for by natural selection, while the intermediate phenotypes are, on average, less fit. Known as diversifying selection (Figure $3.5.1$), this is seen in many populations of animals that have multiple male forms. Large, dominant alpha males obtain mates by brute force, while small males can sneak in for furtive copulations with the females in an alpha male's territory. In this case, both the alpha males and the "sneaking" males will be selected for, but medium-sized males, which can't overtake the alpha males and are too big to sneak copulations, are selected against. Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a population of mice living at the beach where there is light-colored sand interspersed with patches of tall grass.

In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, on the other hand, would not blend in with either the grass or the sand, and would thus be more likely to be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.



(a) **Stabilizing selection**

Robins typically lay four eggs, an example of stabilizing selection. Larger clutches may result in malnourished chicks, while smaller clutches may result in no viable offspring.

(b) **Directional selection**

Light-colored peppered moths are better camouflaged against a pristine environment; likewise, dark-colored peppered moths are better camouflaged against a sooty environment. Thus, as the Industrial Revolution progressed in nineteenth-century England, the color of the moth population shifted from light to dark, an example of directional selection.

(c) **Diversifying selection**

In a hyphothetical population, gray and Himalayan (gray and white) rabbits are better able to blend with a rocky environment than white rabbits, resulting in diversifying selection.

Figure $3.5.1$: Different types of natural selection can impact the distribution of phenotypes within a population. In (a) stabilizing selection, an average phenotype is favored. In (b) directional selection, a change in the environment shifts the spectrum of phenotypes observed. In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

Exercise $3.5.1$

In recent years, factories have become cleaner, and less soot is released into the environment. What impact do you think this has had on the distribution of moth color in the population?

Answer

Moths have shifted to a lighter color.

Frequency-dependent Selection

Another type of selection, called frequency-dependent selection, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection). An interesting example of this type of selection is seen in a unique group of lizards of the Pacific Northwest. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males (Figure $3.5.2$) are the smallest, and look a bit like females, which allows them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. That is, the big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females, the blue males are successful at guarding their mates against yellow sneaker males, and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.

Figure $3.5.2$: A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. (credit: “tinyfroglet”/Flickr)

In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes—in one generation, orange might be predominant, and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for. Finally, when blue males become common, orange males will once again be favored.

Negative frequency-dependent selection serves to increase the population’s genetic variance by selecting for rare phenotypes, whereas positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes.

Sexual Selection

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, like the peacock’s tail, while females tend to be smaller and duller in decoration. Such differences are known as sexual dimorphisms (Figure $3.5.3$), which arise from the fact that in many populations, particularly animal populations, there is more variance in the reproductive success of the males than there is of the females. That is, some males—often the bigger, stronger, or more decorated males—get the vast majority of the total matings, while others receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to get those matings, resulting in the evolution of bigger body size and elaborate ornaments to get the females’ attention. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to select more desirable males.

Sexual dimorphism varies widely among species, of course, and some species are even sex-role reversed. In such cases, females tend to have a greater variance in their reproductive success than males and are correspondingly selected for the bigger body size and elaborate traits usually characteristic of males.

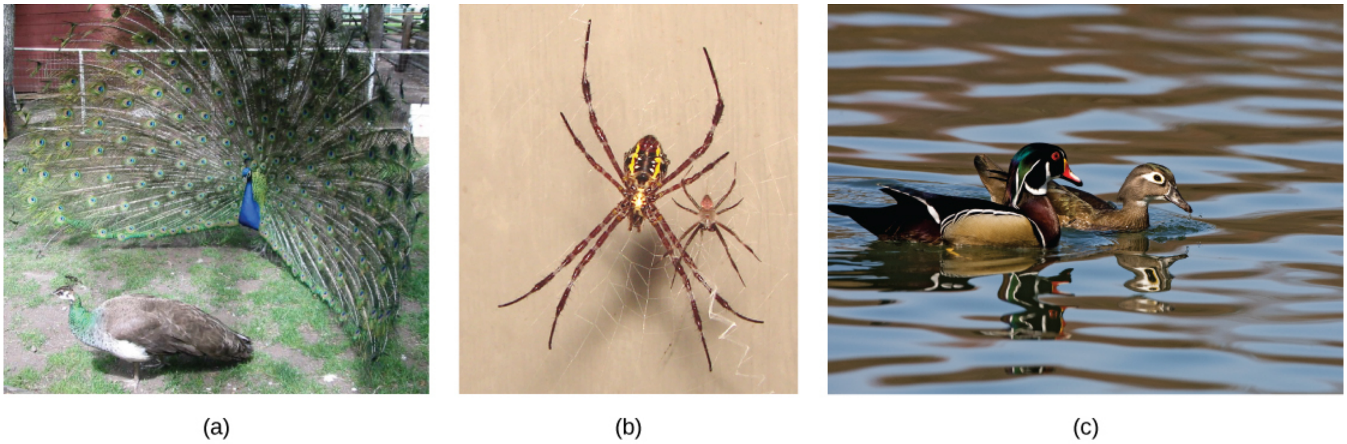


Figure 3.5.3: Sexual dimorphism is observed in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and in (c) wood ducks. (credit "spiders": modification of work by "Sanba38"/Wikimedia Commons; credit "duck": modification of work by Kevin Cole)

The selection pressures on males and females to obtain matings is known as sexual selection; it can result in the development of secondary sexual characteristics that do not benefit the individual's likelihood of survival but help to maximize its reproductive success. Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival. Think, once again, about the peacock's tail. While it is beautiful and the male with the largest, most colorful tail is more likely to win the female, it is not the most practical appendage. In addition to being more visible to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk, in fact, is why females like the big tails in the first place. The speculation is that large tails carry risk, and only the best males survive that risk: the bigger the tail, the more fit the male. This idea is known as the handicap principle.

The good genes hypothesis states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be picky because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.

In both the handicap principle and the good genes hypothesis, the trait is said to be an honest signal of the males' quality, thus giving females a way to find the fittest mates— males that will pass the best genes to their offspring.

No Perfect Organism

Natural selection is a driving force in evolution and can generate populations that are better adapted to survive and successfully reproduce in their environments. But natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population; it does not create anything from scratch. Thus, it is limited by a population's existing genetic variance and whatever new alleles arise through mutation and gene flow.

Natural selection is also limited because it works at the level of individuals, not alleles, and some alleles are linked due to their physical proximity in the genome, making them more likely to be passed on together (linkage disequilibrium). Any given individual may carry some beneficial alleles and some unfavorable alleles. It is the net effect of these alleles, or the organism's fitness, upon which natural selection can act. As a result, good alleles can be lost if they are carried by individuals that also have several overwhelmingly bad alleles; likewise, bad alleles can be kept if they are carried by individuals that have enough good alleles to result in an overall fitness benefit.

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency due to the fact that going from the less beneficial to the more beneficial trait would require going through a less beneficial phenotype. Think back to the mice that live at the beach. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of grass. The dark-colored mice may be, overall, more fit than the light-colored mice, and at first glance, one might expect the light-colored mice be selected for a darker coloration. But remember that the intermediate phenotype, a medium-colored coat, is very bad for the mice—they cannot blend in with either the sand or the grass and are more likely to be eaten by predators. As a result, the light-colored mice would not be selected for a dark coloration because those individuals that began moving in that direction (began being selected for a darker coat) would be less fit than those that stayed light.

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite: introducing deleterious alleles to the population's gene pool. Evolution has no purpose—it is not changing a population into a preconceived ideal. It is simply the sum of the various forces described in this chapter and how they influence the genetic and phenotypic variance of a population.

Summary

Because natural selection acts to increase the frequency of beneficial alleles and traits while decreasing the frequency of deleterious qualities, it is adaptive evolution. Natural selection acts at the level of the individual, selecting for those that have a higher overall fitness compared to the rest of the population. If the fit phenotypes are those that are similar, natural selection will result in stabilizing selection, and an overall decrease in the population's variation. Directional selection works to shift a population's variance toward a new, fit phenotype, as environmental conditions change. In contrast, diversifying selection results in increased genetic variance by selecting for two or more distinct phenotypes.

Other types of selection include frequency-dependent selection, in which individuals with either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection) are selected for. Finally, sexual selection results from the fact that one sex has more variance in the reproductive success than the other. As a result, males and females experience different selective pressures, which can often lead to the evolution of phenotypic differences, or sexual dimorphisms, between the two.

Glossary

adaptive evolution

increase in frequency of beneficial alleles and decrease in deleterious alleles due to selection

directional selection

selection that favors phenotypes at one end of the spectrum of existing variation

diversifying selection

selection that favors two or more distinct phenotypes

evolutionary fitness

(also, Darwinian fitness) individual's ability to survive and reproduce

frequency-dependent selection

selection that favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection)

good genes hypothesis

theory of sexual selection that argues individuals develop impressive ornaments to show off their efficient metabolism or ability to fight disease

handicap principle

theory of sexual selection that argues only the fittest individuals can afford costly traits

honest signal

trait that gives a truthful impression of an individual's fitness

relative fitness

individual's ability to survive and reproduce relative to the rest of the population

sexual dimorphism

phenotypic difference between the males and females of a population

stabilizing selection
selection that favors average phenotypes

3.6: Common Misconceptions about Evolution

Although the theory of evolution initially generated some controversy, by 20 years after the publication of *On the Origin of Species* it was almost universally accepted by biologists, particularly younger biologists. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound. In addition, there are those that reject it as an explanation for the diversity of life.

CONCEPT IN ACTION

This website addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes what scientists understand to be facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge. In contrast, a "theory" in common vernacular means a guess or suggested explanation for something. This meaning is more akin to the concept of a "hypothesis" used by scientists, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization. If this were the case, geneticist Theodosius Dobzhansky would not have said that "nothing in biology makes sense, except in the light of evolution."[1]

Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, but this is called development; it involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there may be enough new individuals with different bill sizes to change the average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics complain that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies—the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, over a very long time, and presumably just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things. The early stages of life included the formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and the external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment," are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in change in the population if the characters are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select for a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic application.

In a larger sense, evolution is also not goal directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the "pinnacle" of evolution, or "perfected" by evolution. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Evolution Is Controversial among Scientists

The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The theory of evolution replaced the predominant theory at the time that species had all been specially created within relatively recent history. Despite the prevalence of this theory, it was becoming increasingly clear to naturalists during the nineteenth century that it could no longer explain many observations of geology and the living world. The persuasiveness of the theory of evolution to these naturalists lay in its ability to explain these phenomena, and it continues to hold extraordinary explanatory power to this day. Its continued rejection by some religious leaders results from its replacement of special creation, a tenet of their religious belief. These leaders cannot accept the replacement of special creation by a mechanistic process that excludes the actions of a deity as an explanation for the diversity of life including the origins of the human species. It should be noted, however, that most of the major denominations in the United States have statements supporting the acceptance of evidence for evolution as compatible with their theologies.

The nature of the arguments against evolution by religious leaders has evolved over time. One current argument is that the theory is still controversial among biologists. This claim is simply not true. The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[2] The support for the theory is reflected in signed statements from many scientific societies such as the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists that reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected.

Other Theories Should Be Taught

A common argument from some religious leaders is that alternative theories to evolution should be taught in public schools. Critics of evolution use this strategy to create uncertainty about the validity of the theory without offering actual evidence. In fact, there are no viable alternative scientific theories to evolution. The last such theory, proposed by Lamarck in the nineteenth century, was replaced by the theory of natural selection. A single exception was a research program in the Soviet Union based on Lamarck's theory during the early twentieth century that set that country's agricultural research back decades. Special creation is not a viable alternative scientific theory because it is not a scientific theory, since it relies on an untestable explanation. Intelligent design, despite the claims of its proponents, is also not a scientific explanation. This is because intelligent design posits the existence of an unknown designer of living organisms and their systems. Whether the designer is unknown or supernatural, it is a cause that cannot be measured; therefore, it is not a scientific explanation. There are two reasons not to teach nonscientific theories. First, these explanations for the diversity of life lack scientific usefulness because they do not, and cannot, give rise to research programs that promote our understanding of the natural world. Experiments cannot test non-material explanations for natural phenomena. For this reason, teaching these explanations as science in public schools is not in the public interest. Second, in the United States, it is illegal to teach them as science because the U.S. Supreme Court and lower courts have ruled that the teaching of religious belief, such as special creation or intelligent design, violates the establishment clause of the First Amendment of the U.S. Constitution, which prohibits government sponsorship of a particular religion.

The theory of evolution and science in general is, by definition, silent on the existence or non-existence of the spiritual world. Science is only able to study and know the material world. Individual biologists have sometimes been vocal atheists, but it is equally true that there are many deeply religious biologists. Nothing in biology precludes the existence of a god, indeed biology as a science has nothing to say about it. The individual biologist is free to reconcile her or his personal and scientific knowledge as they see fit. The Voices for Evolution project (http://ncse.com/voices), developed through the National Center for Science Education, works to gather the diversity of perspectives on evolution to advocate it being taught in public schools.

Section Summary

The theory of evolution is a difficult concept and misconceptions abound. The factual nature of evolution is often challenged by wrongly associating the scientific meaning of a theory with the vernacular meaning. Evolution is sometimes mistakenly interpreted to mean that individuals evolve, when in fact only populations can evolve as their gene frequencies change over time. Evolution is often assumed to explain the origin of life, which it does not speak to. It is often spoken in goal-directed terms by which organisms change through intention, and selection operates on mutations present in a population that have not arisen in response to a particular environmental stress. Evolution is often characterized as being controversial among scientists; however, it is accepted by the vast majority of working scientists. Critics of evolution often argue that alternative theories to evolution should be taught in public schools; however, there are no viable alternative scientific theories to evolution. The alternative religious beliefs should not be taught as science because it cannot be proven, and in the United States it is unconstitutional. Science is silent on the question of the existence of a god while scientists are able to reconcile religious belief and scientific knowledge.

Footnotes

1. 1 Theodosius Dobzhansky. “Biology, Molecular and Organismic.” *American Zoologist* 4, no. 4 (1964): 449.
2. 2 Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.Contributors

Contributors and Attributions

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

CHAPTER OVERVIEW

4: Adaptations to the Physical Environment

Learning Objectives

- Describe what an adaptation is and how it arises, and explain examples of common adaptations in plants and animals.
- Compare and contrast some of the broad strategies organisms employ to deal with a variable environment.
- Explain how individual physiological performance can vary with the environment, and link these concepts with population distribution limits and climate change.

Summary

In biology, adaptation is defined a heritable behavioral, morphological, or physiological trait that has evolved through the process of natural selection, and maintains or increases the fitness of an organism under a given set of environmental conditions. This concept is central to ecology: the study of adaptation is the study of the evolutionary relationship between organisms and their environment. While different groups of plants and animals have adapted to components of their environment in many different ways, more broadly, the two basic solutions for dealing with environmental variation are to conform to the environment or to regulate internal conditions despite the environment. These different strategies influence an organism's physiological performance across variable environmental conditions.

Contributors and Attributions

-

4.1: What is adaptation?

Adaptation

In biology, **adaptation** is defined a heritable behavioral, morphological, or physiological trait that has evolved through the process of natural selection, and maintains or increases the fitness of an organism under a given set of environmental conditions. This concept is central to ecology: the study of adaptation is the study of the evolutionary relationship between organisms and their environment.

Adaptation is related to biological fitness, which governs the rate of evolution as measured by change in gene frequencies. Often, two or more species co-adapt and co-evolve as they develop adaptations that interlock with those of the other species, such as with flowering plants and pollinating insects. Features evolved for one purpose may be co-opted for a different one, as when the insulating feathers of dinosaurs were co-opted for bird flight.

History

Adaptation is an observable fact of life accepted by philosophers and natural historians from ancient times, independently of their views on evolution, but their explanations differed.

In natural theology, adaptation was interpreted as the work of a deity and as evidence for the existence of God.[2] Charles Darwin broke with the tradition by emphasizing the flaws and limitations which occurred in the animal and plant worlds.[5] Jean-Baptiste Lamarck proposed a tendency for organisms to become more complex, moving up a ladder of progress, plus "the influence of circumstances," usually expressed as *use and disuse*.[6] This second, subsidiary element of his theory is what is now called Lamarckism, a proto-evolutionary hypothesis of the inheritance of acquired characteristics, intended to explain adaptations by natural means.[7]

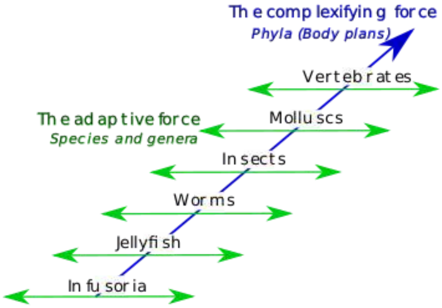


Figure 4.1.1: The second of Jean-Baptiste Lamarck's two factors (the first being a complexifying force) was an adaptive force that causes animals with a given body plan to adapt to circumstances by inheritance of acquired characteristics, creating a diversity of species and genera.

Other natural historians, such as Buffon, accepted adaptation, and some also accepted evolution, without voicing their opinions as to the mechanism. This illustrates the real merit of Darwin and Alfred Russel Wallace, and secondary figures such as Henry Walter Bates, for putting forward a mechanism whose significance had only been glimpsed previously. A century later, experimental field studies and breeding experiments by people such as E.B. Ford and Theodosius Dobzhansky produced evidence that natural selection was not only the 'engine' behind adaptation, but was a much stronger force than had previously been thought.[8][9][10]

General principles

The significance of an adaptation can only be understood in relation to the total biology of the species.

— Julian Huxley, *Evolution: The Modern Synthesis*[11]

What adaptation is

Adaptation is primarily a process rather than a physical form or part of a body.[12] An internal parasite (such as a liver fluke) can illustrate the distinction: such a parasite may have a very simple bodily structure, but nevertheless the organism is highly adapted to its specific environment. From this we see that adaptation is not just a matter of visible traits: in such parasites critical adaptations take place in the life cycle, which is often quite complex.[13] However, as a practical term, "adaptation" often refers to a *product*: those features of a species which result from the process. Many aspects of an animal or plant can be correctly called adaptations, though there are always some features whose function remains in doubt. By using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product), one may distinguish the two different senses of the word.[14][15][16][17]

Adaptation is one of the two main processes that explain the observed diversity of species, such as the different species of Darwin's finches. The other process is speciation, in which new species arise, typically through reproductive isolation.[18][19] An example widely used today to study the interplay of adaptation and speciation is the evolution of cichlid fish in African lakes, where the question of reproductive isolation is complex.[20][21]

Adaptation is not always a simple matter where the ideal phenotype evolves for a given environment. An organism must be viable at all stages of its development and at all stages of its evolution. This places *constraints* on the evolution of development, behavior, and structure of organisms. The main constraint, over which there has been much debate, is the requirement that each genetic and phenotypic change during evolution should be relatively small, because developmental systems are so complex and interlinked. However, it is not clear what "relatively small" should mean, for example polyploidy in plants is a reasonably common large genetic change.[22] The origin of eukaryotic endosymbiosis is a more dramatic example.[23]

All adaptations help organisms survive in their ecological niches. The adaptive traits may be structural, behavioral or physiological. Structural adaptations are physical features of an organism, such as shape, body covering, armament, and internal organization. Behavioral adaptations are inherited systems of behavior, whether inherited in detail as instincts, or as a neuropsychological capacity for learning. Examples include searching for food, mating, and vocalizations. Physiological adaptations permit the organism to perform special functions such as making venom, secreting slime, and phototropism, but also involve more general functions such as growth and development, temperature regulation, ionic balance and other aspects of homeostasis. Adaptation affects all aspects of the life of an organism.[24]

The following definitions are given by the evolutionary biologist Theodosius Dobzhansky:

1. *Adaptation* is the evolutionary process whereby an organism becomes better able to live in its habitat or habitats.[25][26][27]

2. *Adaptedness* is the state of being adapted: the degree to which an organism is able to live and reproduce in a given set of habitats.[28]

3. An *adaptive trait* is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing.[29]

What adaptation is not

Adaptation differs from flexibility, acclimatization, and learning, all of which are changes during life which are not inherited. Flexibility deals with the relative capacity of an organism to maintain itself in different habitats: its degree of specialization. Acclimatization describes automatic physiological adjustments during life;[30] learning means improvement in behavioral performance during life.[31]

Flexibility stems from phenotypic plasticity, the ability of an organism with a given genotype (genetic type) to change its phenotype (observable characteristics) in response to changes in its habitat, or to move to a different habitat.[32][33] The degree of flexibility is inherited, and varies between individuals. A highly specialized animal or plant lives only in a well-defined habitat, eats a specific type of food, and cannot survive if its needs are not met. Many herbivores are like this; extreme examples are koalas which depend on *Eucalyptus*, and giant pandas which require bamboo. A generalist, on the other hand, eats a range of food, and can survive in many different conditions. Examples are humans, rats, crabs and many carnivores. The *tendency* to behave in a specialized or exploratory manner is inherited—it is an adaptation. Rather different is developmental flexibility: "An animal or plant is developmentally flexible if when it is raised in or transferred to new conditions, it changes in structure so that it is better fitted to survive in the new environment," writes evolutionary biologist John Maynard Smith.[34]

Figure 4.1.2: Some generalists, such as birds, have the flexibility to adapt to urban areas.

If humans move to a higher altitude, respiration and physical exertion become a problem, but after spending time in high altitude conditions they acclimatize to the reduced partial pressure of oxygen, such as by producing more red blood cells. The ability to acclimatize is an adaptation, but the acclimatization itself is not. The reproductive rate declines, but deaths from some tropical diseases also go down. Over a longer period of time, some people are better able to reproduce at high altitudes than others. They contribute more heavily to later generations, and gradually by natural selection the whole population becomes adapted to the new conditions. This has demonstrably occurred, as the observed performance of long-term communities at higher altitude is significantly better than the performance of new arrivals, even when the new arrivals have had time to acclimatize.[35]

Adaptedness and fitness

There is a relationship between adaptedness and the concept of fitness used in population genetics. Differences in fitness between genotypes predict the rate of evolution by natural selection. Natural selection changes the relative frequencies of alternative phenotypes, insofar as they are heritable.[36] However, a phenotype with high adaptedness may not have high fitness. Dobzhansky mentioned the example of the Californian redwood, which is highly adapted, but a relict species in danger of extinction.[25] Elliott Sober commented that adaptation was a retrospective concept since it implied something about the history of a trait, whereas fitness predicts a trait's future.[37]

1. Relative fitness- the average contribution to the next generation by a genotype or a class of genotypes, relative to the contributions of other genotypes in the population.[38] This is also known as *Darwinian fitness*, *selection coefficient*, and other terms.

2. Absolute fitness - the absolute contribution to the next generation by a genotype or a class of genotypes. Also known as the Malthusian parameter when applied to the population as a whole.[36][39]

3. Adaptedness - the extent to which a phenotype fits its local ecological niche. Researchers can sometimes test this through a reciprocal transplant, which involves taking organisms evolved in different locations and swapping where they are located to determine if fitness is reduced. Transplant experiments are often used to test if there is a genetic component to differences in populations. [40]

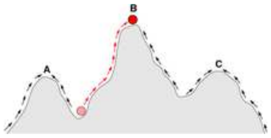


Figure 4.1.3: In this sketch of a fitness landscape, a population can evolve by following the arrows to the adaptive peak at point B, and the points A and C are local optima where a population could become trapped.

Sewall Wright proposed that populations occupy *adaptive peaks* on a fitness landscape. To evolve to another, higher peak, a population would first have to pass through a valley of maladaptive intermediate stages, and might be "trapped" on a peak that is not optimally adapted.[41]

Definition: Reciprocal transplant experiment

Testing for local adaptation requires measuring the fitness of organisms from one population in both their local environment and in foreign environments. This is often done using transplant experiments. Using the stricter definition of reciprocal home site advantage, local adaptation is often tested via reciprocal transplant experiments. In reciprocal transplants, organisms from one population are transplanted into another population, and vice versa, and their fitness is measured (see figure).[42] If local transplants outperform (i.e. have higher fitness than) the foreign transplants at both sites, the local populations are said to be locally adapted.[43] If local adaptation is defined simply as a home site advantage of one population (local sources outperform foreign sources at a common site), it can be tested for using common garden experiments, where multiple source populations are grown in a common site, as long as one of the source populations is local to that site.

Transplant experiments have most often been done with plants or other organisms that do not move.[44] However, evidence for rapid local adaptation in mobile animals has been gathered through transplant experiments with Trinidadian guppies.[45]

Sources

1. Leroi, A.M. (2015). *The lagoon: How Aristotle invented science*. Penguin Books.
2. Desmond, A. (1989). Importing the new morphology. *The politics of evolution* (pp. 25-100). Library of Congress.
3. Voltaire (1759). *Candide ou l'optimisme, traduit de l'allemand de Mr. Le Docteur Ralph*. Cramer et al.
4. Sober, E. (1993). *Philosophy of biology*. Westview Press.
5. Darwin, C. (1872). Mutual affinities of organic beings: Morphology, embryology, rudimentary organs. *The origin of species*, (pp. 363-403). William Clowes and Sons. http://darwin-online.org.uk/content/frameset?pageseq=425&itemID=F391&viewtype=side.
6. Bowler, P.J. (1989). *Evolution: The history of an idea*. University of California Press. https://archive.org/details/evolutionhistory0000bowl/page/86/mode/1up.
7. See, for example, the discussion in Bowler 2003, pp. 86–95: "Whatever the true nature of Lamarck's theory, it was his mechanism of adaptation that caught the attention of later naturalists." (p. 90)
8. Provine, W.B. (1986). *Sewall Bright and evolutionary biology*. University of Chicago Press. https://archive.org/details/sewallwrightevol00will.
9. Ford, E.B. (1975). *Ecological genetics*. Chapman & Hall.
10. Orr, H.A. (2005). The genetic theory of adaptation: A brief history. *Nature Reviews Genetics, 6*(2), pp. 119–127. doi:10.1038/nrg1523. PMID 15716908. S2CID 17772950.
11. Huxley, J. (1942). *Evolution: The modern synthesis*. Allen & Unwin, London.
12. Mayr 1982, p. 483: "Adaptation... could no longer be considered a static condition, a product of a creative past, and became instead a continuing dynamic process."
13. Price, P.W. (1980). The evolutionary biology of parasites. *Monographs in population biology, 15*. Princeton University Press.
14. Daintith, John; Martin, Elizabeth A., eds. (2010) [First published 1984 as *Concise Science Dictionary*]. "adaptation". *A Dictionary of Science*. Oxford Paperback Reference (6th ed.). Oxford University Press. p. 13. ISBN 978-0-19-956146-9. LCCN 2010287468. OCLC 444383696. Any change in the structure or functioning of successive generations of a population that makes it better suited to its environment.
15. Bowler, P.J. (2003). *Evolution: The history of an idea*. University of California Press. https://archive.org/details/evolutionhistory0000bowl/page/86/mode/1up.
16. Patterson, C. (1999). *Evolution*. Comstuck Publishing. p. 1
17. Williams 1966, p. 5: "Evolutionary adaptation is a phenomenon of pervasive importance in biology."
18. Mayr, E. (1963). *Animal species and evolution*. Cambridge, Belknap Press of Harvard University Press.
19. Mayr 1982, pp. 562–566
20. Mack, T., Meyer, A., Salzburger, W., Mack, T., & Verheyen, E. (2005). Out of Tanganyika: Genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evolutionary Biology, 5*(17), pp. 17. doi:10.1186/1471-2148-5-17. PMC 554777. PMID 15723698.
21. Kornfield, I., & Smith, P.F. (2000). African Cichlid fishes: Model systems for evolutionary biology. *Annual Review of Ecology and Systematics, 31*, pp. 163–196. doi:10.1146/annurev.ecolsys.31.1.163.
22. Stebbins, G.L. (1950). Variation and evolution in plants. chs. 8 and 9
23. Margulis, L., & Fester, R. (1991). *Symbiosis as a source of evolutionary innovation: Speciation and morphogenesis*. MIT Press.
24. Hutchinson 1965. The niche is the central concept in evolutionary ecology; see especially part II: "The niche: an abstractly inhabited hypervolume." (pp. 26–78)
25. Dobzhansky, T. (1968). On some fundamental concepts of Darwainian biology. In Dobzhansky, T., Hecht, M.K., Steere, W.C. (Eds.) *Evolutionary Biology*. Springer, Boston, MA. pp. 1–34
26. Wang, G (2014). "Chapter 5.6—Zero Order Adaptivity". *Analysis of Complex Diseases: A Mathematical Perspective*. Taylor Francis. p. 69. ISBN 978-1-4665-7223-2.
27. Sejian, V.; Gaughan, J.; Baumgard, L.; Prasad, C., eds. (2015). *Climate Change Impact on Livestock: Adaptation and Mitigation*. Springer. p. 515. ISBN 978-81-322-2265-1.
28. Dobzhansky, T. (1970). *Genetics of the evolutionary process*. Columbia University Press. pp. 4–6, 79–82
29. Dobzhansky, T. (1956). Genetics of natural populations. XXV. Genetic changes in populations of *Drosophila pseudoobscura* and *Drosophila persimilis* in Some localities in California. *Evolution, 10*(1), pp. 82–92. doi:10.2307/2406099. JSTOR 2406099.
30. Pillay, N., Rymer, T., Schradin, C. (2013). Extinction or survival? Behavioral flexibility in response to environmental change in the African striped mouse Rhabdomys. *Sustainability, 5*(1), pp. 163–186. doi:10.3390/su5010163.
31. Gross, R. (2012). *Psychology: The science of mind and behaviour* (6th ed.). Hodder. p. 335. ISBN 978-1-4441-6436-7.

32. Irwin, D.E., Price, T.D., Qvarnström, A. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B*, *270* (1523), pp. 1433–1440. doi:10.1098/rspb.2003.2372. PMC 1691402. PMID 12965006.
33. Price, T.D. (2006). Phenotypic plasticity, sexual selection and the evolution of colour patterns. *The Journal of Experimental Biology*, *209*,(12), pp. 2368–2376. doi:10.1242/jeb.02183. PMID 16731813.
34. Smith, J.M. (1993). *The theory of evolution*. Cambridge University Press. p. 33
35. Moore, L.G., & Regensteiner, J.G. (1983). Adaptation to High Altitude. *Annual Review of Anthropology*, *12*, pp. 285–304. doi:10.1146/annurev.an.12.100183.001441.
36. Endler, J.A. (1986). *Natural selection in the wild*. Princeton University Press. pp. 33–51
37. Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. MIT Press. p. 210
38. Futuyma, D.J. (1986). *Evolutionary biology*. Sunderland Mass. p. 552
39. Fisher, R.A. (1930). *The genetical theory of natural selection*. Oxford at the Clarendon Press. p. 25
40. Gaggiotti, O.E., Mouterde, M., de Villemereuil, P., Till-Bottraud, I. (2015). Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity*, *116*(3), pp. 249–254. doi:10.1038/hdy.2015.93. PMC 4806574. PMID 26486610.
41. Wright, D.F. (1932). *Proceedings of the sixth international congress of genetics*. Electronic Scholarly Publishing. pp. 356–366
42. Ebert, D., & Kawecki, T.J. (2004) Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), pp. 1225-1241. *doi:10.1111/j.1461-0248.2004.00684.x*. *ISSN 1461-0248*.
43. Fenster, C.B., & Galloway, L.F. (2000). Population differentiation in an annual legume: Local adaptation. *Evolution*, *54*(4), pp. 1173-1181. *doi:10.1111/j.0014-3820.2000.tb00552.x*. *ISSN 1558-5646*. *PMID 11005286*. *S2CID 13652390*.
44. Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist*, *173*(5), pp. 579-588. *doi:10.1086/597611*. *ISSN 0003-0147*. *PMID 19272016*. *S2CID 524423*.
45. Bryant, M., Gordon, S., Hendry, A., Kinnison, M., Millar, N., Räsänen, K., Reznick, D., & Weese, D. (2009). Adaptive changes in life history and survival following a new guppy introduction. *The American Naturalist*, *174*(1), pp. 34-45. *doi:10.1086/599300*. *PMID 19438322*. *S2CID 8589987*.

Contributors and Attributions

Modified by Dan Wetzel from Wikipedia: https://en.wikipedia.org/wiki/Adaptation and https://en.wikipedia.org/wiki/Local_adaptation

---

4.2: Strategies for dealing with a changing environment

There are lots of amazing and sometimes bizarre adaptations out there in the world. For example, some species of frogs (e.g., wood frogs) that live in temperate climates can tolerate the freezing of their blood and other tissues. These frogs allow about 65% of their bodies to freeze solid, stop breathing, and stop their heart when temperatures drop below freezing. Come spring, as temperatures rise, the frog's body thaws and basic motor functions restart, allowing these frogs to survive incredibly harsh winter conditions. Other examples of interesting adaptations include carnivorous plants that obtain their nutrients from insects (e.g., pitcher plants), or rodents (kangaroo rat) that obtain enough water from metabolism that they do not need to drink water at all.

Figure 4.2.1: Frog (photo by Patti Black on Unsplash), pitcher plant (photo by Adrian Pingstone released to the public domain), and kangaroo rat (US Fish & Wildlife).

While each of these examples are fascinating in their own right, perhaps a better place to start when thinking about adaptation are the basic, or broad strategies that organisms have adapted to survive in the environment. Specifically, if we think about the fact that the environment that an organism lives in can vary considerably. The environment can vary temporally, on both short and long-term time scales, and spatially in terms of both abiotic and biotic factors. For example, the environment an organism experiences can change in temperature, precipitation, amount of sunlight, water availability, oxygen concentration, salinity, atmospheric pressure, etc. This can create problems for living things because most cellular functions (think enzymes, or neurotransmitters) require specific conditions for proper function. Biotic components of the environment can also change with time or space, including things like the availability of prey, the abundance of predators or competitors, or access to potential mates. While different groups of plants and animals may have solved different components of dealing with this variability in different ways, more broadly we can think of two basic solutions or strategies for dealing with environmental variation: **conform** or **regulate**.

Conforming is when an organism allows their internal environment to fluctuate with the external environment; we might call an organism that conforms a "conformer" for that particular environmental variable. An example of a conformer to external temperature is a frog that allows its body temperature to fluctuate with the environment (Figure 4.2.2A). As the external temperature increases or decreases, the internal temperature of the frog increases or decreases along with the external environment.

If we're thinking just about temperature, we often describe organisms using conforming strategies using the terms **ectotherm** (an animal that relies on the external environment to regulate its internal body temperature), or **poikilotherm** (an animal that varies its internal body temperature within a wide range of temperatures).

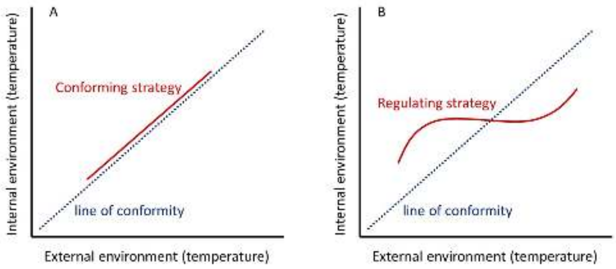


Figure $4.2.2$: Basic strategies for dealing with fluctuations in the environment: conform or regulate.

Regulating is when an organism attempts to regulate or maintain a constant internal environment despite any environmental fluctuations; we might call an organism that regulates a “regulator” for that particular environmental variable. An example of a regulator for external temperature is a dog that attempts to maintain its internal body temperature within a relatively narrow range despite fluctuations in the external environment (Figure $4.2.2$B). As the external temperature increases or decreases, the internal temperature of the dog remains nearly the same with some limitations at extreme temperatures.

If we’re thinking just about temperature, we often describe organisms using regulating strategies using the terms **endotherm** (an animal that regulates its own internal body temperature through metabolic processes), or **homeotherm** (maintains a constant internal body temperature, usually within a narrow range of temperatures).

Some organisms can differ in their strategy for different regulatory processes. For example, salmon are **thermoconformers**, but **osmoregulators** when they move between marine (saline) and freshwater environments..

There are costs and benefits to each of these basic strategies. For example, conformers will invest less energy into maintaining their internal environment, but can experience compromised cellular functions. On the other hand, regulators can live in a wider range of environments without experiencing reduced cellular functions, but they expend a great deal of energy to maintain their internal environment (Figure $4.2.3$).

	Benefits	**Costs**
Regulator	Freedom from environment	High energy demand
Conformer	Low energy demand	Compromised homeostasis

Figure $4.2.3$: Theoretical costs and benefits of an organism regulating their internal environment or conforming to the external environment.

In addition to being a conformer or regulator, organisms may also be **avoiders** that will escape changes in the environment by moving locally or migrating long distances (read more about this in the behavioral ecology chapter). Other types of the “avoiding” strategy could include organisms that undergo some type of **dormancy**, which is when an organism decreases their metabolic activity under extended unfavorable conditions in order to conserve energy.

Examples of dormancy in animals include **hibernation**, a mechanism used by many mammals to reduce energy expenditure and survive food shortages over the winter. During hibernation, the animal undergoes many physiological changes, including decreased heart rate (by as much as 95%) and decreased body temperature. Another type of dormancy in animals, most commonly seen in insects, is **diapause**, when the organism completely suspends development between autumn and spring.

In plants, dormancy is a period of arrested growth, and is a survival strategy exhibited by many plant species that allows them to survive in climates where part of the year is unsuitable for growth, such as winter or dry seasons. A classic example of dormancy in plants is seed dormancy, where seeds are prevented from germinating during unsuitable ecological conditions. Many plant species that exhibit dormancy have a biological clock that tells them when to slow activity and to prepare soft tissues for a period of freezing temperatures or water shortage. On the other hand, dormancy can be triggered after a normal growing season by decreasing temperatures, shortened day length, and/or a reduction in rainfall.

Many bacteria can survive adverse conditions such as temperature, desiccation, and antibiotics by forming endospores, cysts, or states of reduced metabolic activity lacking specialized cellular structures.

For organisms that regulate components of their internal environment to big changes in the external environment, one key question we might have is: how do they do this? Mechanistically, the process of adjusting the internal environment in response to an external change is described as **acclimation**.

Acclimation

Acclimation is the process in which an individual organism adjusts to a change in its environment (such as a change in altitude, temperature, humidity, photoperiod, or pH), allowing it to maintain fitness across a range of environmental conditions. Acclimation occurs in a short period of time (hours to weeks), and within the organism's lifetime (compared to adaptation, which is evolution, taking place over many generations). This may be a discrete occurrence (for example, when mountaineers acclimate to high altitude over hours or days) or may instead represent part of a periodic cycle, such as a mammal shedding heavy winter fur in favor of a lighter summer coat. Organisms can adjust their morphological, behavioral, physical, and/or biochemical traits in response to changes in their environment.[1] While the capacity to acclimate to novel environments has been well documented in thousands of species, researchers still know very little about how and why organisms acclimate the way that they do.

Methods of acclimation

Biochemical

In order to maintain performance across a range of environmental conditions, there are several strategies organisms use to acclimate. In response to changes in temperature, organisms can change the biochemistry of cell membranes making them more fluid in cold temperatures and less fluid in warm temperatures by increasing the number of membrane proteins.[8] In response to certain stressors, some organisms express so-called heat shock proteins that act as molecular chaperones and reduce denaturation by guiding the folding and refolding of proteins. It has been shown that organisms which are acclimated to high or low temperatures display relatively high resting levels of heat shock proteins so that when they are exposed to even more extreme temperatures the proteins are readily available. Expression of heat shock proteins and regulation of membrane fluidity are just two of many biochemical methods organisms use to acclimate to novel environments.

Morphological

Organisms are able to change several characteristics relating to their morphology in order to maintain performance in novel environments. For example, birds often increase their organ size to increase their metabolism. This can take the form of an increase in the mass of nutritional organs or heat-producing organs, like the pectorals (with the latter being more consistent across species[9]).[10]

Examples

Plants

Many plants, such as maple trees, irises, and tomatoes, can survive freezing temperatures if the temperature gradually drops lower and lower each night over a period of days or weeks. The same drop might kill them if it occurred suddenly. Studies have shown that tomato plants that were acclimated to higher temperature over several days were more efficient at photosynthesis at relatively high temperatures than were plants that were not allowed to acclimate.[13]

Animals

Animals acclimatize in many ways. Sheep grow very thick wool in cold, damp climates. Fish are able to adjust only gradually to changes in water temperature and quality. Tropical fish sold at pet stores are often kept in acclimation bags until this process is complete.[15] Lowe & Vance (1995) were able to show that lizards acclimated to warm temperatures could maintain a higher running speed at warmer temperatures than lizards that were not acclimated to warm conditions.[16] Fruit flies that develop at relatively cooler or warmer temperatures have increased cold or heat tolerance as adults, respectively.[17]

Humans

The salt content of sweat and urine decreases as people acclimatize to hot conditions.[18] Plasma volume, heart rate, and capillary activation are also affected.[19]

Acclimation to high altitude continues for months or even years after initial ascent, and ultimately enables humans to survive in an environment that, without acclimation, would kill them. Humans who migrate permanently to a higher altitude naturally acclimatize to their new environment by developing an increase in the number of red blood cells to increase the oxygen carrying capacity of the blood, in order to compensate for lower levels of oxygen intake.[20][21]

Sources

1. (2009) “Acclimatisation” (n.d.) The Unabridged Hutchinson Encyclopedia Retrieved November 5, 2009 from http://encyclopedia.farlex.com/acclimatization
2. Oxford Dictionaries, *Oxford Dictionaries Online*, Oxford University Press.
3. Merriam-Webster, *Merriam-Webster's Collegiate Dictionary*, Merriam-Webster.
4. Merriam-Webster, *Merriam-Webster's Unabridged Dictionary*, Merriam-Webster.
5. Houghton Mifflin Harcourt, *The American Heritage Dictionary of the English Language*, Houghton Mifflin Harcourt, archived from the original on September 25, 2015, retrieved January 31, 2017.
6. Elsevier, *Dorland's Illustrated Medical Dictionary*, Elsevier.
7. Wolters Kluwer, *Stedman's Medical Dictionary*, Wolters Kluwer.
8. Los D.A., Murata N. (2004). "Membrane fluidity and its roles in the perception of environmental signals". *Biochimica et Biophysica Acta (BBA) - Biomembranes*. **0666** (1–2): 142–157. doi:10.1016/j.bbamem.2004.08.002. PMID 15519313.
9. Liknes, Eric T.; Swanson, David L. (2011). "Phenotypic flexibility of body composition associated with seasonal acclimatization in passerine birds". *Journal of Thermal Biology*. **36** (6): 363–370. doi:10.1016/j.jtherbio.2011.06.010. ISSN 0306-4565.
10. McKechnie, Andrew E. (2008). "Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review". *Journal of Comparative Physiology B*. **178** (3): 235–247. doi:10.1007/s00360-007-0218-8. ISSN 0174-1578. PMID 17957373. S2CID 28481792.
11. Angilletta, M.J. (2009). Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University Press, Oxford.
12. DeWitt, Thomas J.; Sih, Andrew; Wilson, David Sloan (February 1, 1998). "Costs and limits of phenotypic plasticity". *Trends in Ecology & Evolution*. **13** (2): 77–81. doi:10.1016/S0169-5347(97)01274-3. PMID 21238209.
13. Camejo, Daymi; Martí, María del C.; Nicolás, Emilio; Alarcón, Juan J.; Jiménez, Ana; Sevilla, Francisca (2007). "Response of superoxide dismutase isoenzymes in tomato plants (Lycopersicon esculentum) during thermo-acclimation of the photosynthetic apparatus". *Physiologia Plantarum*. Wiley. **131** (3): 367–377. doi:10.1111/j.1399-3054.2007.00953.x. ISSN 0031-9317. PMID 18251876.
14. Ali, Mohammad Babar; Khatun, Serida; Hahn, Eun-Joo; Paek, Kee-Yoeup (September 29, 2006). "Enhancement of phenylpropanoid enzymes and lignin in Phalaenopsis orchid and their influence on plant acclimatisation at different levels of photosynthetic photon flux". *Plant Growth Regulation*. Springer Science and Business Media LLC. **49** (2–3): 137–146. doi:10.1007/s10725-006-9003-z. ISSN 0167-6903. S2CID 26821483.
15. "Acclimating Your Fish".
16. Lowe C.H., Vance V.J. (1955). "Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*". *Science*. **122** (3158): 73–74. Bibcode:1955Sci...122...73L. doi:10.1126/science.122.3158.73. PMID 17748800.
17. Slotsbo, Stine; Schou, Mads F.; Kristensen, Torsten N.; Loeschcke, Volker; Sørensen, Jesper G. (September 1, 2016). "Reversibility of developmental heat and cold plasticity is asymmetric and has long-lasting consequences for adult thermal tolerance". *Journal of Experimental Biology*. **219** (17): 2726–2732. doi:10.1242/jeb.143750. ISSN 0022-0949. PMID 27353229.
18. "Heat acclimatization guide" (PDF). US Army. Archived from the original (PDF) on July 2, 2007. Retrieved July 2, 2009.
19. "Heat Acclimatization". *www.sportsci.org*. Retrieved December 3, 2017.
20. Muza, SR; Fulco, CS; Cymerman, A (2004). "Altitude Acclimatization Guide". *US Army Research Inst. Of Environmental Medicine Thermal and Mountain Medicine Division Technical Report* (USARIEM–TN–04–05). Archived from the original on April 23, 2009. Retrieved March 5, 2009.
21. Kenneth Baillie; Alistair Simpson. "Altitude oxygen calculator". Apex (Altitude Physiology EXpeditions). Archived from the original on June 11, 2017. Retrieved August 10, 2006. - Altitude physiology model

Contributors and Attributions

Written by Dan Wetzel, and modified by Dan Wetzel from the following sources:

- Acclimation section from Wikipedia: https://en.wikipedia.org/wiki/Acclimatization

- Information on plant dormancy from: https://en.Wikipedia.org/wiki/Dormancy

---

4.3: Adaptations to avoid harsh conditions

The content for this subtopic is found in two external pages. Please click the links below to access this information.

Extreme Cold Hardiness in Ectotherms

Costanzo, J. P. (2011) Extreme Cold Hardiness in Ectotherms. *Nature Education Knowledge* 3(10):3

Plant-Soil Interactions: Nutrient Uptake

Morgan, J. B. & Connolly, E. L. (2013) Plant-Soil Interactions: Nutrient Uptake. *Nature Education Knowledge* 4(8):2

4.4: Physiological optima and critical limits

The content for this subtopic is found in an external page. Please click the link below to access this information.

Physiological Optima and Critical Limits

Morgan, J. B. & Connolly, E. L. (2013) Plant-Soil Interactions: Nutrient Uptake. *Nature Education Knowledge* 4(8):2

CHAPTER OVERVIEW

5: Terrestrial and Aquatic Biomes

Learning Objectives

- Define biogeography, the study of the geographic distribution of species and the abiotic factors that affect this distribution
- Characterize Earth's terrestrial and aquatic biomes based on their abiotic characteristics
- Differentiate the major driving abiotic factors in terrestrial versus aquatic habitats

Summary

Earth is made up of terrestrial and aquatic biomes that can be defined based on their abiotic (non-living) and biotic (living) characteristics. Biogeographers study how species are geographically distributed and which abiotic factors determine these distributions. The eight major terrestrial biomes vary in abiotic characteristics like temperature, precipitation, and seasonality and, as a result, in primary productivity that they support. Aquatic biomes, which include freshwater and saltwater, vary in light availability and in water temperature and salinity. Earth has experienced natural, periodic cycles in temperature (e.g., through Milankovitch cycles), but humans have altered these natural cycles through the production of greenhouse gases, leading to unnaturally rapid changes in climate.

Contributors and Attributions

5.1: Biogeography

Skills to Develop

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the effect of abiotic factors on net primary productivity

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of biomes: large areas of land with similar climate, flora, and fauna.

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia (Figure 5.1.1).

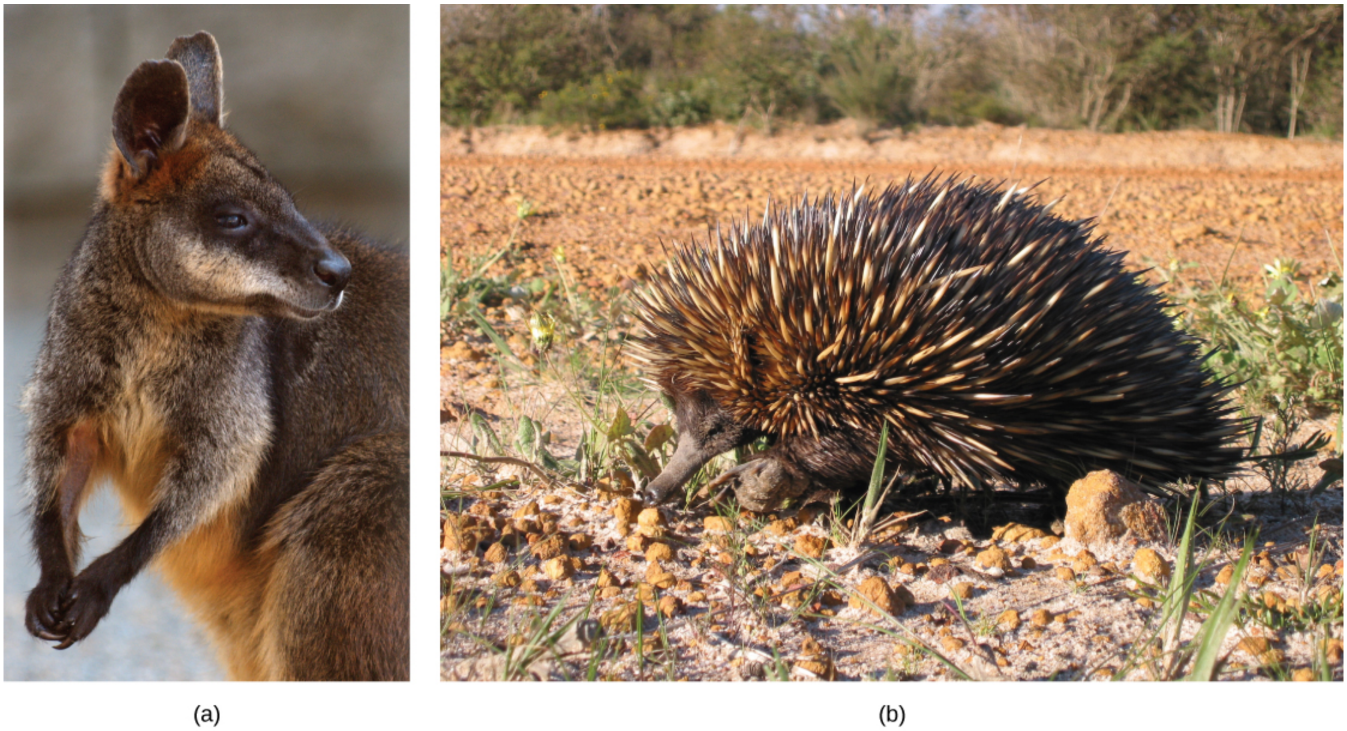


Figure \(\PageIndex{1}\): Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome).

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Link to Learning

Check out this video to observe a platypus swimming in its natural habitat in New South Wales, Australia.

Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist (Figure 5.1.2).

Figure \(\PageIndex{2}\): Listed as federally endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens. *Source: Forest & Kim Starr.*

Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty (Figure 5.1.3). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.

Figure 5.1.3: The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. *Source: John Beetham.*

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants (in the water or above the water's surface), suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis. In small headwater streams in forested areas, very little photosynthesis occurs within the stream because of shading by the forest canopy.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. Ocean upwelling is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline (Figure 5.1.4). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

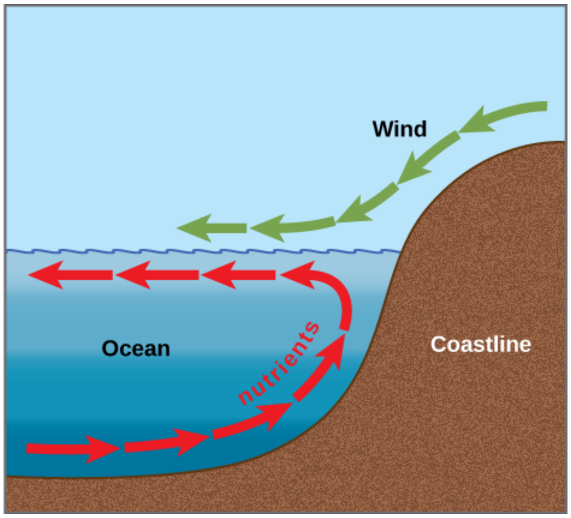


Figure 5.1.4: Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The spring and fall turnover is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water (Figure 5.1.5). These turnovers are caused by the formation of a thermocline: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

Art Connection

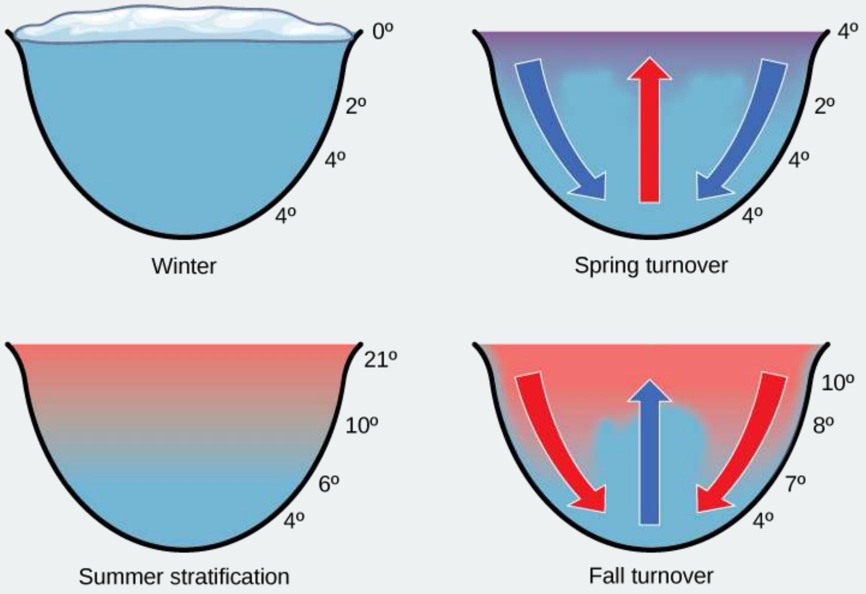


Figure 5.1.5:
The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

Exercise 5.1.1

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

Answer

Tropical lakes don’t freeze, so they don’t undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface (Figure 5.1.5). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

Temperature

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are adapted to surviving in extremely hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine—a coniferous tree—requires heat from fire for its seed cones to open (Figure 5.1.6). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.

Figure 5.1.6: The mature cones of the jack pine (*Pinus banksiana*) open only when exposed to high temperatures, such as during a forest fire. A fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. *Source: USDA.*

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). Net primary productivity is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the aboveground biomass per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Summary

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Endemic species are species that are naturally found only in a specific geographic area. The distribution of living things is influenced by several environmental factors that are, in part, controlled by the latitude or elevation at which an organism is found. Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients and other abiotic factors important in aquatic ecosystems. Energy sources, temperature, water, inorganic nutrients, and soil are factors limiting the distribution of living things in terrestrial systems. Net primary productivity is a measure of the amount of biomass produced by a biome.

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Vermont).

- **44.2: Biogeography** by OpenStax is licensed CC BY 4.0.

5.2: Terrestrial Biomes

The Earth’s biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure 5.2.1).

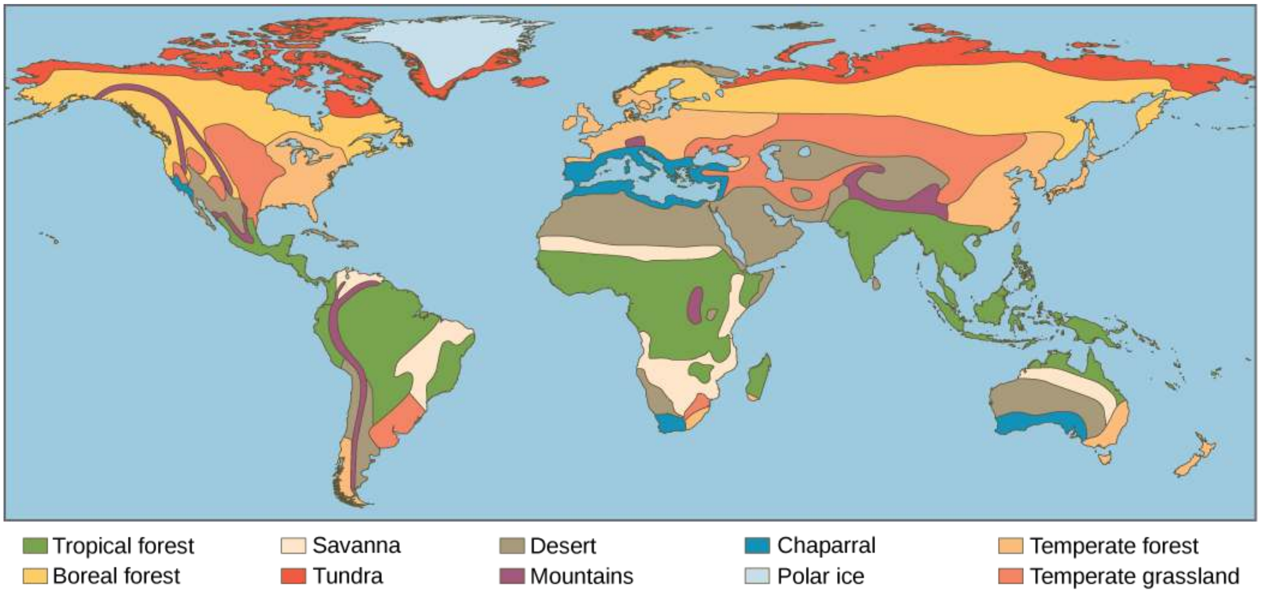


Figure 5.2.1: Each of the world’s major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure 5.2.1). The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are “evergreen” year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities (Figure 5.2.2). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper canopy—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.

Figure 5.2.2: Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. *Source: Roosevelt Garcia.*

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 5.2.3). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 5.2.3). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.

Figure 5.2.3: Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. *Source: Christopher T. Cooper.*

Subtropical Deserts

Subtropical deserts exist between 15 ° and 30 ° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 5.2.4). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The vegetation and low animal diversity of this biome is closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 5.2.4). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.

Figure 5.2.4: To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure 5.2.5). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure 5.2.5, is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.

Figure 5.2.5: The chaparral is dominated by shrubs. *Source: Miguel Vieira.*

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes (Figure 5.2.6). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals Figure 5.2.6. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.

Figure 5.2.6: The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. *Source: Jack Dykinga, USDA Agricultural Research Service.*

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure 5.2.7). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22 °F to 86 °F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure 5.2.7). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.

Figure 5.2.7: Deciduous trees are the dominant plant in the temperate forest. *Source: Oliver Herold.*

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 5.2.8). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 5.2.8). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.

Figure 5.2.8: The boreal forest (taiga) has low lying plants and conifer trees. *Source: L.B. Brubaker.*

Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure 5.2.9). The average winter temperature is -34 °C (-34 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure 5.2.9). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as permafrost. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.

Figure 5.2.9: Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. *Source: USFWS Arctic National Wildlife Refuge.*

Link to Learning

Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Summary

The Earth has terrestrial biomes and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of available water.

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Vermont).

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- **44.3: Terrestrial Biomes** by OpenStax is licensed CC BY 4.0.

5.3: Aquatic Biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure $5.3.1$). All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

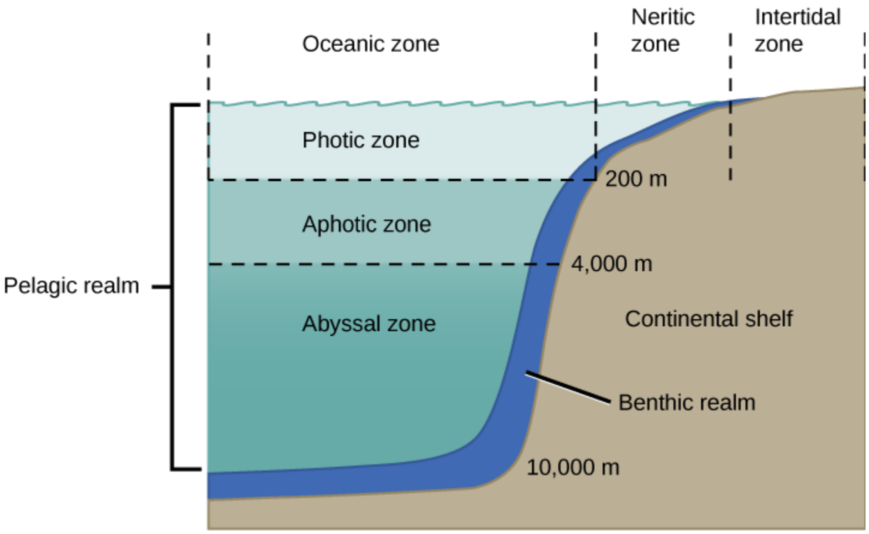


Figure $5.3.1$: The ocean is divided into different zones based on water depth and distance from the shoreline.

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure $5.3.1$). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure $5.3.2$). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.

Figure $5.3.2$: Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. *Source: NOAA.*

The neritic zone (Figure $5.3.1$) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world’s fisheries.

Beyond the neritic zone is the open ocean area known as the oceanic zone (Figure $5.3.1$). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (*phylum Echinodermata*) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf (Figure $5.3.1$). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the abyssal zone, which is at depths of 4000 m or greater. The abyssal zone (Figure $5.3.1$) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30° north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum

Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure $5.3.3$). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the cryptofauna (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, or planktivores. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.

Figure $5.3.3$: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. *Source: Terry Hughes.*

Evolution Connection: Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world’s coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

> Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.
>
> When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.
>
> Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.
>
> Although a rise in global temperatures of 1–2˚C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (*phylum Mollusca*), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as ecosystem services. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. Algal blooms (Figure $5.3.4$) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and stormwater runoff pose significant environmental challenges.

Figure 5.3.4: The uncontrolled growth of algae in this lake has resulted in an algal bloom. *Source: Jeremy Nettleton.*

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as source water. The source water is usually cold, low in nutrients, and clear. The channel (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (*phylum Annelida*) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (*phylum Chordata*) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (*phylum Annelida*) and insects (*phylum Arthropoda*) can be found burrowing into the mud. The higher order predator vertebrates (*phylum Chordata*) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. Emergent vegetation consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water’s surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure 5.3.5). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.

Figure 5.3.5: Located in southern Florida, Everglades National Park is a vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. *Source: NPS.*

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

Contributors and Attributions

This page was modified from the following sources by Kyle Whittinghill (University of Vermont).

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- **44.4: Aquatic Biomes** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

6: The Evolution of Populations and Species

Learning Objectives

- Introduce the concept of evolution at the population level
- Explore mechanisms of evolution with an emphasis on natural selection
- Determine how to quantify evolution using the Hardy-Weinberg equation
- Apply the mechanisms of evolution to the production of new species

Summary

Natural selection is one of the most dominant evolutionary forces. Natural selection acts to promote traits and behaviors that increase an organism’s chances of survival and reproduction, while eliminating those traits and behaviors that are to the organism’s detriment. But natural selection can only, as its name implies, select—it cannot create. The introduction of novel traits and behaviors falls on the shoulders of another evolutionary force—mutation. Mutation and other sources of variation among individuals, as well as the evolutionary forces that act upon them, alter populations and species. This combination of processes has led to the world of life we see today.

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

6.1: Introduction

Figure 6.1.1: Living things may be single-celled or complex, multicellular organisms. They may be plants, animals, fungi, bacteria, or archaea. This diversity results from evolution. (credit "wolf": modification of work by Gary Kramer; credit "coral": modification of work by William Harrigan, NOAA; credit "river": modification of work by Vojtěch Dostál; credit "fish" modification of work by Christian Mehlführer; credit "mushroom": modification of work by Cory Zanker; credit "tree": modification of work by Joseph Kranak; credit "bee": modification of work by Cory Zanker)

All life on Earth is related. Evolutionary theory states that humans, beetles, plants, and bacteria all share a common ancestor, but that millions of years of evolution have shaped each of these organisms into the forms seen today. Scientists consider evolution a key concept to understanding life. Natural selection is one of the most dominant evolutionary forces. Natural selection acts to promote traits and behaviors that increase an organism's chances of survival and reproduction, while eliminating those traits and behaviors that are to the organism's detriment. But natural selection can only, as its name implies, select—it cannot create. The introduction of novel traits and behaviors falls on the shoulders of another evolutionary force—mutation. Mutation and other sources of variation among individuals, as well as the evolutionary forces that act upon them, alter populations and species. This combination of processes has led to the world of life we see today.

- **19.0: Introduction** by OpenStax is licensed CC BY 4.0.

6.2: Population Evolution

Skills to Develop

- Define population genetics and describe how population genetics is used in the study of the evolution of populations
- Define the Hardy-Weinberg principle and discuss its importance

The mechanisms of inheritance, or genetics, were not understood at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to understanding many aspects of evolution. In fact, the predominant (and incorrect) genetic theory of the time, blending inheritance, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of Darwin's book, *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the modern synthesis—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary processes, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this change of a population over time, called microevolution, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called macroevolution.

Everyday Connection: Evolution and Flu Vaccines

Every fall, the media starts reporting on flu vaccinations and potential outbreaks. Scientists, health experts, and institutions determine recommendations for different parts of the population, predict optimal production and inoculation schedules, create vaccines, and set up clinics to provide inoculations. You may think of the annual flu shot as a lot of media hype, an important health protection, or just a briefly uncomfortable prick in your arm. But do you think of it in terms of evolution?

The media hype of annual flu shots is scientifically grounded in our understanding of evolution. Each year, scientists across the globe strive to predict the flu strains that they anticipate being most widespread and harmful in the coming year. This knowledge is based in how flu strains have evolved over time and over the past few flu seasons. Scientists then work to create the most effective vaccine to combat those selected strains. Hundreds of millions of doses are produced in a short period in order to provide vaccinations to key populations at the optimal time.

Because viruses, like the flu, evolve very quickly (especially in evolutionary time), this poses quite a challenge. Viruses mutate and replicate at a fast rate, so the vaccine developed to protect against last year's flu strain may not provide the protection needed against the coming year's strain. Evolution of these viruses means continued adaptions to ensure survival, including adaptations to survive previous vaccines.

Population Genetics

Recall that a gene for a particular character may have several alleles, or variants, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type protein on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists in a field of study known as population genetics began to study how selective forces change a population through changes in allele and genotypic frequencies.

The allele frequency (or gene frequency) is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, the term evolution is defined as a change in the frequency of an allele in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan[1] found a frequency of I^A to be 26.1 percent. The I^B and I^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies added up to 100 percent. A change in this frequency over time would constitute evolution in the population.

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the process of natural selection. Natural selection can alter the population's genetic makeup; for example, if a given allele confers a phenotype that allows an individual to better survive or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus, perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The gene pool is the sum of all the alleles in a population.

Sometimes, allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies. This phenomenon is called genetic drift. Natural selection and genetic drift usually occur simultaneously in populations and are not isolated events. It is hard to determine which process dominates because it is often nearly impossible to determine the cause of change in allele frequencies at each occurrence. An event that initiates an allele frequency change in an isolated part of the population, which is not typical of the original population, is called the founder effect. Natural selection, random drift, and founder effects can lead to significant changes in the genome of a population.

Hardy-Weinberg Principle of Equilibrium

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the genetic makeup of a population. The theory, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population's allele and genotype frequencies are inherently stable— unless some kind of evolutionary force is acting upon the population, neither the allele nor the genotypic frequencies would change. The Hardy-Weinberg principle assumes conditions with no mutations, migration, emigration, or selective pressure for or against genotype, plus an infinite population; while no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes.

Working under this theory, population geneticists represent different alleles as different variables in their mathematical models. The variable p, for example, often represents the frequency of a particular allele, say Y for the trait of yellow in Mendel's peas, while the variable q represents the frequency of y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, $p + q = 1$. In other words, all the p alleles and all the q alleles make up all of the alleles for that locus that are found in the population.

But what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, known as the population's genetic structure, from which scientists can surmise the distribution of phenotypes. If the phenotype is observed, only the genotype of the homozygous recessive alleles can be known; the calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if the allele frequencies (p and q) are known, predicting the frequencies of these genotypes is a simple mathematical calculation to determine the probability of getting these genotypes if two alleles are drawn at random from the gene pool. So in the above scenario, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus producing green peas (Figure $6.2.1$). In other words, the frequency of pp individuals is simply p^2; the frequency of pq individuals is 2pq; and the frequency of qq individuals is q^2. And, again, if p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

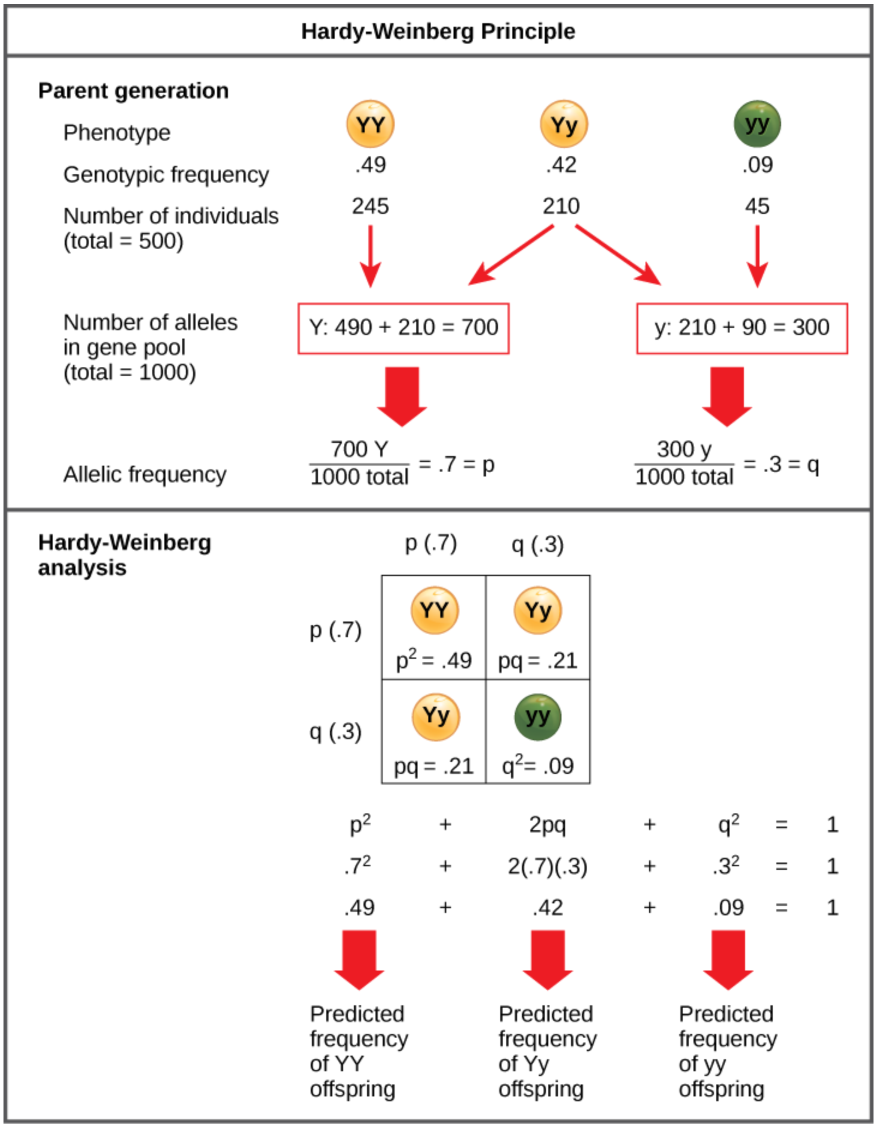


Figure 6.2.1: When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined from the Hardy-Weinberg equation. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.

Exercise 6.2.1

In plants, violet flower color (V) is dominant over white (v). If $p = 0.8$ and $q = 0.2$ in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

Answer

The expected distribution is 320 VV, 160Vv, and 20 vv plants. Plants with VV or Vv genotypes would have violet flowers, and plants with the vv genotype would have white flowers, so a total of 480 plants would be expected to have violet flowers, and 20 plants would have white flowers.

In theory, if a population is at equilibrium—that is, there are no evolutionary forces acting upon it—generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all of the time. Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. But the Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

Summary

The modern synthesis of evolutionary theory grew out of the cohesion of Darwin’s, Wallace’s, and Mendel’s thoughts on evolution and heredity, along with the more modern study of population genetics. It describes the evolution of populations and species, from small-scale changes among individuals to large-scale changes over paleontological time periods. To understand how organisms evolve, scientists can track populations’ allele frequencies over time. If they differ from generation to generation, scientists can conclude that the population is not in Hardy-Weinberg equilibrium, and is thus evolving.

Footnotes

1. 1 Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, “Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population,” *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58.

Glossary

allele frequency	(also, gene frequency) rate at which a specific allele appears within a population
founder effect	event that initiates an allele frequency change in part of the population, which is not typical of the original population
gene pool	all of the alleles carried by all of the individuals in the population
genetic structure	distribution of the different possible genotypes in a population
macroevolution	broader scale evolutionary changes seen over paleontological time
microevolution	changes in a population’s genetic structure
modern synthesis	overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today
population genetics	study of how selective forces change the allele frequencies in a population over time

---

6.3: The Hardy-Weinberg Equilibrium

If two individuals mate that are heterozygous (e.g., **Bb**) for a trait, we find that

- 25% of their offspring are homozygous for the dominant allele (**BB**)
- 50% are heterozygous like their parents (**Bb**)
- 25% are homozygous for the recessive allele (**bb**) and thus, unlike their parents, express the recessive phenotype.

This is what Mendel found when he crossed monohybrids. It occurs because meiosis separates the two alleles of each heterozygous parent so that 50% of the gametes will carry one allele and 50% the other and when the gametes are brought together at random, each **B** (or **b**)-carrying egg will have a 1 in 2 probability of being fertilized by a sperm carrying **B** (or **b**). (Left table)

Results of random union of the two gametes produced by two individuals, each heterozygous for a given trait. As a result of meiosis, half the gametes produced by each parent with carry allele **B**; the other half allele **b**.			Results of random union of the gametes produced by an entire population with a gene pool containing 80% **B** and 20% **b**.		
	0.5 **B**	0.5 **b**		0.8 **B**	0.2 **b**
0.5 **B**	0.25 **BB**	0.25 **Bb**	0.8 **B**	0.64 **BB**	0.16 **Bb**
0.5 **b**	0.25 **Bb**	0.25 **bb**	0.2 **b**	0.16 **Bb**	0.04 **bb**

However, the frequency of two alleles in an **entire population** of organisms is unlikely to be exactly the same. Let us take as a hypothetical case, a population of hamsters in which 80% of all the gametes in the population carry a dominant allele for black coat (**B**) and 20% carry the recessive allele for gray coat (**b**).

Random union of these gametes (right table) will produce a generation:

- 64% homozygous for **BB** (0.8 x 0.8 = 0.64)
- 32% **Bb** heterozygotes (0.8 x 0.2 x 2 = 0.32)
- 4% homozygous (**bb**) for gray coat (0.2 x 0.2 = 0.04)

So 96% of this generation will have black coats; only 4% gray coats.

Will gray coated hamsters eventually disappear? No. Let's see why not.

- All the gametes formed by **BB** hamsters will contain allele **B** as will one-half the gametes formed by heterozygous (**Bb**) hamsters.
- So, 80% (0.64 + .5*0.32) of the pool of gametes formed by this generation with contain **B**.
- All the gametes of the gray (**bb**) hamsters (4%) will contain **b** but one-half of the gametes of the heterozygous hamsters will as well.
- So 20% (0.04 + .5*0.32) of the gametes will contain **b**.

So we have duplicated the initial situation exactly. The proportion of allele **b** in the population has remained the same. The heterozygous hamsters ensure that each generation will contain 4% gray hamsters. Now let us look at an algebraic analysis of the same problem using the expansion of the binomial $(\mathbf{p}+\mathbf{q})^2$.

$$(p+q)^2 = p^2 + 2pq + q^2 \tag{6.3.1}$$

The total number of genes in a population is its *gene pool*.

- Let p represent the frequency of one gene in the pool and q the frequency of its single allele.
- So, $p+q=1$
    - p^2 = the fraction of the population homozygous for p
    - q^2 = the fraction homozygous for q
    - $2pq$ = the fraction of heterozygotes
- In our example, **p** = 0.8, **q** = 0.2, and thus

$$(0.8+0.2)^2 = (0.8)^2 + 2(0.8)(0.2) + (0.2)^2 = 064 + 0.32 + 0.04 \tag{6.3.2}$$

The algebraic method enables us to work backward as well as forward. In fact, because we chose to make **B** fully dominant, the only way that the frequency of **B** and **b** in the gene pool could be known is by determining the frequency of the recessive phenotype (gray) and computing from it the value of **q**.

$q^2 = 0.04$, so $q = 0.2$, the frequency of the **b** allele in the gene pool. Since $p + q = 1$, $p = 0.8$ and allele **B** makes up 80% of the gene pool. Because **B** is completely dominant over **b**, we cannot distinguish the **Bb** hamsters from the **BB** ones by their phenotype. But substituting in the middle term (**2pq**) of the expansion gives the percentage of heterozygous hamsters. $2pq = (2)(0.8)(0.2) = 0.32$

So, recessive genes do not tend to be lost from a population no matter how small their representation.

Hardy-Weinberg law

> So long as certain conditions are met (discussed below), **gene frequencies** and **genotype ratios** in a randomly-breeding population remain constant from generation to generation. This is known as the Hardy-Weinberg law.

The Hardy-Weinberg law is named in honor of the two men who first realized the significance of the binomial expansion to population genetics and hence to evolution. Evolution involves changes in the gene pool. A population in Hardy-Weinberg equilibrium shows no change. What the law tells us is that populations are able to maintain a reservoir of variability so that if future conditions require it, the gene pool can change. If recessive alleles were continually tending to disappear, the population would soon become homozygous. Under Hardy-Weinberg conditions, genes that have no present selective value will nonetheless be retained.

When the Hardy-Weinberg Law Fails

To see what forces lead to evolutionary change, we must examine the circumstances in which the Hardy-Weinberg law may fail to apply. There are five:

1. mutation
2. gene flow
3. genetic drift
4. nonrandom mating
5. natural selection

Mutation

The frequency of gene **B** and its allele **b** will not remain in Hardy-Weinberg equilibrium if the rate of mutation of **B** -> **b** (or vice versa) changes. By itself, this type of mutation probably plays only a minor role in evolution; the rates are simply too low. However, gene (and whole genome) duplication - a form of mutation - probably has played a major role in evolution. In any case, evolution absolutely depends on mutations because this is the only way that new alleles are created. After being shuffled in various combinations with the rest of the gene pool, these provide the raw material on which natural selection can act.

Gene Flow

Many species are made up of local populations whose members tend to breed within the group. Each local population can develop a gene pool distinct from that of other local populations. However, members of one population may breed with occasional immigrants from an adjacent population of the same species. This can introduce new genes or alter existing gene frequencies in the residents.

In many plants and some animals, gene flow can occur not only between subpopulations of the same species but also between different (but still related) species. This is called **hybridization**. If the hybrids later breed with one of the parental types, new genes are passed into the gene pool of that parent population. This process is called **introgression**. It is simply gene flow between species rather than within them.

Comparison of the genomes of contemporary humans with the genome recovered from Neanderthal remains shows that from 1–3% of our genes were acquired by introgression following mating between members of the two populations tens of thousands of years ago.

Whether within a species or between species, gene flow increases the variability of the gene pool.

Genetic Drift

As we have seen, interbreeding often is limited to the members of local populations. If the population is small, Hardy-Weinberg may be violated. Chance alone may eliminate certain members out of proportion to their numbers in the population. In such cases, the frequency of an allele may begin to drift toward higher or lower values. Ultimately, the allele may represent 100% of the gene pool or, just as likely, disappear from it.

Drift produces evolutionary change, but there is no guarantee that the new population will be more fit than the original one. Evolution by drift is aimless, not adaptive.

Nonrandom Mating

One of the cornerstones of the Hardy-Weinberg equilibrium is that mating in the population must be random. If individuals (usually females) are choosy in their selection of mates, the gene frequencies may become altered. Darwin called this **sexual selection**.

Nonrandom mating seems to be quite common. Breeding territories, courtship displays, "pecking orders" can all lead to it. In each case certain individuals do not get to make their proportionate contribution to the next generation.

Assortative mating

Humans seldom mate at random preferring phenotypes like themselves (e.g., size, age, ethnicity). This is called *assortative mating*. Marriage between close relatives is a special case of assortative mating. The closer the kinship, the more alleles shared and the greater the degree of **inbreeding**. Inbreeding can alter the gene pool. This is because it predisposes to **homozygosity**. Potentially harmful recessive alleles — invisible in the parents — become exposed to the forces of natural selection in the children.

Figure 18.6.1: Assortative mating. (Drawing by Koren © 1977 The New Yorker Magazine, Inc.)

It turns out that many species - plants as well as animals - have mechanisms be which they avoid inbreeding. Examples:

- Link to discussion of self-incompatibility in plants.
- Male mice use olfactory cues to discriminate against close relatives when selecting mates. The preference is learned in infancy - an example of imprinting. The distinguishing odors are controlled by the MHC alleles of the mice and are detected by the vomeronasal organ (VNO).

Natural Selection

If individuals having certain genes are better able to produce mature offspring than those without them, the frequency of those genes will increase. This is simply expressing Darwin's natural selection in terms of alterations in the gene pool. (Darwin knew nothing of genes.) Natural selection results from *differential mortality* and/or *differential fecundity*.

Mortality Selection

Certain genotypes are less successful than others in surviving through to the end of their reproductive period. The evolutionary impact of mortality selection can be felt anytime from the formation of a new zygote to the end (if there is one) of the organism's period of fertility. Mortality selection is simply another way of describing Darwin's criteria of fitness: **survival**.

Fecundity Selection

Certain phenotypes (thus genotypes) may make a disproportionate contribution to the gene pool of the next generation by producing a disproportionate number of young. Such fecundity selection is another way of describing another criterion of fitness described by Darwin: **family size**. In each of these examples of natural selection, certain phenotypes are better able than others to contribute their genes to the next generation. Thus, by Darwin's standards, they are more **fit**. The outcome is a gradual change in the gene frequencies in that population.

Calculating the Effect of Natural Selection on Gene Frequencies

The effect of natural selection on gene frequencies can be quantified. Let us assume a population containing

- 36% homozygous dominants (**AA**)
- 48% heterozygotes (**Aa**) and
- 16% homozygous recessives (**aa**)

The gene frequencies in this population are $p = 0.6$ and $q = 0.4$. The heterozygotes are just as successful at reproducing themselves as the homozygous dominants, but the homozygous recessives are only 80% as successful. That is, for every 100 **AA** (or **Aa**) individuals that reproduce successfully only 80 of the **aa** individuals succeed in doing so. The *fitness* (w) of the recessive phenotype is thus 80% or 0.8.

Their relative disadvantage can also be expressed as a *selection coefficient*, s, where

$$s = 1 - w \tag{6.3.3}$$

In this case,

$$s = 1 - 0.8 = 0.2. \tag{6.3.4}$$

The change in frequency of the dominant allele (Δp) after one generation is expressed by the equation

$$\Delta p = \frac{s p_0 q_0^2}{1 - s q_0^2} \tag{6.3.5}$$

where p_0 and q_0 are the initial frequencies of the dominant and recessive alleles respectively. Substituting, we get

$$\Delta p = \frac{(0.2)(0.6)(0.4)^2}{1-(0.2)(0.4)^2} \tag{6.3.6}$$

$$= \frac{0.019}{0.968} \tag{6.3.7}$$

$$= 0.02 \tag{6.3.8}$$

So, in one generation, the frequency of allele **A** rises from its initial value of 0.6 to 0.62 and that of allele **a** declines from 0.4 to 0.38 ($q = 1 - p$).

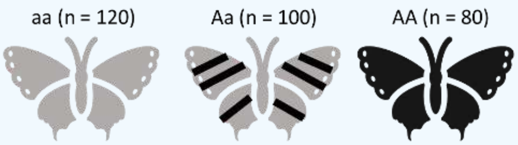
The new equilibrium produces a population of

- 38.4% homozygous dominants (an increase of 2.4%) ($\mathbf{p^2}$ = 0.384)
- 47.1% heterozygotes (a decline of 0.9%)(**2pq** = 0.471) and
- 14.4% homozygous recessives (a decline of 1.6%)($\mathbf{q^2}$ = 0.144)

If the fitness of the homozygous recessives continues unchanged, the calculations can be reiterated for any number of generations. If you do so, you will find that although the frequency of the recessive genotype declines, the **rate** at which **a** is removed from the gene pool declines; that is, the process becomes less efficient at purging allele **a**. This is because when present in the heterozygote, **a** is protected from the effects of selection.

? Hardy-Weinberg Application 6.3.1

A population of 300 butterflies has three phenotypes. One type has gray wings (aa; left), one has wings with gray and black stripes (Aa; middle), and one has black wings (AA; right). The abundance of each phenotype is provided below.



1) What is the proportion of each allele (A and a) in the gene pool?

2) What are the expected frequencies of each genotype in the next generation.

Answer

1) a = (120+120+100)/600 alleles = 0.57 = q

A = (80+80+100)/600 alleles = 0.43 = p

2) AA = 0.19 (p^2), so AA = 0.19 (0.43^2) = 0.03513 or 3.51%

aa = 0.32 (q^2), so aa = 0.32 (0.57^2) = 0.1040 or 10.4%

Aa = 0.49 (2pq), so Aa = 0.49 (2 * 0.43 * 0.57) = 0.24020 or 24.02%

Hardy-Weinberg Application 6.3.2

Based on the Hardy-Weinberg equilibrium, the next generation of a population of randomly-mating laboratory mice is expected to contain 35% white mice (genotype = aa). What are the allele frequencies in this population and what are the expected frequencies of the other two genotypes?

Answer

aa= q^2 = 0.35

so, q = √0.35 = 0.59

p + q = 1

so, p = 0.41

AA = p^2 = (0.41 * 0.41) = 0.17

Aa = 2pq =(2 * 0.41 * 0.59) = 0.48

aa = q^2 =(0.59 * 0.59) = 0.35

6.4: Population Genetics

Skills to Develop

- Describe the different types of variation in a population
- Explain why only heritable variation can be acted upon by natural selection
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence the allele frequencies of a population

Individuals of a population often display different phenotypes, or express different alleles of a particular gene, referred to as polymorphisms. Populations with two or more variations of particular characteristics are called polymorphic. The distribution of phenotypes among individuals, known as the population variation, is influenced by a number of factors, including the population's genetic structure and the environment (Figure 6.4.1). Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.

Figure 6.4.1: The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

Genetic Variance

Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected for, while deleterious alleles may be selected against. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a body builder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

Heritability is the fraction of phenotype variation that can be attributed to genetic differences, or genetic variance, among individuals in a population. The greater the hereditability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

The diversity of alleles and genotypes within a population is called genetic variance. When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves, they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with inbreeding, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease. For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as inbreeding depression.

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and environmental variances.

Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular selection pressure, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is genetic drift (Figure $6.4.2$), which is simply the effect of chance. By chance, some individuals will have more offspring than others—not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

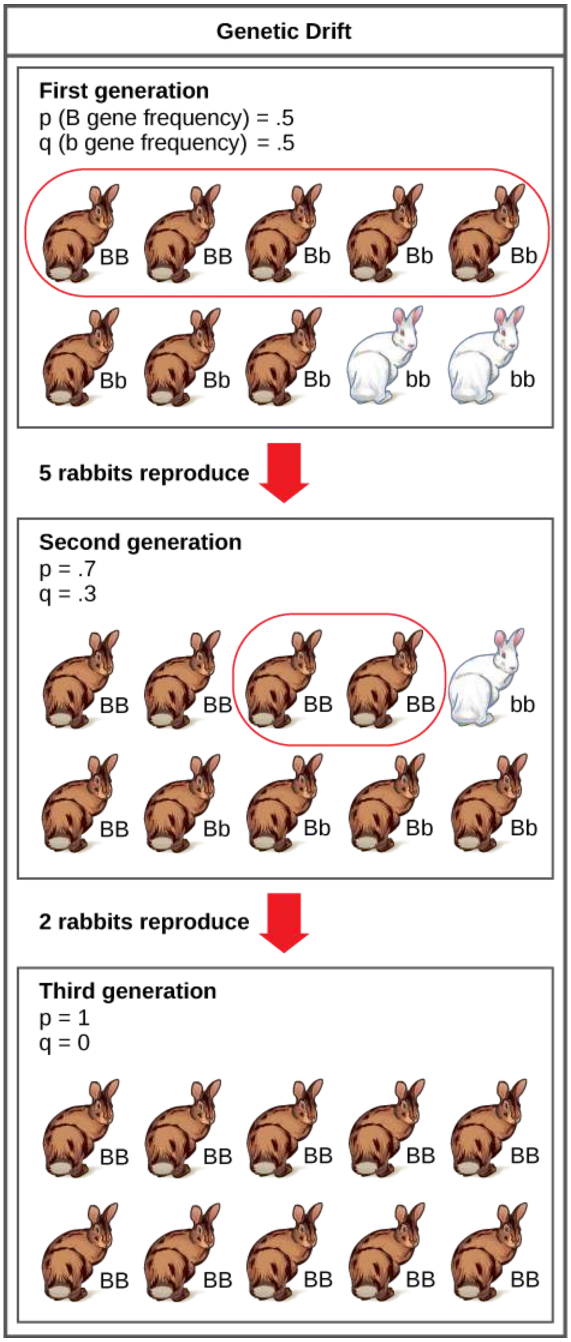


Figure 6.4.2: Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of 0.5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive *b* allele is lost.

Exercise 6.4.1

Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known as the bottleneck effect, it results in a large portion of the genome suddenly being wiped out (Figure $6.4.3$). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

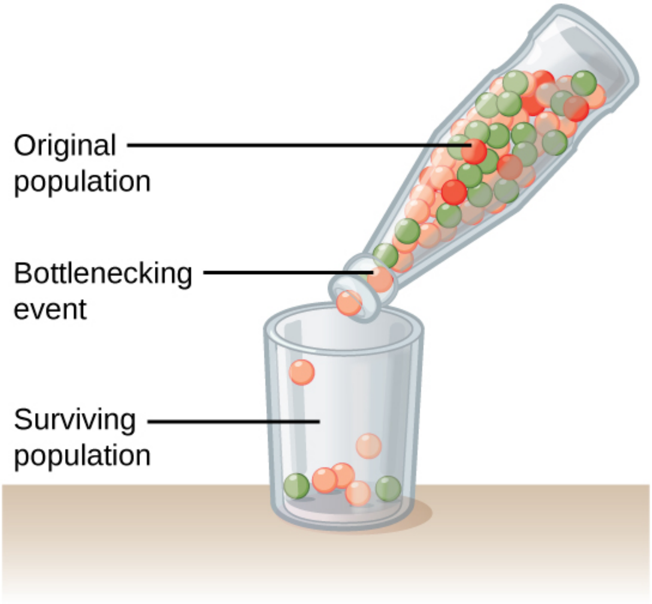


Figure $6.4.3$: A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population, which results in the founder effect. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.[1]

Link to Learning

Watch this short video to learn more about the founder and bottleneck effects.

Scientific Method Connection: Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out the original population using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour 1/3 of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the populations all contain the same number of different colored beads, or do they vary? Remember, these populations all came from the same exact parent population.

Form a conclusion: Most likely, the five resulting populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

Gene Flow

Another important evolutionary force is gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes (Figure 6.4.4). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but it can also introduce new genetic variation to populations in different geological locations and habitats.

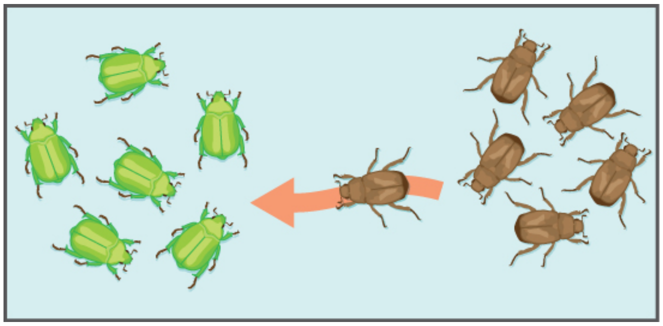


Figure 6.4.4: Gene flow can occur when an individual travels from one geographic location to another.

Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome. Some can have a dramatic effect on a gene and the resulting phenotype.

Nonrandom Mating

If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons nonrandom mating occurs. One reason is simple mate choice; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual become selected for by natural selection. One common form of mate choice, called assortative mating, is an individual's preference to mate with partners who are phenotypically similar to themselves.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment (Figure 6.4.5). A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.

Figure 6.4.5: The sex of the American alligator (*Alligator mississippiensis*) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C produce males. (credit: Steve Hillebrand, USFWS)

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such geographical variation is seen between most populations and can be significant. One type of geographic variation, called a cline, can be seen as populations of a given species vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

Summary

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can be passed to its offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the germ line have more offspring than others. When individuals leave or join the population, allele frequencies can change as a result of gene flow. Mutations to an individual's DNA may introduce new variation into a population. Allele frequencies can also be altered when individuals do not randomly mate with others in the group.

Footnotes

1. 1 A. J. Tipping et al., “Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa,” *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

Glossary

assortative mating	when individuals tend to mate with those who are phenotypically similar to themselves
bottleneck effect	magnification of genetic drift as a result of natural events or catastrophes
cline	gradual geographic variation across an ecological gradient
gene flow	flow of alleles in and out of a population due to the migration of individuals or gametes
genetic drift	effect of chance on a population’s gene pool
genetic variance	diversity of alleles and genotypes in a population
geographical variation	differences in the phenotypic variation between populations that are separated geographically
heritability	fraction of population variation that can be attributed to its genetic variance
inbreeding	mating of closely related individuals
inbreeding depression	increase in abnormalities and disease in inbreeding populations
nonrandom mating	changes in a population’s gene pool due to mate choice or other forces that cause individuals to mate with certain phenotypes more than others
population variation	distribution of phenotypes in a population
selective pressure	environmental factor that causes one phenotype to be better than another

---

6.5: Formation of New Species

Skills to Develop

- Define species and describe how species are identified as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation

Although all life on earth shares various genetic similarities, only certain organisms combine genetic information by sexual reproduction and have offspring that can then successfully reproduce. Scientists call such organisms members of the same biological species.

Species and the Ability to Reproduce

A species is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People’s DNA is likely to be more like their father or mother’s DNA than their cousin or grandparent’s DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

Species’ appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce (Figure 6.5.1).

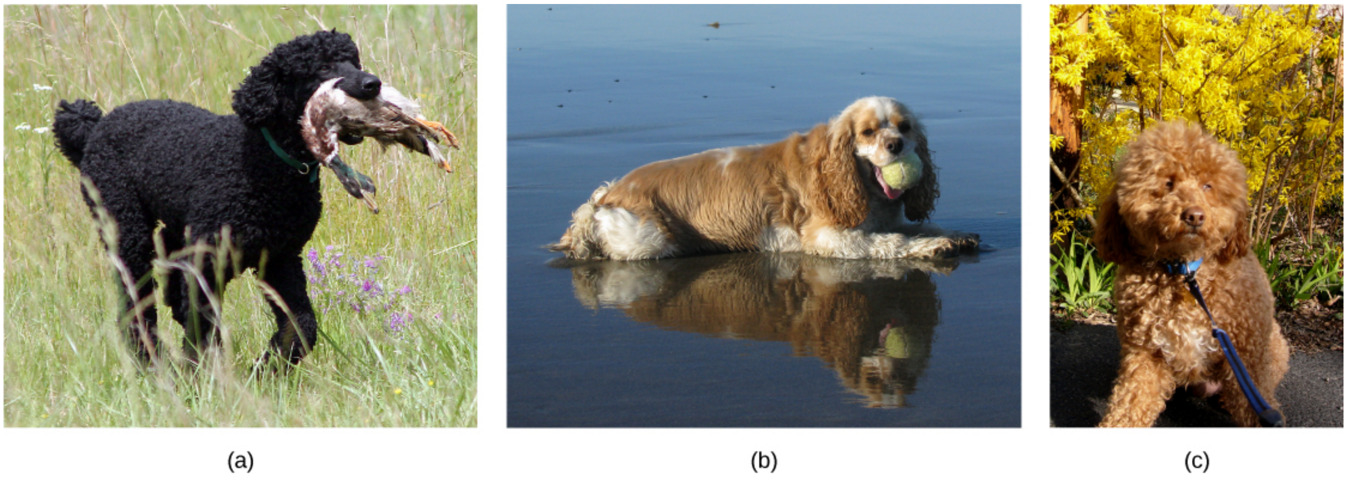


Figure 6.5.1: The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin).

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group (Figure 6.5.2). If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a hybrid (a cross between two species), would probably be infertile —unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.

Figure 6.5.2: The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service).

Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for speciation: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (Figure 6.5.3a). Compare this illustration to the diagram of elephant evolution (Figure 6.5.3b), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.

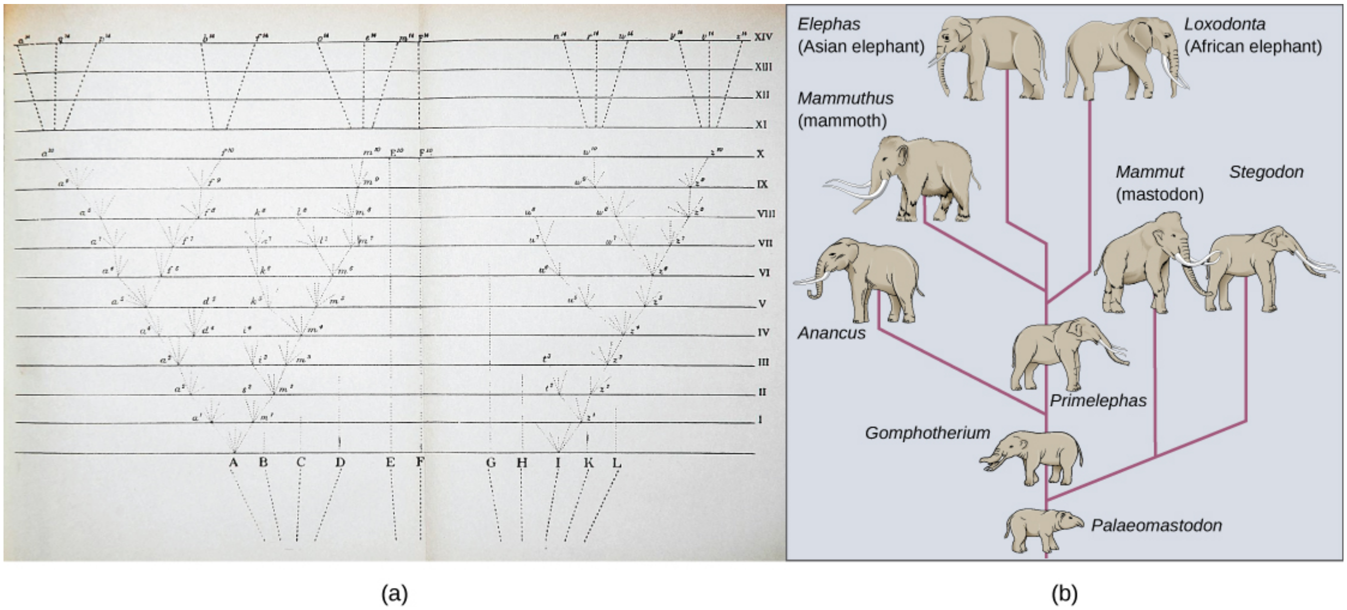


Figure 6.5.3: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must be formed from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. Allopatric speciation (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and multiple events can be conceptualized as single splits occurring close in time.

Allopatric Speciation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. Dispersal is when a few members of a species move to a new geographical area, and vicariance is when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative: the Mexican spotted owl, which lives in the south (Figure 6.5.4).

Figure 6.5.4: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke).

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south; the types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called adaptive radiation because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the six shown in Figure 6.5.5.

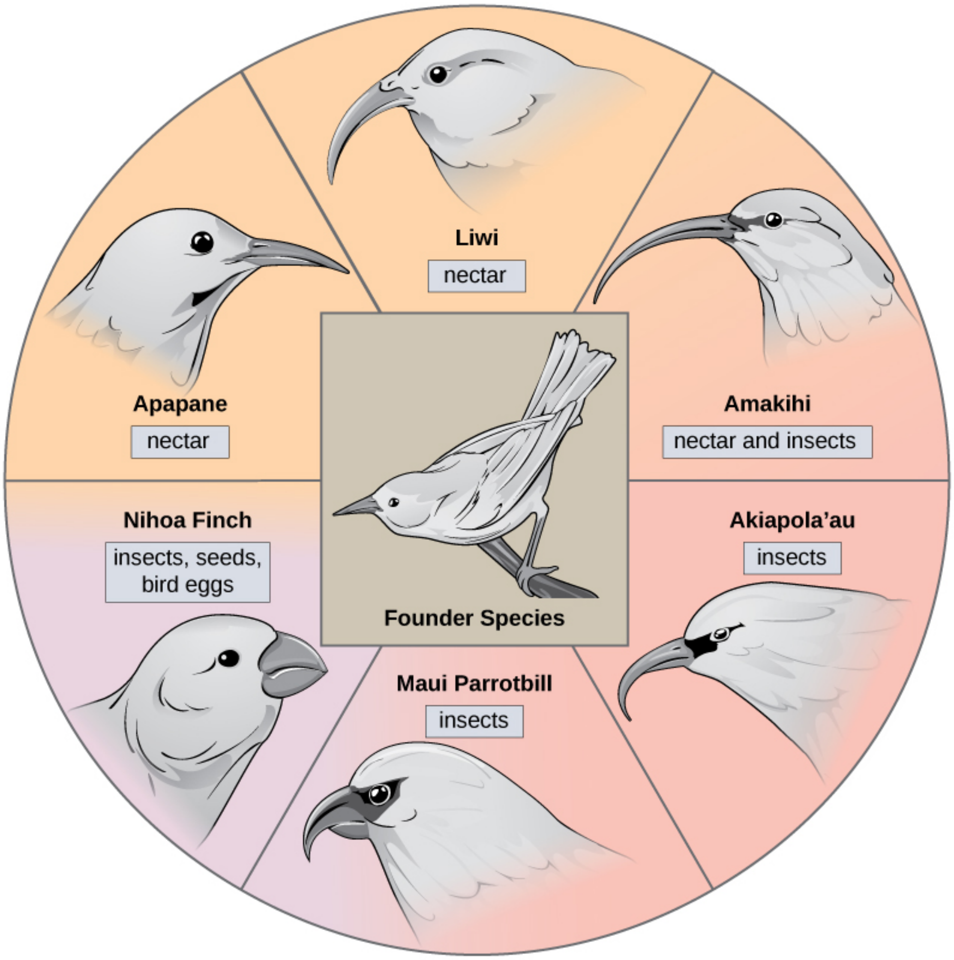


Figure 6.5.5: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 6.5.5. Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

Link to Learning

Click through this interactive site to see how island birds evolved in evolutionary increments from 5 million years ago to today.

Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called *sympatric speciation*; the prefix “sym” means same, so “sympatric” means “same homeland” in contrast to “allopatric” meaning “other homeland.” A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called **aneuploidy** (Figure 6.5.6).

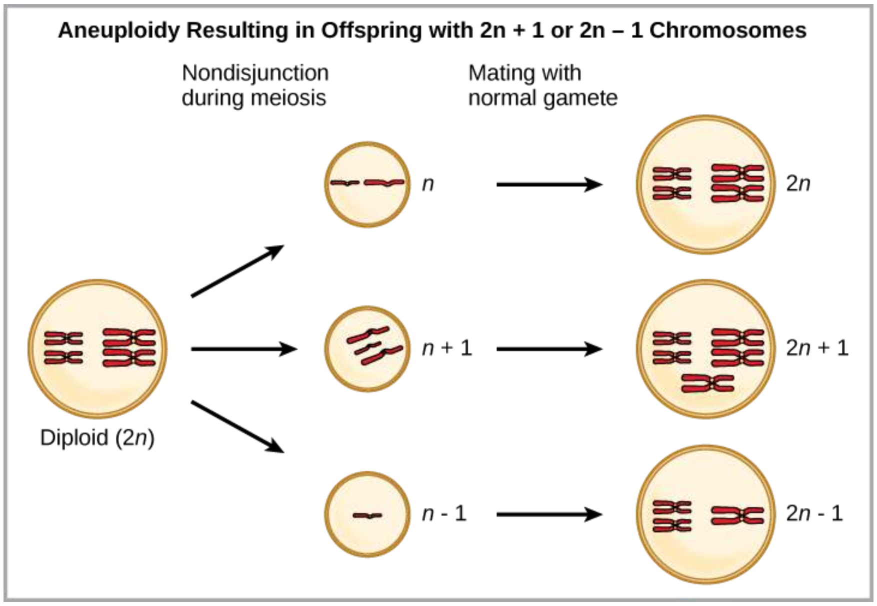


Figure 6.5.6: Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n-1 chromosomes.

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy (Figure 6.5.7). The prefix “auto-” means “self,” so the term means multiple chromosomes from one’s own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

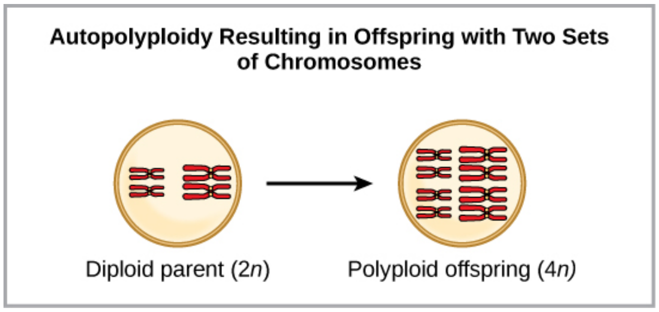


Figure 6.5.7: Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix “allo-” means “other” (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. Figure $6.5.8$ illustrates one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

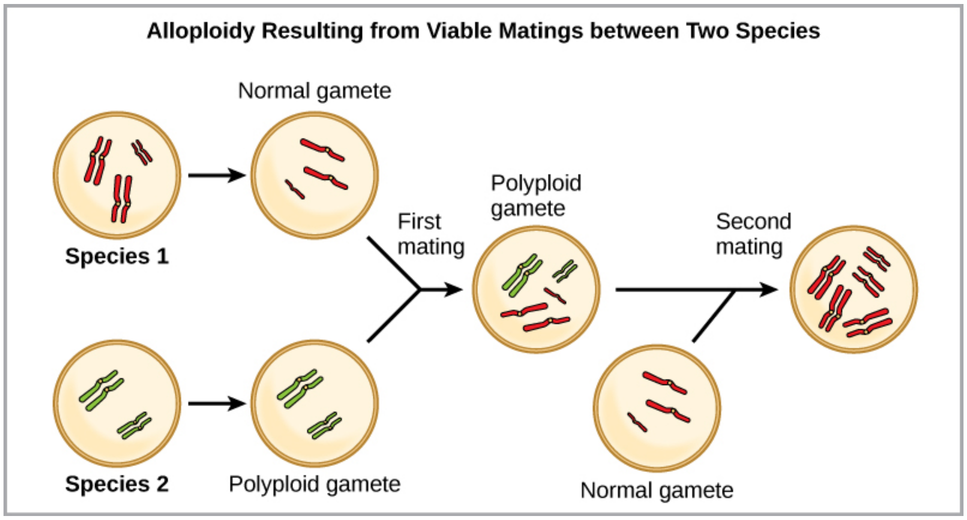


Figure $6.5.8$: Allopolyploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring. Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together, mating would be less likely, but if mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the reproductive isolation, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A postzygotic barrier occurs after zygote formation; this includes organisms that don’t survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called temporal isolation, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May (Figure $6.5.9$).

Figure 6.5.9: These two related frog species exhibit temporal reproductive isolation. (a) *Rana aurora* breeds earlier in the year than (b) *Rana boylii* (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi).

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the other populations of the same species. This situation is called habitat isolation. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups (Figure 6.5.10).

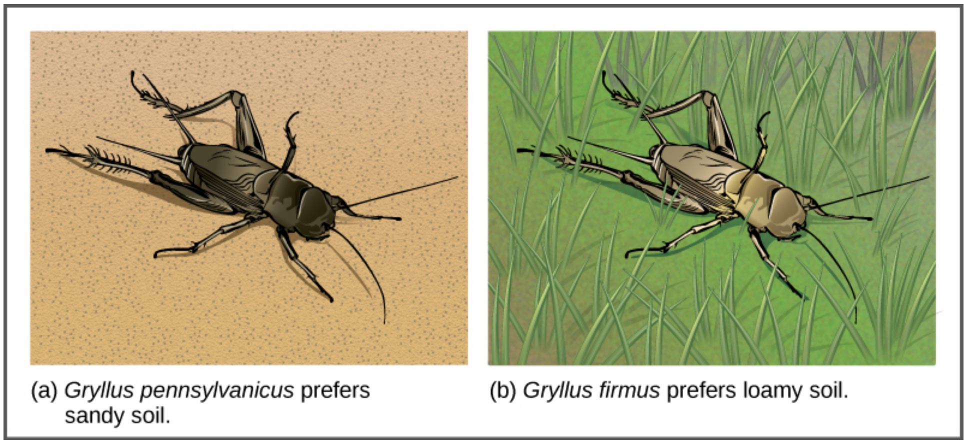

(a) *Gryllus pennsylvanicus* prefers sandy soil.
(b) *Gryllus firmus* prefers loamy soil.

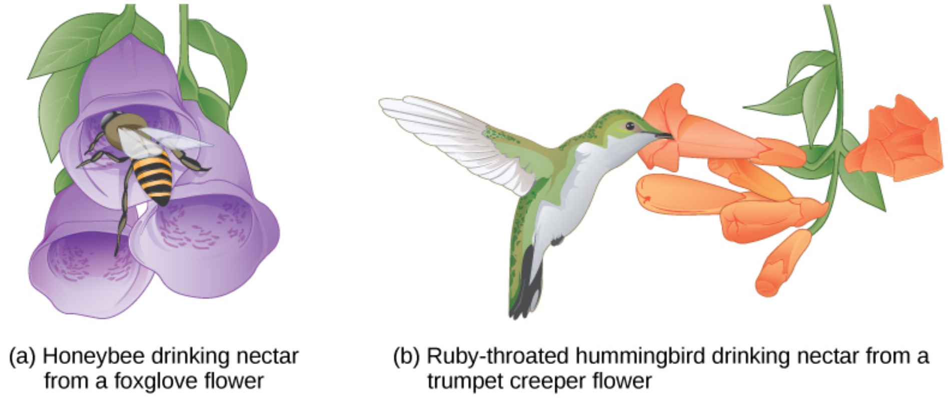
Figure 6.5.10: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species of fireflies display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place; this is called a gametic barrier. Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together (Figure 6.5.11).

Figure 6.5.11: The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from being cross-pollinated with a different species (Figure $6.5.12$).


(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

Figure $6.5.12$: Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. This is called hybrid inviability because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Habitat Influence on Speciation

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a species of fish that lives in a lake. As the population grows, competition for food also grows. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure $6.5.13$ shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.

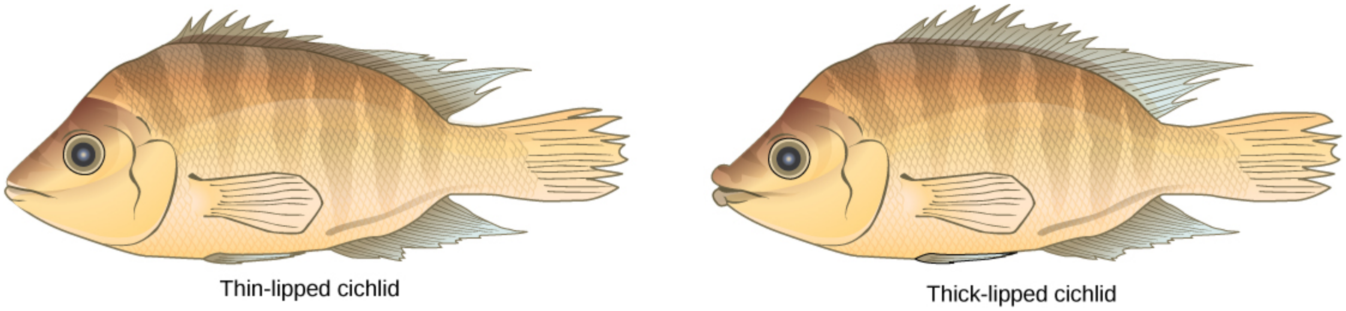


Figure $6.5.13$: Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways isolate a population reproductively in some form. Mechanisms of reproductive isolation act as barriers between closely related species, enabling them to diverge and exist as genetically independent species. Prezygotic barriers block reproduction prior to formation of a zygote, whereas postzygotic barriers block reproduction after fertilization occurs. For a new species to develop, something must cause a breach in the reproductive barriers. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes (polyploidy). Autopolyploidy occurs within a single species, whereas allopolyploidy occurs between closely related species.

Glossary

adaptive radiation
speciation when one species radiates out to form several other species

allopatric speciation
speciation that occurs via geographic separation

allopolyploid
polyploidy formed between two related, but separate species

aneuploidy
condition of a cell having an extra chromosome or missing a chromosome for its species

autopolyploid
polyploidy formed within a single species

behavioral isolation
type of reproductive isolation that occurs when a specific behavior or lack of one prevents reproduction from taking place

dispersal
allopatric speciation that occurs when a few members of a species move to a new geographical area

gametic barrier
prezygotic barrier occurring when closely related individuals of different species mate, but differences in their gamete cells (eggs and sperm) prevent fertilization from taking place

habitat isolation
reproductive isolation resulting when populations of a species move or are moved to a new habitat, taking up residence in a place that no longer overlaps with the other populations of the same species

hybrid
offspring of two closely related individuals, not of the same species

postzygotic barrier
reproductive isolation mechanism that occurs after zygote formation

prezygotic barrier
reproductive isolation mechanism that occurs before zygote formation

reproductive isolation
situation that occurs when a species is reproductively independent from other species; this may be brought about by behavior, location, or reproductive barriers

speciation	formation of a new species
species	group of populations that interbreed and produce fertile offspring
sympatric speciation	speciation that occurs in the same geographic space
temporal isolation	differences in breeding schedules that can act as a form of prezygotic barrier leading to reproductive isolation
vicariance	allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

6.6: Reconnection and Rates of Speciation

Skills to Develop

- Describe pathways of species evolution in hybrid zones
- Explain the two major theories on rates of speciation

Speciation occurs over a span of evolutionary time, so when a new species arises, there is a transition period during which the closely related species continue to interact.

Reconnection

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual who they are capable of breeding with. An area where two closely related species continue to interact and reproduce, forming hybrids, is called a hybrid zone. Over time, the hybrid zone may change depending on the fitness of the hybrids and the reproductive barriers (Figure 6.6.1). If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species continue to diverge until they can no longer mate and produce viable offspring. If reproductive barriers weaken, fusion occurs and the two species become one. Barriers remain the same if hybrids are fit and reproductive: stability may occur and hybridization continues.

Art Connection

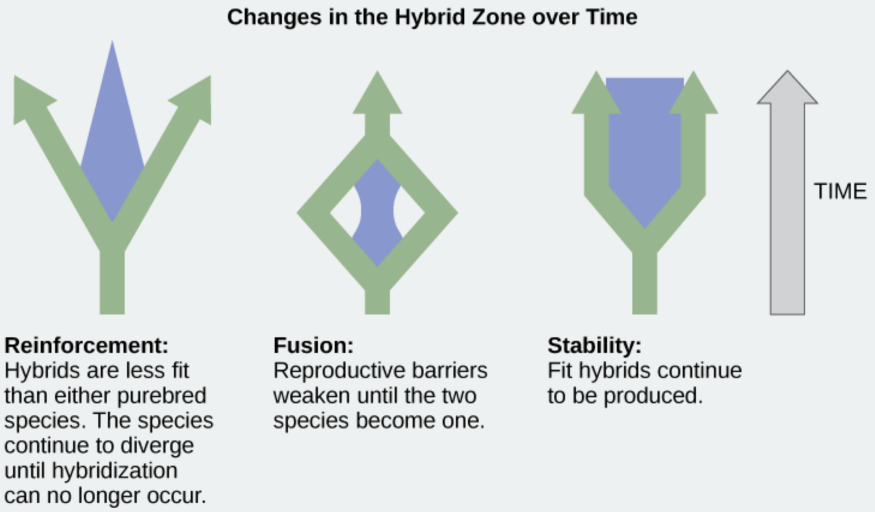


Figure 6.6.1: After speciation has occurred, the two separate but closely related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

If two species eat a different diet but one of the food sources is eliminated and both species are forced to eat the same foods, what change in the hybrid zone is most likely to occur?

Hybrids can be either less fit than the parents, more fit, or about the same. Usually hybrids tend to be less fit; therefore, such reproduction diminishes over time, nudging the two species to diverge further in a process called reinforcement. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are as fit or more fit than the parents, the two species may fuse back into one species ([link]). Scientists have also observed that sometimes two species will remain separate but also continue to interact to produce some hybrid individuals; this is classified as stability because no real net change is taking place.

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: gradual speciation model and punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In the punctuated equilibrium model, a new species undergoes changes quickly from the parent species, and then remains largely unchanged for long periods of time afterward (Figure 6.6.2). This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

Art Connection

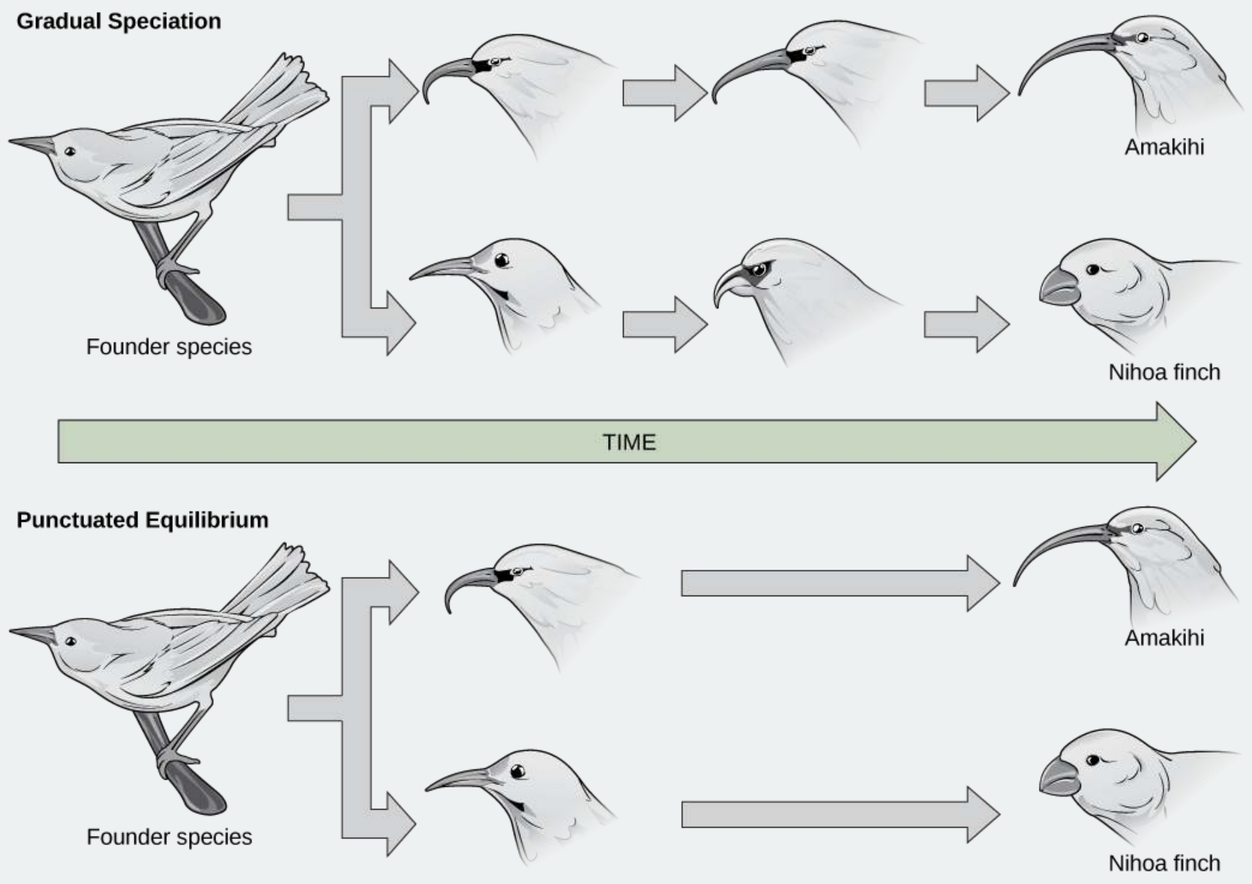


Figure 6.6.2: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

Which of the following statements is false?

A. Punctuated equilibrium is most likely to occur in a small population that experiences a rapid change in its environment.
B. Punctuated equilibrium is most likely to occur in a large population that lives in a stable climate.
C. Gradual speciation is most likely to occur in species that live in a stable climate.
D. Gradual speciation and punctuated equilibrium both result in the divergence of species.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Layers of their fossils would appear similar for a long time. When a change in the environment takes place—such as a drop in the water level—a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

Link to Learning

Visit this website to continue the speciation story of the snails.

Summary

Speciation is not a precise division: overlap between closely related species can occur in areas called hybrid zones. Organisms reproduce with other similar organisms. The fitness of these hybrid offspring can affect the evolutionary path of the two species. Scientists propose two models for the rate of speciation: one model illustrates how a species can change slowly over time; the other model demonstrates how change can occur quickly from a parent generation to a new species. Both models continue to follow the patterns of natural selection.

Glossary

gradual speciation model

model that shows how species diverge gradually over time in small steps

hybrid zone

area where two closely related species continue to interact and reproduce, forming hybrids

punctuated equilibrium

model for rapid speciation that can occur when an event causes a small portion of a population to be cut off from the rest of the population

reinforcement

continued speciation divergence between two related species due to low fitness of hybrids between them

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

CHAPTER OVERVIEW

7: Phylogenies and the History of Life

Learning Objectives

- Introduce classification systems
- Describe how systematics and taxonomy relate to phylogeny
- Discuss the components, purpose, and important concepts regarding phylogenetic trees
- Discuss the purpose of cladistics
- Discuss horizontal gene transfer and going beyond the phyologenetic tree

Summary

By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swam, flown, and walked on this planet.

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

7.1: Introduction

This bee and *Echinacea* flower could not look more different, yet they are related, as are all living organisms on Earth. By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swam, flown, and walked on this planet.

Figure 7.1.1: The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

7.2: Organizing Life on Earth

In scientific terms, the evolutionary history and relationship of an organism or group of organisms is called phylogeny. Phylogeny describes the relationships of an organism, such as from which organisms it is thought to have evolved, to which species it is most closely related, and so forth. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

Phylogenetic Trees

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure $7.2.1$).

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains— Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don’t show a common ancestor but do show relationships among species.

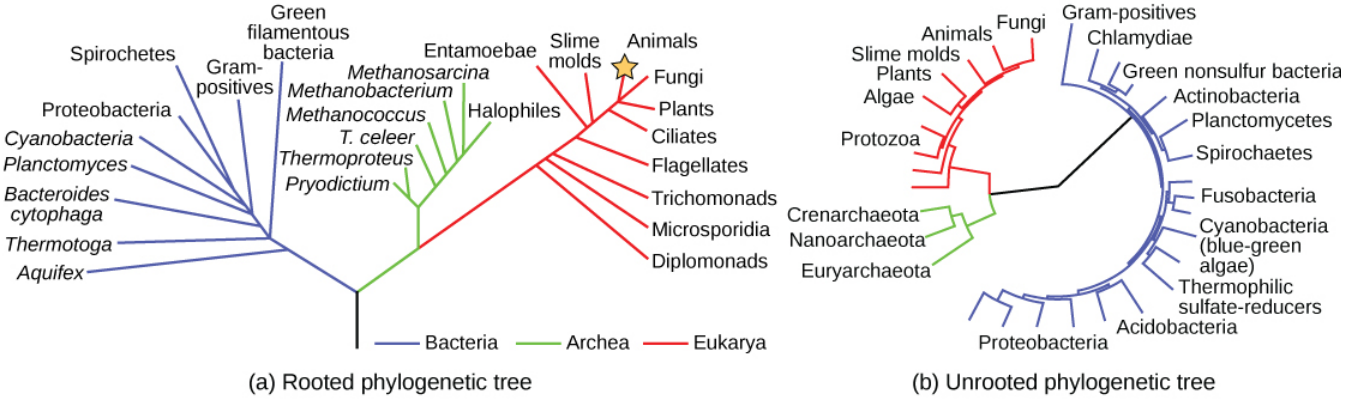


Figure $7.2.1$: Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not (credit a: modification of work by Eric Gaba).

In a rooted tree, the branching indicates evolutionary relationships (Figure $7.2.2$). The point where a split occurs, called a branch point, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called basal taxon. When two lineages stem from the same branch point, they are called sister taxa. A branch with more than two lineages is called a polytomy and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

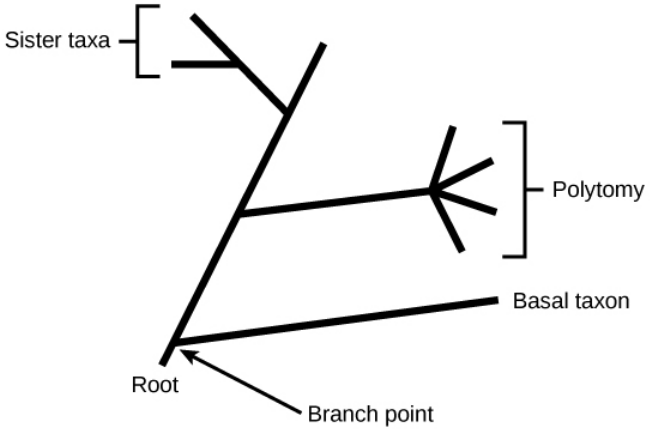


Figure 7.2.2: The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

The diagrams above can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover that species' ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called systematics. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

Limitations of Phylogenetic Trees

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree in Figure 7.2.3 shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.

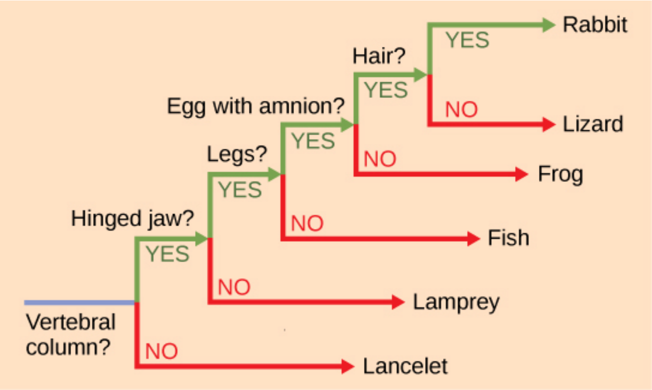


Figure 7.2.3: This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in Figure $7.2.3$, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using Figure $7.2.3$, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure $7.2.3$, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.

Link to Learning

Head to this website to see interactive exercises that allow you to explore the evolutionary relationships among species.

The Levels of Classification

Taxonomy (which literally means “arrangement law”) is the science of classifying organisms to construct internationally shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then finally a single product. This organization from larger to smaller, more specific categories is called a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a kingdom. After kingdoms, the subsequent categories of increasing specificity are: phylum, class, order, family, genus, and species (Figure $7.2.4$).

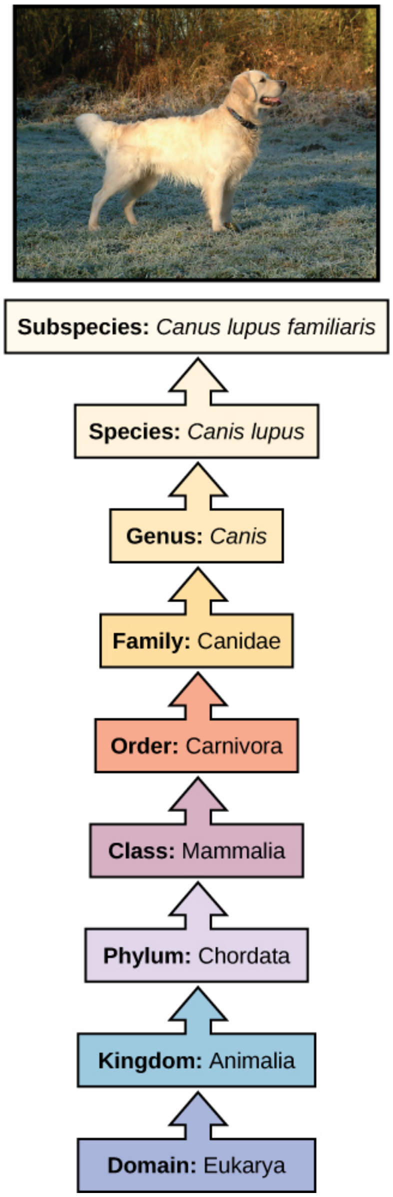


Figure 7.2.4: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo (credit “dog”: modification of work by Janneke Vreugdenhil).

The kingdom Animalia stems from the Eukarya domain. For the common dog, the classification levels would be as shown in Figure 7.2.4. Therefore, the full name of an organism technically has eight terms. For the dog, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called binomial nomenclature. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a taxon. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the “*familiaris*” in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

Figure $7.2.5$ shows how the levels move toward specificity with other organisms. Notice how the dog shares a domain with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists classified organisms using characteristics, but as DNA technology developed, more precise phylogenies have been determined.

Art Connection

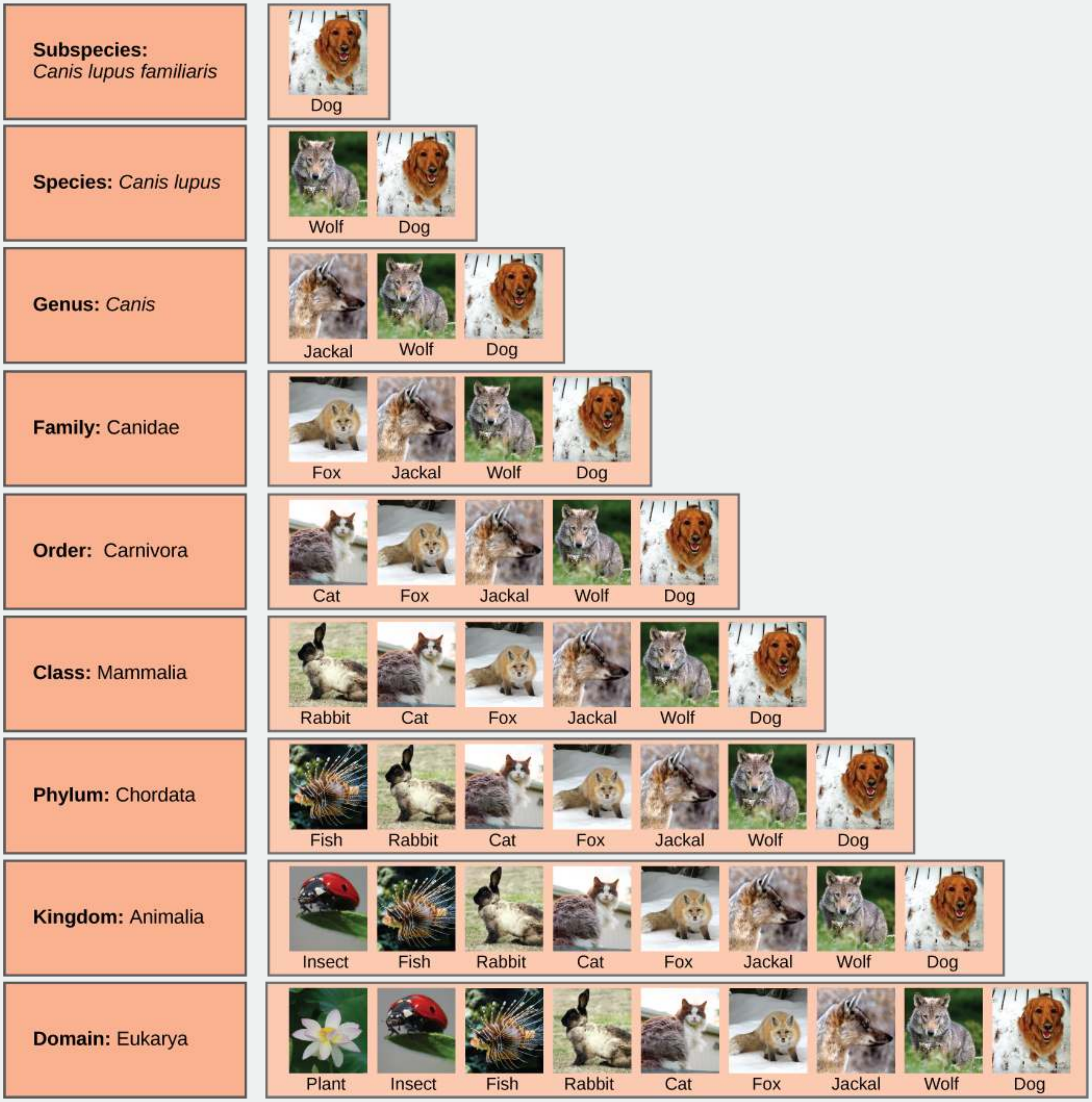


Figure $7.2.5$: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of "Lotus Flower Losing Petals" by berduchwal, licensed under CC BY 2.0; credit “insect”: modification of "Ladybird" by Jon Sullivan, available in the public domain; credit “fish”: modification of "Rotfeuerfisch" by Christian Mehlführer, licensed under CC BY 2.5; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of "Neighborhood Cat" by Jonathan Lidbeck, licensed under CC BY 2.0; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf”: modification of "Wolf" by Robert Dewar, licensed under CC BY 2.0; credit “dog”: modification of "Golden" by digital_image_fan, available under CC BY 2.0)

Exercise 7.2.1

At what levels are cats and dogs considered to be part of the same group?

Answer

Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative of the whale.

Summary

Scientists continually gain new information that helps understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

Glossary

basal taxon

branch on a phylogenetic tree that has not diverged significantly from the root ancestor

binomial nomenclature

system of two-part scientific names for an organism, which includes genus and species names

branch point

node on a phylogenetic tree where a single lineage splits into distinct new ones

class

division of phylum in the taxonomic classification system

family

division of order in the taxonomic classification system

genus

division of family in the taxonomic classification system; the first part of the binomial scientific name

kingdom

division of domain in the taxonomic classification system

order

division of class in the taxonomic classification system

phylogenetic tree

diagram used to reflect the evolutionary relationships among organisms or groups of organisms

phylogeny

evolutionary history and relationship of an organism or group of organisms

phylum

(plural: phyla) division of kingdom in the taxonomic classification system

polytomy

branch on a phylogenetic tree with more than two groups or taxa

rooted

single ancestral lineage on a phylogenetic tree to which all organisms represented in the diagram relate

sister taxa

two lineages that diverged from the same branch point

systematics

field of organizing and classifying organisms based on evolutionary relationships

taxon

(plural: taxa) single level in the taxonomic classification system

taxonomy

science of classifying organisms

7.3: Determining Evolutionary Relationships

Scientists must collect accurate information that allows them to make evolutionary connections among organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures (Figure $7.3.1$).

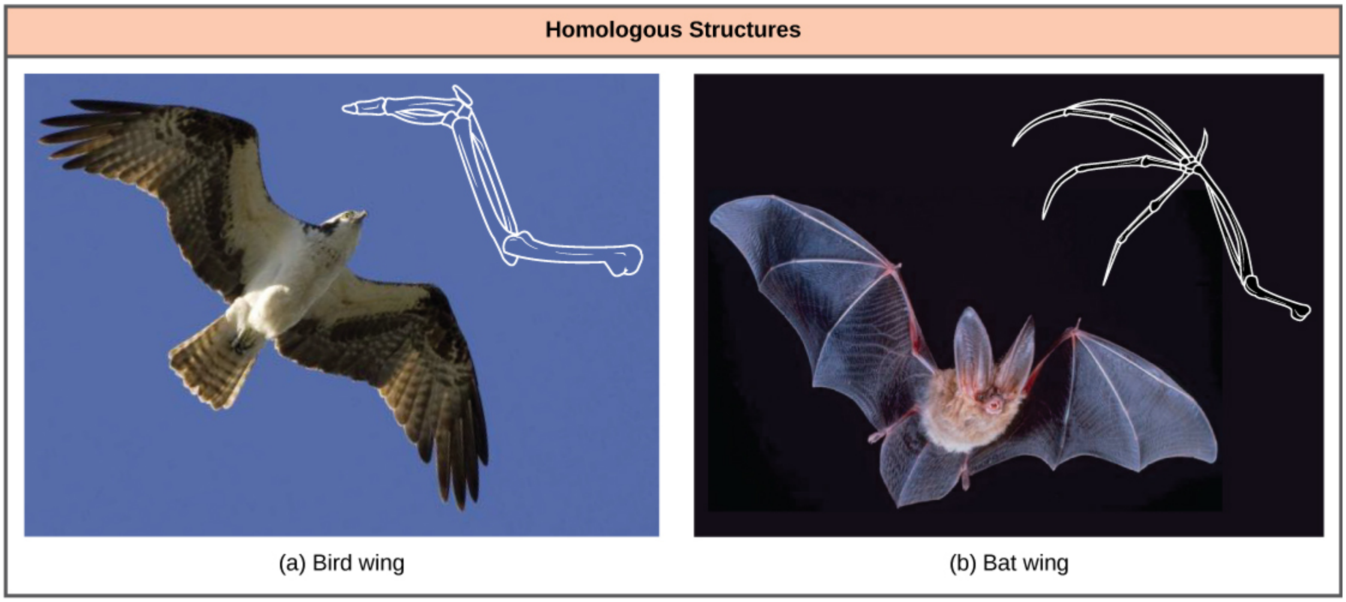


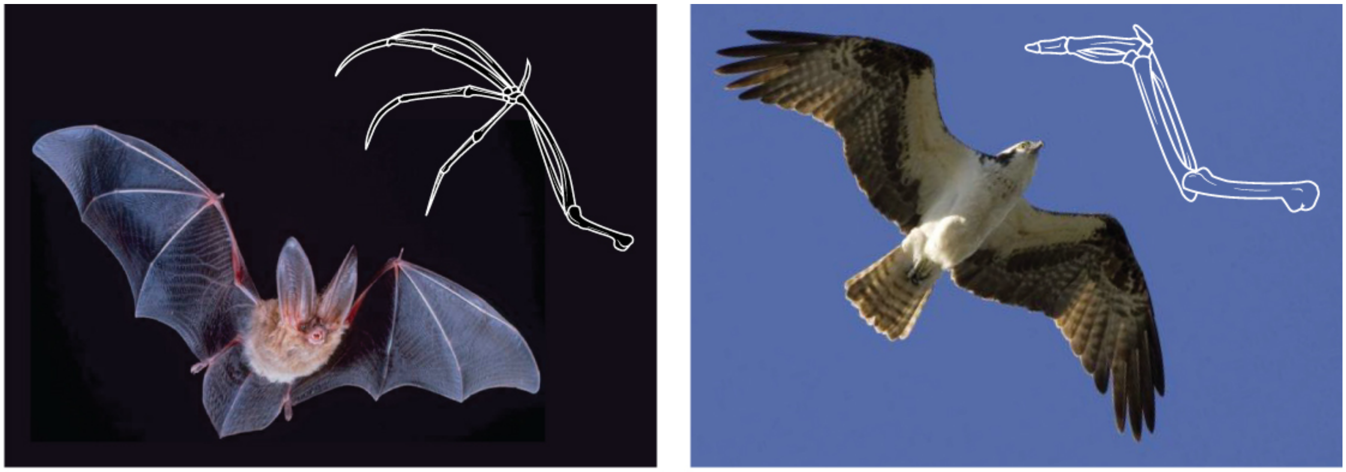
Figure $7.3.1$: Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM).

Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures (Figure $7.3.2$).

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous but not homologous. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.



(a) Bat wing

(b) Bird wing

(c) Insect wing

Figure 7.3.2: The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan).

Molecular Comparisons

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For both of these situations, computer technologies have been developed to help identify the actual relationships, and, ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

Evolution Connection: Why Does Phylogeny Matter?

Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the relatives of that plant for other useful drugs.

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment (Figure $7.3.3$). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Figure $7.3.3$: *Dalbergia sissoo* is in the Fabaceae, or legume family. Scientists found that *D. sissoo* shares a DNA marker with species within the Fabaceae family that have antifungal properties. Subsequently, *D. sissoo* was shown to have fungicidal activity, supporting the idea that DNA markers can be used to screen for plants with potential medicinal properties.

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called cladistics. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, in Figure $7.3.4$, all of the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a monophyletic group. Clades must include all of the descendants from a branch point.

Art Connection

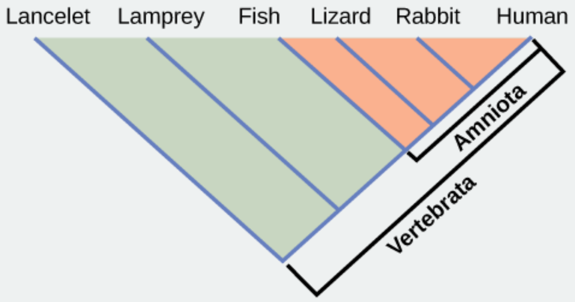


Figure 7.3.4: Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Exercise 7.3.1

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

Answer

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair because the Amniota clade is larger than the clade that encompasses animals with hair.

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. Figure 7.3.5 shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

Art Connection

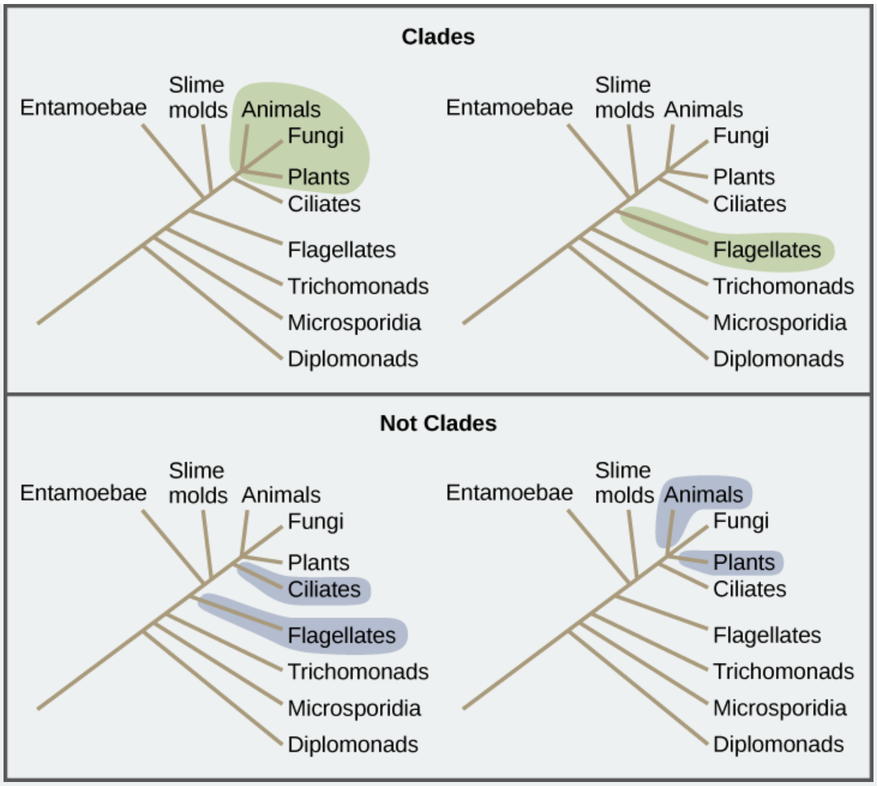


Figure 7.3.5: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

Exercise 7.3.2

What is the largest clade in this diagram?

Answer

The largest clade encompasses the entire tree.

Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats over and over as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a shared ancestral character because all of the organisms in the taxon or clade have that trait. The vertebrate in Figure 7.3.4 is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in Figure 7.3.4 have this trait, and to those that do, it is called a shared derived character because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to Figure 7.3.5, note that the amniotic egg is a shared ancestral character for the Amniota clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.

Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to go hiking, based on the principle of maximum parsimony, one could predict that most of the people would hike on established trails rather than forge new ones.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

Summary

To build phylogenetic trees, scientists must collect accurate information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). Newer technologies can be used to help distinguish homologies from analogies. After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the concept of maximum parsimony, which states that the order of events probably occurred in the most obvious and simple way with the least amount of steps. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Glossary

analogy

(also, homoplasy) characteristic that is similar between organisms by convergent evolution, not due to the same evolutionary path

cladistics

system used to organize homologous traits to describe phylogenies

maximum parsimony

applying the simplest, most obvious way with the least number of steps

molecular systematics

technique using molecular evidence to identify phylogenetic relationships

monophyletic group

(also, clade) organisms that share a single ancestor

shared ancestral character

describes a characteristic on a phylogenetic tree that is shared by all organisms on the tree

shared derived character

describes a characteristic on a phylogenetic tree that is shared only by a certain clade of organisms

---

7.4: Perspectives on the Phylogenetic Tree

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists' ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community.

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure 7.4.1a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (Figure 7.4.1b). However, evidence from modern DNA sequence analysis and newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.

(a)

(b)

Figure 7.4.1: The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches (credit b: modification of work by "Amada44"/Wikimedia Commons).

Limitations to the Classic Model

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonally. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern-day and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree model. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships.

The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table $7.4.1$).

Table $7.4.1$: Summary of Mechanisms of Prokaryotic and Eukaryotic HGT

	Mechanism	Mode of Transmission	Example
Prokaryotes	transformation	DNA uptake	many prokaryotes
	transduction	bacteriophage (virus)	bacteria
	conjugation	pilus	many prokaryotes
	gene transfer agents	phage-like particles	purple non-sulfur bacteria
Eukaryotes	from food organisms/viral infections	unknown	aphid
	jumping genes	transposons	rice and millet plants
	epiphytes/parasites	unknown	yew tree fungi

HGT in Prokaryotes

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the Endosymbiont Theory, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species.

The fact that genes are transferred among common bacteria is well known to microbiology students. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms:

1. Transformation: naked DNA is taken up by a bacteria
2. Transduction: genes are transferred using a virus
3. Conjugation: the use of a hollow tube called a pilus to transfer genes between organisms

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called gene transfer agents (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as 10^{13} per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

As a consequence of this modern DNA analysis, the idea that eukaryotes evolved directly from Archaea has fallen out of favor. While eukaryotes share many features that are absent in bacteria, such as the TATA box (found in the promoter region of many genes), the discovery that some eukaryotic genes were more homologous with bacterial DNA than Archaea DNA made this idea less tenable. Furthermore, the fusion of genomes from Archaea and Bacteria by endosymbiosis has been proposed as the ultimate event in eukaryotic evolution.

HGT in Eukaryotes

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are but single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species, and it is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves, a clear example of gene transfer.

In animals, a particularly interesting example of HGT occurs within the aphid species (Figure $7.4.2$). Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure $7.4.2$).

Figure $7.4.2$: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones (credit a: modification of "Blood-Red Aphids" by Benny Mazur, licensed under CC BY 2.0; credit b: modification of work by Mick Talbot).

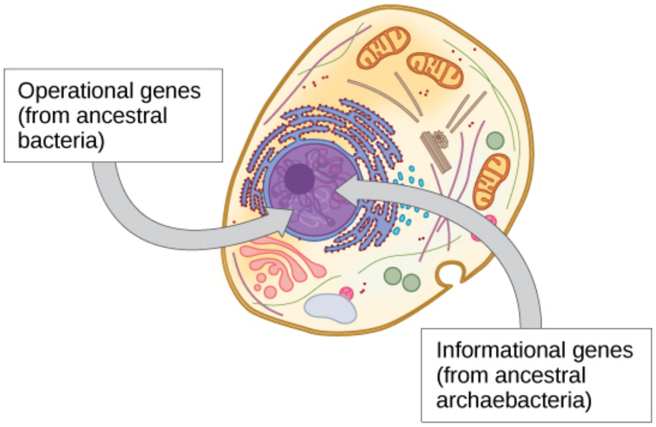
Genome Fusion and the Evolution of Eukaryotes

Scientists believe the ultimate in HGT occurs through genome fusion between different species of prokaryotes when two symbiotic organisms become endosymbiotic. This occurs when one species is taken inside the cytoplasm of another species, which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Interestingly enough, mitochondrial DNA is inherited only from the mother. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure 7.4.3a). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (Figure 7.4.3b) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake’s work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake’s hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.

(a) Genome fusion by endosymbiosis



(b) Endosymbiotic formation of Gram-negative bacteria

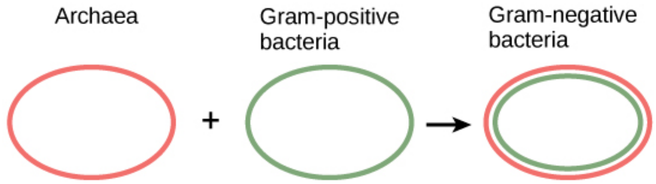


Figure 7.4.3: The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane.

The nucleus-first hypothesis proposes that the nucleus evolved in prokaryotes first (Figure 7.4.4a), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis proposes that mitochondria were first established in a prokaryotic host (Figure 7.4.4b), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (Figure 7.4.4c). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

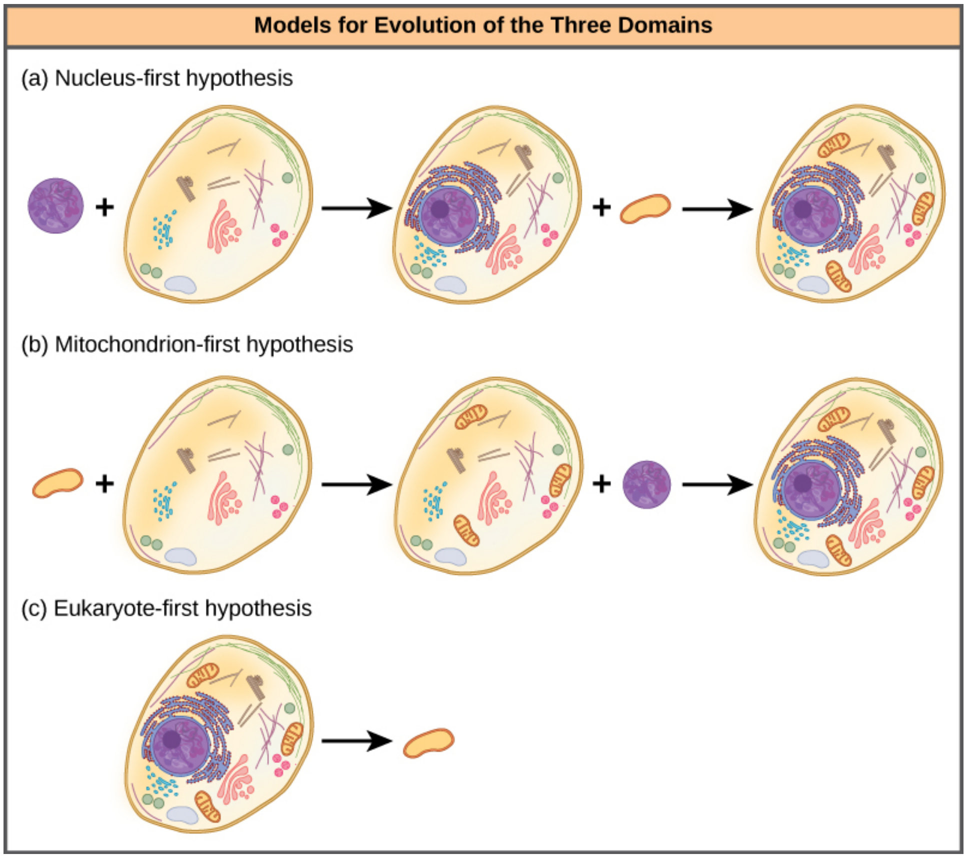
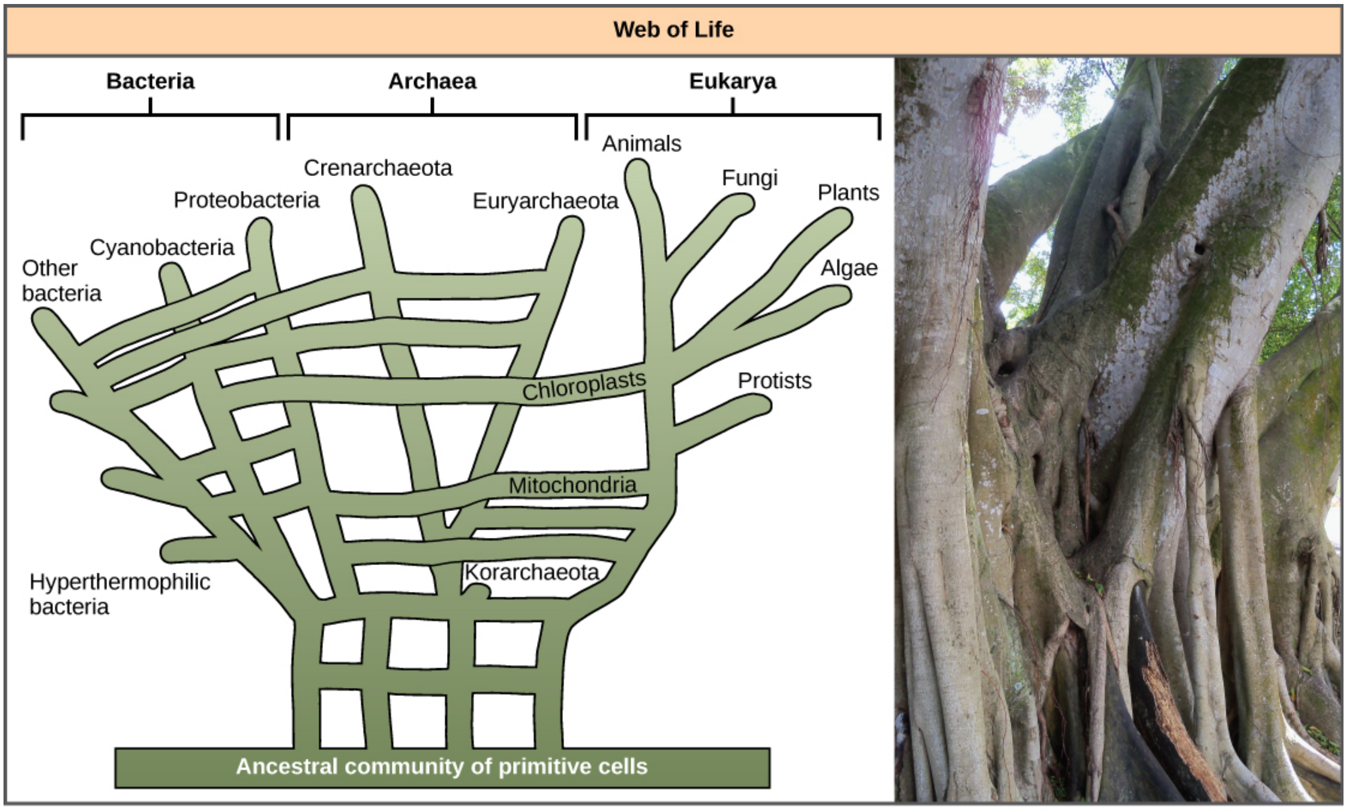


Figure 7.4.4: Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.

Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic “tree of life” model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure 7.4.5a, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the “web of life.” In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure 7.4.5b) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.



(a) (b)

Figure 7.4.5: In the (a) phylogenetic model proposed by W. Ford Doolittle, the “tree of life” arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked *Ficus* than by the single trunk of the oak similar to the tree drawn by Darwin in Figure 7.4.1 (credit b: modification of work by "psyberartist"/Flickr).

Ring of Life Models

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called “ring of life” (Figure 7.4.6); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

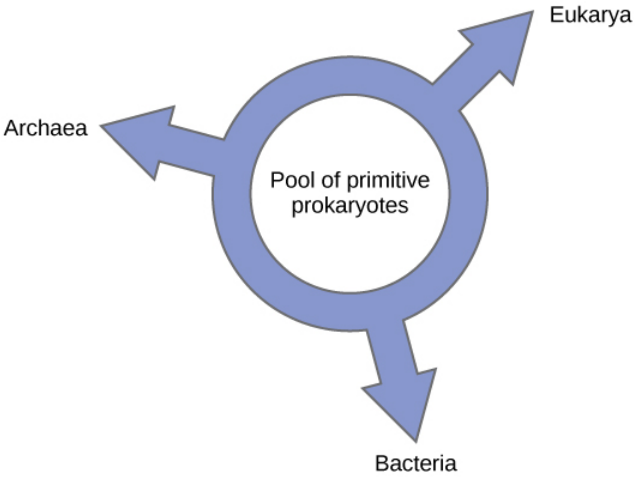


Figure 7.4.6: According to the “ring of life” phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

In summary, the “tree of life” model proposed by Darwin must be modified to include HGT. Does this mean abandoning the tree model completely? Even Lake argues that all attempts should be made to discover some modification of the tree model to allow it to accurately fit his data, and only the inability to do so will sway people toward his ring proposal.

This doesn’t mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin’s original conception of the phylogenetic tree is too simple, but made sense based on what was known at the time. However, the search for a more useful model moves on: each model serving as hypotheses to be tested with the possibility of developing new models. This is how science advances. These models are used as visualizations to help construct hypothetical evolutionary relationships and understand the massive amount of data being analyzed.

Summary

The phylogenetic tree, first used by Darwin, is the classic “tree of life” model describing phylogenetic relationships among species, and the most common model used today. New ideas about HGT and genome fusion have caused some to suggest revising the model to resemble webs or rings.

Glossary

eukaryote-first hypothesis

proposal that prokaryotes evolved from eukaryotes

gene transfer agent (GTA)

bacteriophage-like particle that transfers random genomic segments from one species of prokaryote to another

genome fusion

fusion of two prokaryotic genomes, presumably by endosymbiosis

horizontal gene transfer (HGT)

(also, lateral gene transfer) transfer of genes between unrelated species

mitochondria-first hypothesis

proposal that prokaryotes acquired a mitochondrion first, followed by nuclear development

nucleus-first hypothesis

proposal that prokaryotes acquired a nucleus first, and then the mitochondrion

ring of life

phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes

web of life

phylogenetic model that attempts to incorporate the effects of horizontal gene transfer on evolution

7.5: A Brief History of Life on Earth

The diversity of species, ecosystems and landscapes that surround us today are the product of perhaps 3.7 billion (i.e., 3.7×1093.7×109) to 3.85 billion years of evolution of life on Earth (Mojzsis et al., 1996; Fedo and Whitehouse, 2002). Life may have first evolved under harsh conditions, perhaps comparable to the deep-sea thermal vents where chemo-autotrophic bacteria are currently found (these are organisms that obtain their energy only from inorganic, chemical sources).

A subterranean evolution of life has also been suggested. Rock layers deep below the continents and ocean floors, that were previously thought to be too poor in nutrients to sustain life, have now been found to support thousands of strains of microorganisms. Types of bacteria have been collected from rock samples almost 2 miles below the surface, at temperatures up to 75 degrees Celsius. These chemo-autotrophic microorganisms derive their nutrients from chemicals such as carbon, hydrogen, iron and sulphur. Deep subterranean communities could have evolved underground or originated on the surface and become buried or otherwise transported down into subsurface rock strata, where they have subsequently evolved in isolation. Either way, these appear to be very old communities, and it is possible that these subterranean bacteria may have been responsible for shaping many geological processes during the history of the Earth (e.g., the conversion of minerals from one form to another, and the erosion of rocks) (Fredrickson and Onstott, 1996).

The earliest evidence for photosynthetic bacteria - suspected to be cyanobacteria - is dated at sometime between 3.5 and 2.75 billion years ago (Schopf, 1993; Brasier et al., 2002; Hayes, 2002). These first photosynthetic organisms would have been responsible for releasing oxygen into the atmosphere. (Photosynthesis is the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen). Prior to this, the atmosphere was mainly composed of carbon dioxide, with other gases such as nitrogen, carbon monoxide, methane, hydrogen and sulphur gases present in smaller quantities.

It probably took over 2 billion years, from the initial advent of photosynthesis for the oxygen concentration in the atmosphere to reach the level it is at today (Hayes, 2002). As oxygen levels rose, some of the early anaerobic species probably became extinct, and others probably became restricted to habitats that remained free of oxygen. Some assumed a lifestyle permanently lodged inside aerobic cells. The anaerobic cells might, initially, have been incorporated into the aerobic cells after those aerobes had engulfed them as food. Alternatively, the anaerobes might have invaded the aerobic hosts and become parasites within them. Either way, a more intimate symbiotic relationship subsequently evolved between these aerobic and anaerobic cells. In these cases the survival of each cell was dependent on the function of the other cell.

The evolution of this symbiotic relationship was an extremely important step in the evolution of more complex cells that have a nucleus, which is a characteristic of the Eucarya or eucaryotes (eu = good, or true; and karyon = kernel, or nucleus). Recent studies of rocks from Western Australia have suggested that the earliest forms of single-celled eucaryotes might be at least 2.7 billion years old (Anon, 2001). According to contemporary theories, there has been sufficient time, over those 2.7 billion years, for some of the genes of the invading anaerobe to have been lost, or even transferred to the nucleus of the host aerobe cell. As a result, the genomes of the ancestral invader and ancestral host have become mingled and the two entities can now be considered as one from a genetic standpoint.

The evolutionary history of the Eucarya is described in various standard references and so is not covered in detail here. Briefly, eucaryotes constitute three well known groups - the Viridiplantae or green plants, the Fungi, and the Metazoa or animals. There are also many basal groups of eucaryotes that are extremely diverse - and many of which are evolutionarily ancient. For example, the Rhodophyta, or red algae, which might be the sister-group to the Viridiplantae, includes fossil representatives dating from the Precambrian, 1025 billion years ago. The Stramenopiles includes small, single-celled organisms such as diatoms, fungus-like species of water moulds and downy mildews, and extremely large, multicellular brown seaweeds such as kelps.

The earliest known green plants are green algae, dating from the Cambrian, at least 500 million years ago. By the end of the Devonian, 360 million years ago, plants had become quite diverse and included representatives similar to modern plants. Green plants have been extremely important in shaping the environment. Fueled by sunlight, they are the primary producers of carbohydrates, sugars that are essential food resources for herbivores that are then prey to predatory carnivores. The evolution and ecology of pollinating insects is closely associated with the evolution of the Angiosperms, or flowering plants, since the Jurassic and Cretaceous periods.

Fungi, which date back to the Precambrian times about 650 to 540 million years ago, are also important in shaping and sustaining biodiversity. By breaking down dead organic material and using this for their growth, they recycle nutrients back through ecosystems. Fungi are also responsible for causing several plant and animal diseases. Fungi also form symbiotic relationships with tree species, often in nutrient-poor soils such as are found in the humid tropics, allowing their symbiont trees the ability to flourish in what would otherwise be a difficult environment.

Metazoa, which date to over 500 million years ago have also been responsible for shaping many ecosystems, from the specialized tubeworms of deep sea, hydrothermal vent communities of the ocean floor, to the birds living in the high altitudes of the Himalayas, such as the impeyan pheasant and Tibetan snow cock. Many species of animals are parasitic on other species and can significantly affect the behavior and life-cycles of their hosts.

Thus, the evolutionary history of Earth has physically and biologically shaped our contemporary environment. Many existing landscapes are based on the remains of earlier life forms. For example, some existing large rock formations are the remains of ancient reefs formed 360 to 440 million years ago by communities of algae and invertebrates (Veron, 2000).

Glossary

Photosynthesis

the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen

---

CHAPTER OVERVIEW

8: Life Histories

Learning Objectives

- Describe life history theory, the traits typically associated with the study of life histories.
- Explain the role of trade-offs and the principle of allocation in shaping life history traits.
- Explain correlated life history patterns we often observe across species (e.g., the concepts of **r**- versus **K**-selection), and conditions that could favor different life history strategies.
- Describe why organisms experience senescence, and compare and contrast hypotheses of aging.

Summary

A species’ life history describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species’ life history is genetically determined and shaped by the environment and natural selection. Studying life histories can help us understand larger evolutionary questions, like why does biological aging, a deleterious reduction in fecundity and survival, exist?

8.1: What is life history?

Life history theory

Life history theory is an analytical framework[1] designed to study the diversity of life history strategies used by different organisms throughout the world, as well as the causes and results of the variation in their life cycles.[2] It is a theory of biological evolution that seeks to explain aspects of organisms' anatomy and behavior by reference to the way that their life histories—including their reproductive development and behaviors, post-reproductive behaviors, and life span (length of time alive)—have been shaped by natural selection. A life history strategy is the "age- and stage-specific patterns"[2] and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc.[3] These events, notably juvenile development, age of sexual maturity, first reproduction, number of offspring and level of parental investment, senescence and death, depend on the physical and ecological environment of the organism.

The theory was developed in the 1950s[4] and is used to answer questions about topics such as organism size, age of maturation, number of offspring, life span, and many others.[5] In order to study these topics, life history strategies must be identified, and then models are constructed to study their effects. Finally, predictions about the importance and role of the strategies are made,[6] and these predictions are used to understand how evolution affects the ordering and length of life history events in an organism's life, particularly the life span and period of reproduction.[7] Life history theory draws on an evolutionary foundation, and studies the effects of natural selection on organisms, both throughout their lifetime and across generations.[8] It also uses measures of evolutionary fitness to determine if organisms are able to maximize or optimize this fitness,[9] by allocating resources to a range of different demands throughout the organism's life.[1] It serves as a method to investigate further the "many layers of complexity of organisms and their worlds".[10]

Organisms have evolved a great variety of life histories, from Pacific salmon, which produce thousands of eggs at one time and then die, to human beings, who produce a few offspring over the course of decades. The theory depends on principles of evolutionary biology and ecology and is widely used in other areas of science.

Figure 8.1.1: A swallowtail butterfly hatches from a chrysalis. *Source: Pixabay.*

Life cycle

All organisms follow a specific sequence in their development,[9] beginning with gestation and ending with death, which is known as the life cycle. Events in between usually include birth, childhood, maturation, reproduction, and senescence, and together these comprise the life history strategy of that organism.[3] The major events in this life cycle are usually shaped by the demographic qualities of the organism.[2] Some are more obvious shifts than others, and may be marked by physical changes—for example, teeth erupting in young children.[8] Some events may have little variation between individuals in a species, such as length of gestation, but other events may show a lot of variation between individuals,[3] such as age at first reproduction. Life cycles can be divided into two major stages: growth and reproduction. These two cannot take place at the same time, so once reproduction has begun, growth usually ends.[9] This shift is important because it can also affect other aspects of an organism's life, such as the organization of its group or its social interactions.[8]

Each species has its own pattern and timing for these events, often known as its ontogeny, and the variety produced by this is what life history theory addresses.[12] Evolution then works upon these stages to ensure that an organism adapts to its environment.[5] For example, a human, between being born and reaching adulthood, will pass through an assortment of life stages, which include: birth, infancy, weaning, childhood and growth, adolescence, sexual maturation, and reproduction.[3][12] All of these are defined in a specific biological way, which is not necessarily the same as the way that they are commonly used.[12] In life history theory, evolution works on the life stages of particular species (e.g., length of juvenile period) but is also discussed for a single organism's functional, lifetime adaptation. In both cases, researchers assume adaptation—processes that establish fitness.[5]

Traits

There are at least seven traits that are traditionally recognized as important in life history theory.[4] The trait that is seen as the most important for any given organism is the one where a change in that trait creates the most significant difference in that organism's level of fitness. In this sense, an organism's fitness is determined by its changing life history traits.[6] The way in which evolutionary forces act on these life history traits serves to limit the genetic variability and heritability of the life history strategies,[4] although there are still large varieties that exist in the world.

Commonly studied life history traits:

1. size at birth
2. growth pattern
3. age and size at maturity
4. number, size, and sex ratio of offspring
5. age- and size-specific reproductive investments
6. age- and size-specific mortality schedules
7. length of life

Strategies

Combinations of these life history traits and life events create the life history strategies. As an example, Winemiller and Rose propose three types of life history strategies in the fish they study: opportunistic, periodic, and equilibrium.[13] These types of strategies are defined by the body size of the fish, age at maturation, high or low survivorship, and the type of environment they are found in. A fish with a large body size, a late age of maturation, and low survivorship, found in a seasonal environment, would be classified as having a periodic life strategy.[13] The type of behaviors taking place during life events can also define life history strategies. For example, an exploitative life history strategy would be one where an organism benefits by using more resources than others, or by taking these resources from other organisms.[14]

Ecological conditions favor organisms with certain life history strategies through natural selection and evolution, rather than organisms favoring certain strategies based on ecological conditions.

Characteristics

Life history characteristics are traits that affect the life table of an organism, and can be imagined as various investments in growth, reproduction, and survivorship. The goal of life history theory is to understand the variation in such life history strategies. This knowledge can be used to construct models to predict what kinds of traits will be favored in different environments. Without constraints, the highest fitness would belong to a Darwinian demon, a hypothetical organism for whom such trade-offs do not exist. The key to life history theory is that there are limited resources available, and focusing on only a few life history characteristics is necessary.

Examples of some major life history characteristics include:

- Age at first reproductive event
- Reproductive life span and aging
- Number and size of offspring

Variations in these characteristics reflect different allocations of an individual's resources (i.e., time, effort, and energy expenditure) to competing life functions. For any given individual, available resources in any particular environment are finite. Time, effort, and energy used for one purpose diminishes the time, effort, and energy available for another.

For example, birds with larger broods are unable to afford more prominent secondary sexual characteristics.[15] Life history characteristics will, in some cases, change according to the population density, since genotypes with the highest fitness at high population densities will not have the highest fitness at low population densities.[16] Other conditions, such as the stability of the environment, will lead to selection for certain life history traits. Experiments have found that unstable environments select for flies with both shorter life spans and higher fecundity—in unreliable conditions, it is better for an organism to breed early and abundantly than waste resources promoting its own survival.[17]

Trade-offs

An essential component of studying life history strategies is identifying the **trade-offs**[26] that take place for any given organism. Energy use in life history strategies is regulated by thermodynamics and the conservation of energy,[3] and the "inherent scarcity of resources",[9] so not all traits or tasks can be invested in at the same time. Thus, organisms must choose between tasks, such as growth, reproduction, and survival,[9] prioritizing some and not others. For example, there is a trade-off between maximizing body size and maximizing life span, and between maximizing offspring size and maximizing offspring number.[5][6] This is also sometimes seen as a choice between quantity and quality of offspring.[7] These choices are the trade-offs that life history theory studies.

One significant trade-off is between somatic effort (towards growth and maintenance of the body) and reproductive effort (towards producing offspring).[7][9] Since an organism cannot put energy towards doing these simultaneously, many organisms have a period where energy is put just toward growth, followed by a period where energy is focused on reproduction, creating a separation of the two in the life cycle.[3] Thus, the end of the period of growth marks the beginning of the period of reproduction. Another fundamental trade-off associated with reproduction is between mating effort and parenting effort. If an organism is focused on raising its offspring, it cannot devote that energy to pursuing a mate.[9]

An important trade-off in the dedication of resources to breeding has to do with predation risk: organisms that have to deal with an increased risk of predation often invest less in breeding. This is because it is not worth as much to invest a lot in breeding when the benefit of such investment is uncertain.[27]

These trade-offs, once identified, can then be put into models that estimate their effects on different life history strategies and answer questions about the selection pressures that exist on different life events.[7] Over time, there has been a shift in how these models are constructed. Instead of focusing on one trait and looking at how it changed, scientists are looking at these trade-offs as part of a larger system, with complex inputs and outcomes.[6]

The idea of **constraints** is closely linked to the idea of trade-offs discussed above. Because organisms have a finite amount of energy, the process of trade-offs acts as a natural limit on the organism's adaptations and potential for fitness. These limits can be physical, developmental, or historical, and they are imposed by the existing traits of the organism.[2]

Populations can adapt and thereby achieve an **"optimal" life history strategy** that allows the highest level of fitness possible (fitness maximization). There are several methods from which to approach the study of optimality, including energetic and demographic. Achieving optimal fitness also encompasses multiple generations, because the optimal use of energy includes both the parents and the offspring. For example, "optimal investment in offspring is where the decrease in total number of offspring is equaled by the increase of the number who survive".[7] Optimality is important for the study of life history theory because it serves as the basis for many of the models used, which work from the assumption that natural selection, as it works on a life history traits, is moving towards the most optimal group of traits and use of energy.[6] This base assumption, that over the course of its life span an organism is aiming for optimal energy use,[7] then allows scientists to test other predictions. However, actually gaining this optimal life history strategy cannot be guaranteed for any organism.[6]

An organism's **allocation of resources** ties into several other important concepts, such as trade-offs and optimality. The best possible allocation of resources is what allows an organism to achieve an optimal life history strategy and obtain the maximum level of fitness,[9] and making the best possible choices about how to allocate energy to various trade-offs contributes to this. The allocation of resources also plays a role in variation, because the different resource allocations by different species create the variety of life history strategies.[3]

Reproductive value and costs of reproduction

Reproductive value models the trade-offs between reproduction, growth, and survivorship. An organism's reproductive value (RV) is defined as its expected contribution to the population through both current and future reproduction:[19]

RV = Current Reproduction + Residual Reproductive Value (RRV)

The residual reproductive value represents an organism's future reproduction through its investment in growth and survivorship. The cost of reproduction hypothesis[20] predicts that higher investment in current reproduction hinders growth and survivorship and reduces future reproduction, while investments in growth will pay off with higher fecundity (number of offspring produced) and reproductive episodes in the future. This cost-of-reproduction trade-off influences major life history characteristics. For example, a 2009 study by Creighton et al. on burying beetles provided support for the costs of reproduction.[21] The study found that beetles that had allocated too many resources to current reproduction also had the shortest life spans. In their lifetimes, they also had the fewest reproductive events and offspring, reflecting how over-investment in current reproduction lowers residual reproductive value.

The related terminal investment hypothesis describes a shift to current reproduction with higher age. At early ages, RRV is typically high, and organisms should invest in growth to increase reproduction at a later age. As organisms age, this investment in growth gradually increases current reproduction. However, when an organism grows old and begins losing physiological function, mortality increases while fecundity decreases. This senescence shifts the reproduction trade-off towards current reproduction: the effects of aging and higher risk of death make current reproduction more favorable. The burying beetle study also supported the terminal investment hypothesis: the authors found beetles that bred later in life also had increased brood sizes, reflecting greater investment in those reproductive events.[22]

r/K selection theory

For more information on r/K selection see the Population Ecology chapter.

The selection pressures that determine the reproductive strategy, and therefore much of the life history, of an organism can be understood in terms of r/K selection theory. The central trade-off to life history theory is the number of offspring vs. the timing of reproduction. Organisms that are r-selected have a high growth rate (*r*) and tend to produce a high number of offspring with minimal parental care; their life spans also tend to be shorter. *r*-selected organisms are suited to life in an unstable environment, because they reproduce early and abundantly and allow for a low survival rate of offspring. *K*-selected organisms subsist near the carrying capacity of their environment (*K*), produce a relatively low number of offspring over a longer span of time, and have high parental investment. They are more suited to life in a stable environment in which they can rely on a long life span and a low mortality rate that will allow them to reproduce multiple times with a high offspring survival rate.[23]

Some organisms that are very *r*-selected are **semelparous**, only reproducing once before they die. Semelparous organisms may be short-lived, like annual crops. However, some semelparous organisms are relatively long-lived, such as the African flowering plant *Lobelia telekii* which spends up to several decades growing an inflorescence that blooms only once before the plant dies,[24] or the periodical cicada which spends 17 years as a larva before emerging as an adult. Organisms with longer life spans are usually **iteroparous**, reproducing more than once in a lifetime. However, iteroparous organisms can be more *r*-selected than *K*-selected, such as a sparrow, which gives birth to several chicks per year but lives only a few years, as compared to a wandering albatross, which first reproduces at ten years old and breeds every other year during its 40-year life span.[25]

Characteristic	K-selected species	r-selected species
life span	long	short
time to reproductive maturity	long	short
amount of reproductive events	many	few (or semelparous)
number of offspring	few	many
parental care	high	absent
population growth rate	slow	fast
associated with	Type I	Type III
example species	elephants	rabbits

Figure 8.1.2: Typical variations seen between r- and K-selected species

Figure 8.1.3: A litter of mice with their mother. The reproduction of mice follows an *r*-selection strategy, with many offspring, short gestation, less parental care, and a short time until sexual maturity. *Source: Seweryn Olkowicz.*

Unpredictable environments

Many factors can determine the evolution of an organism's life history, especially the unpredictability of the environment. A very unpredictable environment—one in which resources, hazards, and competitors may fluctuate rapidly—selects for organisms that produce more offspring earlier in their lives, because it is never certain whether they will survive to reproduce again. Mortality rate may be the best indicator of a species' life history: organisms with high mortality rates—the usual result of an unpredictable environment—typically mature earlier than those species with low mortality rates, and give birth to more offspring at a time.[32] A highly unpredictable environment can also lead to plasticity, in which individual organisms can shift along the spectrum of r-selected vs. K-selected life histories to suit the environment.[33]

Evolution Connection: Energy Budgets, Reproductive Costs, and Sexual Selection in *Drosophila*

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings (Figure 8.1.3). Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed "resource-depleted," while males that had not mated were termed "non-resource-depleted." The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

Figure 8.1.4: Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's life span, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

Adapted from Phillip G. Byrne and William R. Rice, "Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*," Proc Biol Sci. 273, no. 1589 (2006): 917-922, doi: 10.1098/rspb.2005.3372.

Human life history

In studying humans, life history theory is used in many ways, including in biology, psychology, economics, anthropology, and other fields.[9][34][35] For humans, life history strategies include all the usual factors—trade-offs, constraints, reproductive effort, etc.—but also includes a culture factor that allows them to solve problems through cultural means in addition to through adaptation.[5] Humans also have unique traits that make them stand out from other organisms, such as a large brain, later maturity and age of first reproduction,[7] a long life span,[7][36] and a high level of reproduction, often supported by fathers and older (post-menopausal) relatives.[36][37][38] There are a variety of possible explanations for these unique traits. For example, a long juvenile period may have been adapted to support a period of learning the skills needed for successful hunting and foraging.[7][36] This period of learning may also explain the longer life span, as a longer amount of time over which to use those skills makes the period needed to acquire them worth it.[8][36] Cooperative breeding and the "grandmother hypothesis" have been proposed as the reasons that humans continue to live for many years after they are no longer capable of reproducing.[7][38] The large brain allows for a greater learning capacity, and the ability to engage in new behaviors and create new things.[7] The change in brain size may have been the result of a dietary shift —towards higher quality and difficult to obtain food sources[36]—or may have been driven by the social requirements of group living, which promoted sharing and provisioning.[8] Research has also indicated that humans may pursue different reproductive strategies.[39][40][41]

Survivorship Curves

Another tool used by population ecologists is a survivorship curve, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure 8.1.4). Humans and most primates exhibit a **Type I survivorship curve** because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or **Type II survivorship curve** because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a **Type III survivorship curve** because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are "on their own" and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

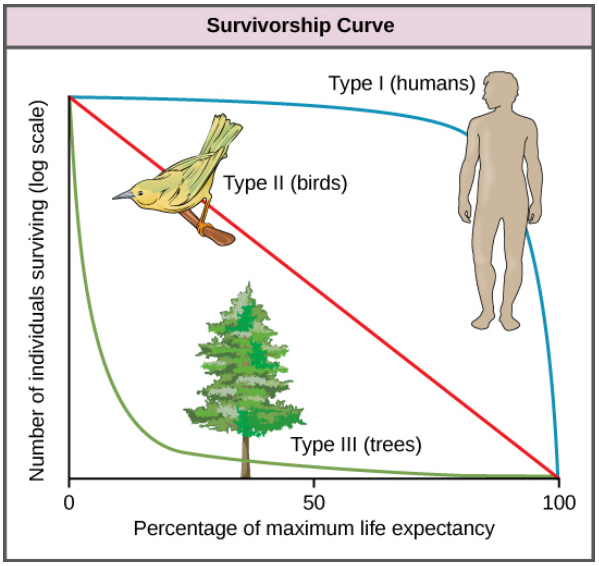


Figure 8.1.5: Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Sources

1. Vitzthum, V. (2008). Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*, *37*, 53-73
2. Flatt, T., & Heyland, A. (Eds.). (2011). Mechanisms of Life History Evolution : The Genetics and Physiology of Life History Traits and Trade-Offs. Oxford, GB: OUP Oxford.
3. Ahlström, T. (2011). Life-history theory, past human populations and climatic perturbations. *International Journal of Osteoarchaeology*, *21*(4), 407-419.
4. Stearns, S. (1992). *The Evolution of Life Histories*. Oxford ; New York: Oxford University Press.
5. Hochberg, Z. (2011). Evo-Devo of Child Growth : Treatise on Child Growth and Human Evolution (1). Hoboken, US: Wiley-Blackwell.
6. Stearns, S. (1976). Life-History Tactics: A Review of the Ideas. *The Quarterly Review of Biology, 51*(1), 3-47. JSTOR 2825234
7. Hill, K., & Kaplan, H. (1999). Life history traits in humans: Theory and empirical studies. *Annual Review Of Anthropology*, *28*(1), 397.
8. Bolger, D. (Ed.). (2012). Wiley Blackwell Companions to Anthropology Ser. : A Companion to Gender Prehistory (1). Somerset, US: Wiley-Blackwell.
9. Preston, S. D., Kringelbach, M. L., & Knutson, B. (2014). The Interdisciplinary Science of Consumption. Cambridge, US: The MIT Press.
10. Morbeck, M., Galloway, A., & Zihlman, A. *The Evolving Female : A Life-history Perspective*. (1997). Princeton, N.J.: Princeton University Press
11. Roff, D. (2002). *Life History Evolution*. Sunderland, Mass.: Sinauer.
12. Hawkes K., ed. *The Evolution of Human Life History*. (2006). Santa Fe : Oxford: School of American Research ; James Currey. Gen ed.
13. Lartillot, N., & Delsuc, F. (2012). "Joint reconstruction of divergence times and life-history evolution in placental mammals using a phylogenetic covariance model". *Evolution*, *66*(6), 1773-1787.JSTOR 41503481
14. Reynolds, J., & McCrea, S. (2016). Life history theory and exploitative strategies. *Evolutionary Psychology*, *14*(3),
15. Gustafsson, L., Qvarnström, A., and Sheldon, B.C. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature 375, 311—313
16. Mueller, L.D., Guo, P., and Ayala, F.J. 1991. Density dependent natural selection and trade-offs in life history traits. Science, 253: 433-435.
17. Rose, M. and Charlesworth, B. A Test of Evolutionary Theories of Senescence. 1980. Nature 287, 141-142
18. Keen, E. C. (2014). "trade-offs in bacteriophage life histories". *Bacteriophage*. **4** (1): e28365. doi:10.4161/bact.28365. PMC 3942329. PMID 24616839.

19. Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.
20. Jasienska, Grazyna (2009-07-01). "Reproduction and life span: Trade-offs, overall energy budgets, intergenerational costs, and costs neglected by research". *American Journal of Human Biology*. **21** (4): 524–532. doi:10.1002/ajhb.20931. ISSN 1520-6300. PMID 19367577. S2CID 11440141.
21. J. Curtis Creighton, Nicholas D. Heflin, and Mark C. Belk. 2009. Cost of Reproduction, Resource Quality, and Terminal Investment in a Burying Beetle. The American Naturalist, 174:673–684.
22. J. Curtis Creighton, Nicholas D. Heflin, and Mark C. Belk. 2009. Cost of Reproduction, Resource Quality, and Terminal Investment in a Burying Beetle. The American Naturalist, 174:673–684.
23. Stearns, S.C. 1977. The Evolution of Life History Traits: A Critique of the Theory and a Review of the Data. Annual Review of Ecology and Systematics, 8: 145-171
24. Young, Truman P. 1984. The Comparative Demography of Semelparous Lobelia Telekii and Iteroparous Lobelia Keniensis on Mount Kenya. Journal of Ecology, 72: 637–650
25. Ricklefs, Robert E. 1977. On the Evolution of Reproductive Strategies in Birds: Reproductive Effort. The American Naturalist, 111: 453–478.
26. "105_2013_12_05_Trade-offs_1". *idea.ucr.edu*.
27. Dillon, Kristen G; Conway, Courtney J; Skelhorn, John (2018). "Nest predation risk explains variation in avian clutch size". *Behavioral Ecology*. **29** (2): 301–311. doi:10.1093/beheco/arx130. ISSN 1045-2249.
28. Houston, Alasdair I.; Stephens, Philip A.; Boyd, Ian L.; Harding, Karin C.; McNamara, John M. (2007). "Capital or income breeding? A theoretical model of female reproductive strategies". *Behavioral Ecology*. **18** (1): 241–250. doi:10.1093/beheco/arl080. ISSN 1465-7279.
29. Drent, R. H.; Daan, S. (1980). "The prudent parent: energetic adjustments in avian breeding". *Ardea*. 38–90: 225–252. doi:10.5253/arde.v68.p225. ISSN 0373-2266.
30. Ejsmond, Maciej Jan; Varpe, Øystein; Czarnoleski, Marcin; Kozłowski, Jan (2015). "Seasonality in offspring value and trade-offs with growth explain capital breeding". *The American Naturalist*. **186** (5): E111–E125. doi:10.1086/683119. ISSN 0003-0147. S2CID 87515085.
31. Sainmont, Julie; Andersen, Ken H.; Varpe, Øystein; Visser, André W. (2014). "Capital versus income breeding in a seasonal environment". *The American Naturalist*. **184** (4): 466–476. doi:10.1086/677926. ISSN 0003-0147. PMID 25226182. S2CID 28848120.
32. Promislow, D.E.L. and P.H. Harvey. 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. Journal of Zoology, 220:417-437.
33. Baird, D. G., L. R. Linton and Ronald W. Davies. 1986. Life-History Evolution and Post-Reproductive Mortality Risk. *Journal of Animal Ecology* 55: 295-302.
34. Mittal, C., Griskevicius, V., Simpson, J., & Kawakami, K. (2014). Sense of control under uncertainty depends on people's childhood environment: A life history theory approach. *Journal of Personality and Social Psychology*, *107*(4), 621-637.
35. Schmitt, D., & Rhode, P. (2013). The human polygyny index and its ecological correlates: Testing sexual selection and life history theory at the cross-national level. *Social Science Quarterly*, *94*(4), 1159-1184.
36. Kaplan, H., Hill, K., Lancaster, J. and Hurtado, A. M. (2000), A theory of human life history evolution: Diet, intelligence, and longevity. Evol. Anthropol., 9: 156–185. doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7
37. Barton, R., Capellini, I., & Stevens, C. (2011). Maternal investment life histories, and the costs of brain growth in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(15), 6169-6174. JSTOR 41126625
38. Isler, K., & van Schaik, C. (2012). Allomaternal care, life history and brain size evolution in mammals. *Journal of Human Evolution*, *63*(1), 52-63.
39. Kim, Yuri, and James J. Lee. "The genetics of human fertility." Current opinion in psychology 27 (2019): 41-45.
40. Yao, Shuyang, Niklas Långström, Hans Temrin, and Hasse Walum. "Criminal offending as part of an alternative reproductive strategy: Investigating evolutionary hypotheses using Swedish total population data." Evolution and Human Behavior 35, no. 6 (2014): 481-488.
41. Vall, Gemma, Fernando Gutiérrez, Josep M. Peri, Miguel Gárriz, Eva Baillés, Juan Miguel Garrido, and Jordi E. Obiols. "Seven dimensions of personality pathology are under sexual selection in modern Spain." Evolution and Human Behavior 37, no. 3 (2016): 169-178.

Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) from the following sources:

- Wikipedia: https://en.wikipedia.org/wiki/Life_history_theory
- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

8.2: Semelparity versus Iteroparity

Semelparity versus Iteroparity

Semelparity and **iteroparity** are two contrasting reproductive strategies available to living organisms. A species is considered **semelparous** if it is characterized by a single reproductive episode before death, and **iteroparous** if it is characterized by multiple reproductive cycles over the course of its lifetime.

In truly semelparous species, death after reproduction is part of an overall strategy that includes putting all available resources into maximizing reproduction, at the expense of future life. In any iteroparous population there will be some individuals who die between their first and second reproductive episodes, but unless this is part of a syndrome of programmed death after reproduction, this would not be called semelparity.

This distinction is also related to the difference between annual and perennial plants. An annual is a plant that completes its life cycle in a single season, and is usually semelparous. Perennials live for more than one season and are usually (but not always) iteroparous.[1]

Semelparity and iteroparity are not, strictly speaking, alternative strategies, but extremes along a continuum of possible modes of reproduction. Many organisms considered to be semelparous can, under certain conditions, separate their single bout of reproduction into two or more episodes.[2][3]

Semelparity

The word semelparity was coined by evolutionary biologist Lamont Cole[4], and comes from the Latin *semel* 'once, a single time' and *pario* 'to beget'. This differs from iteroparity in that iteroparous species are able to have multiple reproductive cycles and therefore can mate more than once in their lifetime. Semelparity is also known as "big bang" reproduction, since the single reproductive event of semelparous organisms is usually large as well as fatal[5]. A classic example of a semelparous organism is Pacific salmon (*Oncorhynchus* spp.), which lives for many years in the ocean before swimming to the freshwater stream of its birth, spawning, and dying. Other semelparous animals include many insects, including some species of butterflies, cicadas, and mayflies, many arachnids, and some molluscs such as some species of squid and octopus. Annual plants, including all grain crops and most domestic vegetables, are semelparous. Long-lived semelparous plants include century plant (agave), *Lobelia telekii*, and some species of bamboo.

Figure 8.2.1: Many Pacific salmon, like this sockeye salmon (*Oncorhynchus nerka*) are semelparous and only reproduce once in their lifetime. *Source: Milton Love, Marine Science Institute, available in the public domain.*

This form of lifestyle is consistent with **r-selected strategies** as many offspring are produced and there is low parental input, as one or both parents die after mating. All of the male’s energy is diverting into mating and the immune system is repressed. High levels of corticosteroids are sustained over long periods of time. This triggers immune and inflammatory system failure and gastrointestinal hemorrhage, which eventually leads to death.

Iteroparity

The term iteroparity comes from the Latin *itero*, to repeat, and *pario*, to beget. An example of an iteroparous organism is a human—humans are biologically capable of having offspring many times over the course of their lives. Iteroparous vertebrates include all birds, most reptiles, virtually all mammals, and most fish. Among invertebrates, most mollusca and many insects (for example, mosquitoes and cockroaches) are iteroparous. Most perennial plants are iteroparous.

Figure 8.2.2: Most mammals, like this domestic pig are iteroparous and reproduce multiple times in their life. *Source: Scott Bauer, USDA, available in the public domain.*

Trade-offs

Within its lifetime, an organism has a limited amount of energy/resources available to it and must always partition it among various functions such as collecting food and finding a mate. Of relevance here is the trade-off between fecundity, growth, and survivorship in its life history strategy. These trade-offs come into play in the evolution of iteroparity and semelparity. It has been repeatedly demonstrated that semelparous species produce more offspring in their single fatal reproductive episode than do closely related iteroparous species in any one of theirs. However, the opportunity to reproduce more than once in a lifetime, and possibly with greater care for the development of offspring produced, can offset this strictly numerical benefit.

Models based on non-linear trade-offs

One class of models that tries to explain the differential evolution of semelparity and iteroparity examines the shape of the trade-off between offspring produced and offspring forgone (offspring that will not be produced). In economic terms, offspring produced is equivalent to a benefit function, while offspring forgone is comparable to a cost function. The reproductive effort of an organism—the proportion of energy that it puts into reproducing, as opposed to growth or survivorship—occurs at the point where the distance between offspring produced and offspring forgone is the greatest (Figure 3).

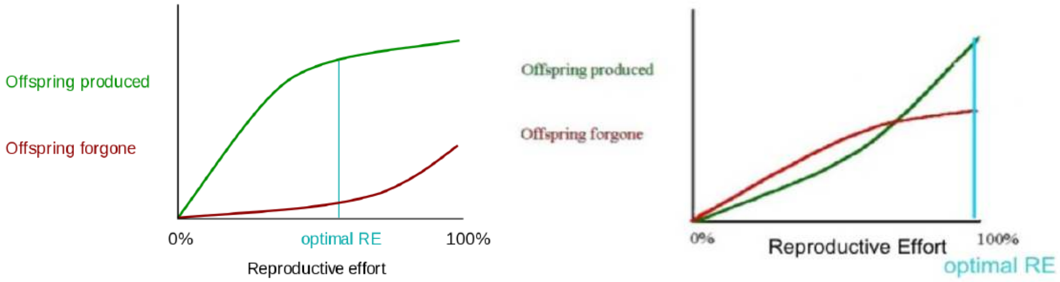


Figure 8.2.3: A visual model to explain the evolution of semelparity and iteroparity based on different cost/benefit curves. In the first graph, the marginal cost of offspring produced is decreasing (each additional offspring is less "expensive" than the average of all previous offspring) and the marginal cost of offspring forgone is increasing. In this situation, the organism only devotes a portion of its resources to reproduction, and uses the rest of its resources on growth and survivorship so that it can reproduce again in the future[6]. However, it is also possible (second graph) for the marginal cost of offspring produced to *increase*, and for the marginal cost of offspring forgone to decrease. When this is the case, it is favorable for the organism to reproduce a single time. The organism devotes all of its resources to that one episode of reproduction, so it then dies. This mathematical/graphical model has found only limited quantitative support from nature. *Source: Paul Moorcroft, Harvard University, licensed under CC BY-SA 3.0.*

Bet-hedging models

A second set of models examines the possibility that iteroparity is a hedge against unpredictable juvenile survivorship (avoiding putting all one's eggs in one basket). Again, mathematical models have not found empirical support from real-world systems. In fact, many semelparous species live in habitats characterized by high (not low) environmental unpredictability, such as deserts and early successional habitats.

Cole's paradox and demographic models

The models that have the strongest support from living systems are demographic. In Lamont Cole's classic 1954 paper, he came to the conclusion that: "For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size." [7]

For example, imagine two species—an iteroparous species that has annual litters averaging three offspring each, and a semelparous species that has one litter of four, and then dies. These two species have the same rate of population growth, which suggests that even a tiny fecundity advantage of one additional offspring would favor the evolution of semelparity. This is known as Cole's paradox. In his analysis, Cole assumed that there was no mortality of individuals of the iteroparous species, even seedlings. Twenty years later, Charnov and Schaffer[8] showed that reasonable differences in adult and juvenile mortality yield much more reasonable costs of semelparity, essentially solving Cole's paradox. An even more general demographic model was produced by Young[9]. These demographic models have been more successful than the other models when tested with real-world systems. It has been shown that semelparous species have higher expected adult mortality, making it more economical to put all reproductive effort into the first (and therefore final) reproductive episode.[10][11]

Sources

1. Gotelli, N.J. (2008). *A primer of ecology.* Sunderland, Mass.: Sinauer Associates, Inc. ISBN 978-0-87893-318-1
2. Futami, K., & Akimoto, S. (2005). Facultative second oviposition as an adaptation to egg loss in a semelparous crab spider. *Ethlogy, 111*(12), pp. 1126-1138. *Bibcode:2005Ethol.111.1126F. doi:10.1111/j.1439-0310.2005.01126.x. ISSN 1439-0310.*
3. Hughes, P.W., & Simons, A.M. (2014). Changing reproductive effort within a semelparous reproductive episode. *American Journal of Botany, 101*(8), pp. 1323-1331. *doi:10.3732/ajb.1400283. ISSN 0002-9122. PMID 25156981.*
4. Cole, L.C. (1954). The population consequences of life history phenomena. *The Quarterly Review of Biology, 29*(2), pp. 103-137. *doi:10.1086/400074. JSTOR 2817654. PMID 13177850. S2CID 26986186.*
5. Ricklefs, R.E., & Miller, G.L. (1999). *Ecology.* Macmillan ISBN 0-7167-2829-X
6. Roff, D.A. (1992). *The evolution of life histories*. Springer ISBN 0-412-02391-1
7. Lamont, C.C. (1954). The population consequences of life history phenomena. *The Quarterly Review of Biology, 29*(2), pp. 103-137.
8. Charnov, E.L., & Schaffer, W.M. (1973). Life history consequences of natural selection: Cole's result revisited. *American Naturalist, 107*(958), pp. 791-793. *doi:10.1086/282877. S2CID 83561052.*
9. Young, T.P. (1981). A general mode of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist, 118*, pp. 27-36. *doi:10.1086/283798. S2CID 83860904.*
10. Young, T.P. (1990). The evolution of semelparity in Mount Kenya lobelias. *Evolutionary Ecology, 4*(2), pp. 157-171. *doi:10.1007/bf02270913. S2CID 25993809.*
11. Lesica, P., & Young, T.P. (2005). Demographic model explains life history evolution in *Arabis fecunda*. *Functional Ecology, 19*(3), pp. 471-477. *doi:10.1111/j.1365-2435.2005.00972.x. S2CID 31222891.*

Contributors and Attributions

This chapter was written by D. Wetzel with text taken from the following CC-BY resources:

- Wikipedia: https://en.wikipedia.org/wiki/Semelparity_and_iteroparity

---

8.3: Life History Evolution

The content for this subtopic is found in an external page. Please click the link below to access this information.

Life History Evolution

Fabian, D. & Flatt, T. (2012). Life History Evolution. *Nature Education Knowledge, 3*(10):24

8.4: The Evolution of Aging

The Evolution of Aging

Senescence or **biological aging** is the gradual deterioration of functional characteristics in living organisms. The word *senescence* can refer to either cellular senescence or to senescence of the whole organism. Organismal senescence involves an increase in death rates and/or a decrease in fecundity with increasing age, at least in the latter part of an organism's life cycle. Environmental factors may affect aging - for example, overexposure to ultraviolet radiation accelerates skin aging. Different parts of the body may age at different rates. Two organisms of the same species can also age at different rates, making biological aging and chronological aging distinct concepts.

The occurrence of aging in nature poses an evolutionary puzzle: why would such a deleterious, maladaptive process evolve? This puzzle is deepened by the fact that aging is apparently neither inevitable nor universal: germ lines and several organisms do not exhibit senescent decline.

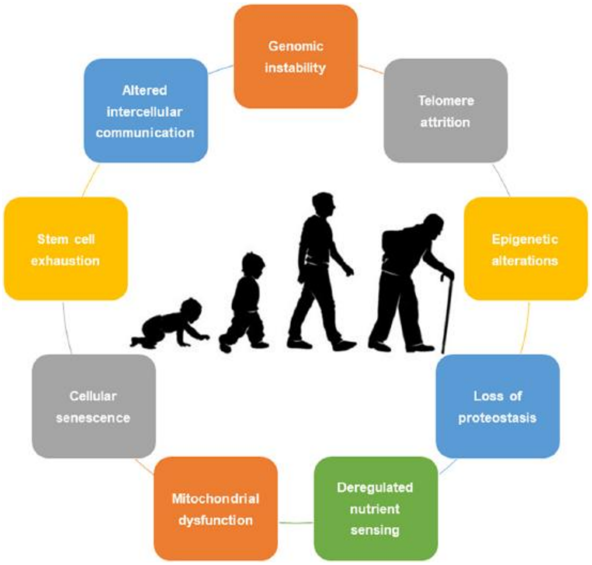


Figure 8.4.1 : The nine hallmarks of aging that are common among organisms: genomic instability, telomere attrition, epigenetic alterations, loss of proteostasis, deregulated nutrient sensing, mitochondrial dysfunction, cellular senescence, stem cell exhaustion, and altered intercellular communication. *Source: Rebelo-Marques, De Sousa Lages, Andrade, Ribeiro, Mota-Pinto, Carrilho and Espregueira-Mendes* - *https://www.frontiersin.org/articles/10.3389/fendo.2018.00258/full*.

Is aging universal? Diverse patterns of senescence among species

Classic theories of aging pertain mainly to relatively short-lived species with increasing mortality and decreasing fertility after maturity, but patterns of aging—including reproductive senescence—are very diverse (Finch 1990, Shefferson et al. 2017, Comfort 1956, Jones et al. 2014, Baudisch et al. 2013, Garcia et al. 2011, Schaible et al. 2015, Ruby et al. 2018, Lemaitre & Gaillard 2017). In particular, although many species do age, some appear to show ‘negligible’ senescence (i.e., only weak or no signs of aging with advancing age; Finch 1990, Shefferson et al. 2017, Finch & Austad 2001, Finch 2009, Finch 1998), whereas others could—at least theoretically—exhibit ‘negative’ senescence (i.e., physiological improvement with age; Vaupel et al. 2004). In freshwater polyps of the genus *Hydra* (Figure 3.2), for instance, survival and fertility do not decline with age (Schaible et al. 2015). Similarly, many plants (e.g., ~ 93% of angiosperms) show no signs of aging (Salguero-Gómez et al. 2013, Baudisch et al. 2013); some trees, for example, live thousands of years (Figure 8.4.2). However, a caveat is that aging might in many cases exist but not be detectable because the studied individuals were not old enough (Peron et al. 2010); for example, a recent study of turtles—typically thought of as exhibiting strongly ‘negligible’ senescence—has shown that reproduction and survival do in fact decline with age, contrary to previous expectations. Many organisms, such as numerous invertebrates and fish, start to reproduce before they are fully grown. Increasing body size can then lead to increased fecundity and also to protection against size-specific predators and other sources of mortality. Under these circumstances, the force of natural selection can increase over part of adult life, because the reproductive value of the organism increases (Baudisch 2008, Baudisch 2005, Charlesworth 1994, Partridge & Barton 1996). Non- or slow-aging species, including some animals (e.g., basal metazoans such as *Hydra* and sea anemones) and most higher plants, are characterized by modular organization, indeterminate (including clonal) growth, and the capacity to regenerate due to stem cell activity; often such organisms start to reproduce before they have finished growing, or they can grow indefinitely (Munné-Bosch 2015, Petralia et al. 2014, Bythell et al. 2017). Some clones of grasses, for example, have been estimated to become 15,000 years old (Noodén 1988). In addition, unlike the standard laboratory model organisms, which set aside and sequestrate their germline early in development, in organisms such as *Hydra* and higher plants the cells that will become the germline are only identified during adulthood, and these organisms therefore maintain cell lineages with high regenerative potential. Thus, the force of natural selection does not always decline monotonically with age (Baudisch 2008, Munné-Bosch 2015, Shefferson et al. 2017 Baudisch 2005, Charlesworth 1994).

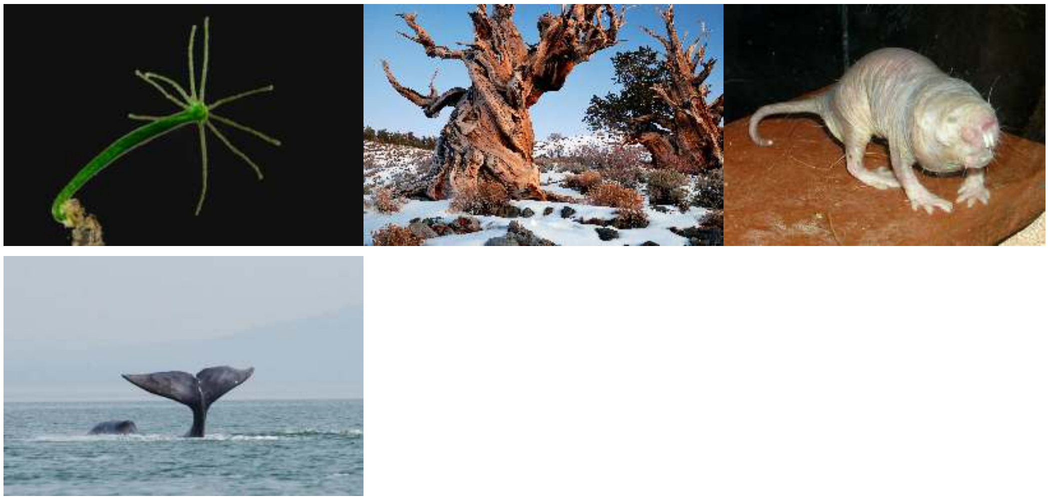


Figure 8.4.2: Long-lived organisms; many organisms age very slowly, if at all. Left: the freshwater polyp *Hydra* is potentially immortal ("Hydra" by Frank Fox is licensed under CC BY-SA 3.0). Second from left: some trees like this bristlecone pine (*Pinus longaeva*) live for thousands of years ("Gnarly" by Rick Goldwaser is licensed under CC BY 2.0). Third from left: in the naked mole-rat (*Heterocephalus glaber*) mortality does not increase with age ("Nacktmull" by Roman Klementschitz is licensed under CC BY-SA 3.0). Right: the bowhead whale (*Balaena mysticetus*) is the longest-lived mammal, with an estimated maximum life span of 211 years ("A bowhead whale" by Olga Shpak is licensed under CC BY-SA 3.0).

Hypotheses of aging

More than 300 different hypotheses have been posited to explain the nature and causes of aging. Aging hypotheses fall into two broad categories, evolutionary hypotheses of aging and mechanistic hypotheses of aging. Evolutionary hypotheses of aging primarily explain why aging happens, but do not concern themselves with how (the molecular mechanism(s)). All evolutionary hypotheses of aging rest on the basic mechanisms that the force of natural selection declines with age. Mechanistic hypotheses of aging can be divided into hypotheses that propose aging is programmed (i.e., aging follows a biological timetable), and damage accumulation hypotheses (i.e., those that propose aging to be caused by specific molecular changes occurring over time).

Evolutionary aging hypotheses

Antagonistic pleiotropy

One hypothesis proposed by George C. Williams involves **antagonistic pleiotropy**. Pleiotropy occurs when a single gene has two or more apparently unrelated effects. The idea of antagonistic pleiotropy is that one gene can positively affect a fitness related trait early in life, but can also have negative effects later in life and thus contribute to senescence. Because many more individuals are alive at young ages than at old ages, even small positive effects early can be strongly selected for, and large negative effects later may be very weakly selected against. Williams suggested the following example: Perhaps a gene codes for calcium deposition in bones, which promotes juvenile survival and will therefore be favored by natural selection; however, this same gene promotes calcium deposition in the arteries, causing negative atherosclerotic effects in old age. Thus, harmful biological changes in old age may result from selection for pleiotropic genes that are beneficial early in life but harmful later on. In this case, selection pressure is relatively high when Fisher's reproductive value is high and relatively low when Fisher's reproductive value is low.

Cancer versus cellular senescence trade-off

Senescent cells within a multicellular organism can be purged by competition between cells, but this increases the risk of cancer. This leads to an inescapable dilemma between two possibilities—the accumulation of physiologically useless senescent cells, and cancer—both of which lead to increasing rates of mortality with age.

Disposable soma

The **disposable soma hypothesis** of aging was proposed by Thomas Kirkwood in 1977. The hypothesis suggests that aging occurs due to a strategy in which an individual only invests in maintenance of the soma for as long as it has a realistic chance of survival. A species that uses resources more efficiently will live longer, and therefore be able to pass on genetic information to the next generation. The demands of reproduction are high, so less effort is invested in repair and maintenance of somatic cells, compared to germline cells, in order to focus on reproduction and species survival.

Damage accumulation hypotheses

The free radical hypothesis

One of the most prominent hypotheses of aging was first proposed by Harman in 1956. It posits that free radicals produced by dissolved oxygen, radiation, cellular respiration and other sources cause damage to the molecular machines in the cell and gradually wear them down. This is also known as oxidative stress. Under normal aerobic conditions, approximately 4% of the oxygen metabolized by mitochondria is converted to superoxide ion, which can subsequently be converted to hydrogen peroxide, hydroxyl radical and eventually other reactive species including other peroxides and singlet oxygen, which can, in turn, generate free radicals capable of damaging structural proteins and DNA.

There is substantial evidence to back up this theory. Old animals have larger amounts of oxidized proteins, DNA and lipids than their younger counterparts.

Chemical damage

One of the earliest aging hypotheses was the *Rate of Living Hypothesis* described by Raymond Pearl in 1928, which states that fast basal metabolic rate corresponds to shortened maximum life span.

While there may be some validity to the idea that for various types of specific damage detailed below that are byproducts of metabolism, all other things being equal, a fast metabolism may reduce life span, in general this hypothesis does not adequately explain the differences in life span either within, or between, species. Calorically restricted animals process as much, or more, calories per gram of body mass, as their *ad libitum* fed counterparts, yet exhibit substantially longer life spans. Similarly, metabolic rate is a poor predictor of life span for birds, bats and other species that, it is presumed, have reduced mortality from predation, and therefore have evolved long life spans even in the presence of very high metabolic rates. In a 2007 analysis it was shown that, when modern statistical methods for correcting for the effects of body size and phylogeny are employed, metabolic rate does not correlate with longevity in mammals or birds.

With respect to specific types of chemical damage caused by metabolism, it is suggested that damage to structural proteins or DNA caused by ubiquitous chemical agents in the body such as oxygen and sugars, are in part responsible for aging. The damage can include breakage of biopolymer chains, cross-linking of biopolymers, or chemical attachment of unnatural substituents to biopolymers. Sugars such as glucose and fructose can react with certain amino acids such as lysine and arginine and certain DNA bases such as guanine to produce sugar adducts, in a process called *glycation*. These adducts can further rearrange to form reactive species, which can then cross-link the structural proteins or DNA to similar biopolymers or other biomolecules such as non-structural proteins. There is evidence that sugar damage is linked to oxidant damage in a process termed *glycoxidation*.

Mutation accumulation

Natural selection can support lethal and harmful alleles, if their effects are felt after reproduction. The geneticist J. B. S. Haldane wondered why the dominant mutation that causes Huntington's disease remained in the population, and why natural selection had not eliminated it. The onset of this neurological disease is (on average) at age 45 and is invariably fatal within 10–20 years. Haldane assumed that, in human prehistory, few survived until age 45. Since few were alive at older ages and their contribution to the next generation was therefore small relative to the large cohorts of younger age groups, the force of selection against such late-acting deleterious mutations was correspondingly small. Therefore, a genetic load of late-acting deleterious mutations could be substantial at mutation–selection balance. This concept came to be known as the **selection shadow** (Figure $8.4.3$).

Peter Medawar formalized this observation in his mutation accumulation hypothesis of aging. "The force of natural selection weakens with increasing age—even in a theoretically immortal population, provided only that it is exposed to real hazards of mortality. If a genetic disaster... happens late enough in individual life, its consequences may be completely unimportant".

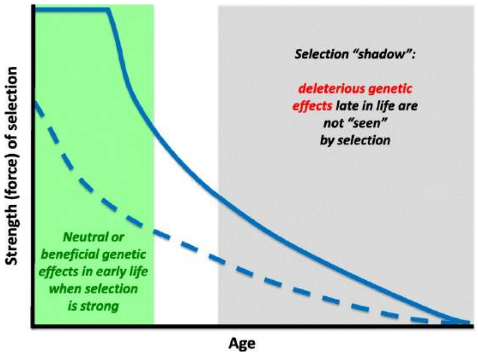


Figure $8.4.3$: The declining force of selection. The strength ('force') of selection measures how strongly natural selection acts on changes in survival and/or fecundity. Often, but not always, the force of selection declines with age. If this is the case, then alleles with neutral effects on fitness early in life but with deleterious effects late in life can accumulate in a population, unchecked by selection (mutation accumulation). Similarly, alleles with positive effects on fitness components early in life can be selectively favored even if they have negative effects late in life (antagonistic pleiotropy). The late-life negative effects in the 'selection shadow' cannot be effectively eliminated by selection, leading to senescence. While the force acting on survival (solid line) only starts to decrease with age after the onset of reproduction, the strength of selection on fecundity (dashed line) can increase or decrease before the onset of reproduction. *Source: Flatt and Partridge,* https://doi.org/10.1186/s12915-018-0562-z.

Trade-offs with life span are pervasive but can be uncoupled

Studies of natural populations have also found support for phenotypic trade-offs consistent with the notion of antagonistic pleiotropy / disposable soma (Nussey et al. 2013, Peron et al. 2010). In bats, for example, species that produce more offspring are shorter-lived than those that produce fewer offspring (Kim et al. 2011). Similarly, a recent review of 26 studies of free-ranging populations of 24 vertebrate species (birds, mammals, reptiles) has identified clear-cut trade-offs between early and late fitness components (Lemaitre et al. 2015), and data in humans have unraveled a genetically based trade-off between reproduction and life span (Wang et al. 2013). Trade-offs thus seem to be pervasive: high resource allocation to growth or reproduction early in life is often associated with earlier or more rapid aging. However, there is also growing evidence that trade-offs between life span and other fitness components are context-dependent and can be 'uncoupled', as is observed in some long-lived *C. elegans* or *Drosophila* mutants (Flatt & Schmidt 2009, Flatt 2011, Rodrigues & Flatt 2016, Flatt & Heyland 2011), or upon manipulation of specific dietary amino acids in flies (Grandison et al. 2009, Selman et al. 2008; see below), without any apparent fitness costs of longevity. In these cases, a likely explanation is the artificially benign laboratory environment occupied by these organisms, which may allow them to realize their physiologically maximal possible investments into both survival and reproduction.

The most famous example of an 'uncoupling' of the fecundity–longevity trade-off is seen in eusocial insects (i.e., ants, bees, termites). In many ants, for example, queens are extraordinarily long-lived and highly fertile as compared to the short-lived and sterile workers (Rodrigues & Flatt 2016, Keller & Genoud 1997, Keller & Jemielity 2006, Kuhn & Korb 2016, Heinze & Schrempf 2008, Schrempf et al. 2017, von Wyschetzki et al. 2015, Hartmann & Heinze 2003, Kramer et al. 2015), even though within the worker caste reproductive costs have been found among fertile bumblebee workers (Blacher et al. 2017). On the other hand, in naked mole rats, which are also eusocial, queens and workers have approximately equivalent life spans but workers do not reproduce while queens can produce up to 900 pups (Buffenstein & Jarvis 2002). How can social insect queens (or kings in termites) escape this trade-off? Surprisingly little formal analysis of this problem exists; the standard explanation that has been put forward is that queens and kings live much longer because they are shielded from extrinsic mortality by the workers (Keller & Genoud 1997, Heinze & Schrempf 2008). In addition, queens or kings may defy the fecundity–longevity trade-off because of trade-offs at the colony level (Kramer et al. 2016), with resources provided by workers freeing them from individual-level trade-offs; at the colony level, queens and kings might be viewed, metaphorically, as representing the 'immortal germline', whereas workers can be seen as representing the 'disposable soma' (Kramer & Schaible 2013). Classic theories of aging may also not fully apply to eusocial insects (Kramer et al. 2016): their populations exhibit not only age structure but also strong social structure and division of labor. Since in such a situation survival is not only age- but also state-dependent, the force of selection does not necessarily decline with age (Williams & Day 2003). More theoretical work on aging in eusocial insects is warranted, especially the development of class-structured inclusive fitness (kin selection) models (Rodrigues & Flatt 2016, Kramer et al. 2016, Kramer & Schaible 2013, Bourke 2007).

An important insight into the likely explanation for the 'breaking' or 'uncoupling' of trade-offs comes from the different outcomes of attempts to measure reproductive costs by looking at natural correlations across individuals as opposed to experimental manipulation of reproductive rate. Generally, *across* individuals in natural populations, there is a positive phenotypic correlation between fecundity and life span. However, the causal connection between the two traits may be the opposite, as experimental manipulations of, for instance, increasing clutch size in birds, often lead to reduced future fecundity or survival (Partridge 1992). This difference occurs because the *individual variation* in condition and circumstances may obscure the underlying cost of reproduction: healthy individuals in a rich environment may have high fecundity and life span despite the cost of reproduction, which is only revealed by experimental manipulations. This concept has been termed the '**big house, big car effect**' (van Noordwijk & de Jong 1986). This underlying cost of reproduction may then constrain the combinations of life history traits that can evolve (van Noordwijk & de Jong 1986, Metcalf 2016). Organisms that live in an environment that is beneficial for development may indeed not experience costs of reproduction (van Noordwijk & de Jong 1986, Metcalf 2016), as often seems to be the case in laboratory animals (Klepsatel et al. 2013). In addition, positive correlations between fitness-related traits can also be caused by mutational variation in recessive deleterious effects (Charlesworth 1990). This arises because such deleterious mutations can have negative pleiotropic effects on two or more traits but the extent of these negative effects varies genetically among individuals.

Definition: The big house, big car effect

The *big house, big car effect* says that individuals differ in the amount of resources (energy, time, or space) they can allocate to competing demands. For example, in humans, each of us has a limited amount of monetary resources. If we were forced to choose between spending our money on a nice house or a nice car (an allocation trade-off), most of us would end up with either a nice house or a nice car, but some people are super wealthy and can afford *both* a big house and a nice car. If we are only looking *across* individuals and not accounting for the amount of resources each has accumulated, we often see patterns like this, which suggest an uncoupling of trade-offs. But because individuals differ in their available resources, this observation is not an accurate representation of the true trade-off that is being experience by each individual at the *within-individual level*.

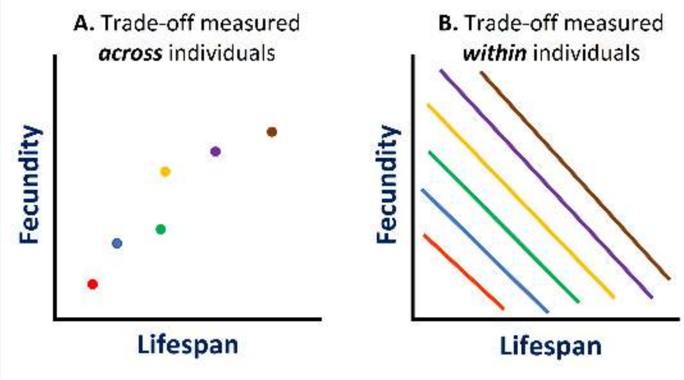


Figure 8.4.4: The 'big house, big car effect' states that individuals differ in the amount of resources they can allocate to competing demands, and thus if we were to correlate life history traits across individuals (A), we can observe an uncoupling of the trade-off. However, because individuals differ in their available resources, this observation is not an accurate representation of the true trade-off that is being experience by each individual at the within-individual level (B). Each color of dot or line represents a different individual with a different amount of resources. *Source: Dan Wetzel.*

The evolution of aging in humans

Human life expectancy worldwide has increased dramatically. During the ~300,000 generations since the divergence from our most recent common ancestor with the great apes, life span evolved to double its previous value (Finch 2010). In the last ~200 years there has been a further substantial increase, on average about 2.5 years per decade, attributable to environmental changes, including improved food, water, hygiene, and living conditions, reduced impact of infectious disease with immunization and antibiotics, and improved medical care at all ages (Vaupel et al. 1998, Wilmoth 2000, Oeppen & Vaupel 2002, Vaupel 2010). Many modern humans inhabit a very different environment from that in which their life history evolved, with both protection from many of its dangers, such as predators, infectious diseases, and harsh physical conditions, and freedom from the need to forage extensively to avoid starvation (Finch 2010). As a result, most people are now living long beyond the ages at which most would have been dead in the past. Natural selection has therefore not had an opportunity to maintain evolutionary fitness at older ages.

In humans, where age-related changes are particularly well documented, aging has proved to be a complex process of functional decline and accumulation of diverse pathologies in different tissues (Lopez-Otin et al. 2013, Kirkwood et al. 1999). Williams predicted in 1957 that aging is likely to be a genetically complex trait, and different lineages and taxa might well exhibit different proximate mechanisms of senescence. Indeed, natural variation in the rate of aging is likely influenced by many genes (Burke et al. 2014, Highfill et al. 2016, Ivanov et al. 2015), since survival and reproduction between them harness the activity of much of the genome.

Figure 8.4.5: Aging in humans. *Source: RODNAE Productions and Andrea Piacquadio.*

Prevention of late-life morbidity in humans ideally would involve interventions that could be started at the earliest in middle age. Pharmacological prevention of cardiovascular disease, with statins and blood pressure lowerers, is already routine in clinical practice (Sundstrom et al. 2018). Unsurprisingly, many of the proteins that have turned out to be important in aging also play prominent roles in the etiology of age-related diseases, and are already the targets of licensed drugs. Consideration is hence starting to be given to widening the preventative, pharmacological approach, for instance by repurposing drugs that are used to treat cancer, prevent rejection of transplanted organs, and diabetes because they have been found to extend life span in model organisms (Blenis 2017, Mannick et al. 2014, Barzilai et al. 2016, Johnson & Kaeberlein 2016). Other possible approaches to emerge from experimental work with animals include removal of damaging senescent cells that accumulate during aging (Childs et al. 2015, Rando & Chang 2012), use of factors from young blood that restore the age-related loss of function of stem cells or synapses between nerve cells in the brain (Rando & Chang 2012, Mair & Dillin 2008), and alteration of the composition of the microorganisms in the gut to a younger profile (Clark & Walker 2018, Kundu et al. 2017, Schmidt et al. 2018), which has already been shown to extend life span in the turquoise killifish (Smith et al. 2017).

However, despite the considerable promise of these approaches, the extent to which they can yield health benefits free of side effects needs detailed study, since they could pose some new challenges for an aged system. For instance, removal of senescent cells, or restoration of stem cell function, could be beneficial in the short term, but in the longer term could lead to stem cell exhaustion and tissue dysfunction.

Sources

- Barzilai, N., Crandall, J.P., Espeland, M.A., & Kritchevsky, S.B. (2016). Metformin as a tool to target aging. *Cell Metab, 23*(6), pp. 1060–5.

- Baudisch A. (2005). Hamilton’s indicators of the force of selection. *Proc Natl Acad Sci USA, 102*(23), pp. 8263–8.
- Baudisch A. (2008). Inevitable aging? *Berlin: Springer*.
- Baudisch, A., Salguero-Gómez, R., Jones, O.R., Wrycza, T., Mbeau-Ache, C., Franco, M., et al. (2013). The pace and shape of senescence in angiosperms. *J Ecol*, *101*(3), pp. 596–06.
- Blacher, P., Bourke, A.F.G, & Huggins, T.J. (2017). Evolution of ageing, costs of reproduction and the fecundity–longevity trade-off in eusocial insects. *Proc R Soc Lond B, 284*. 20170380.
- Blenis, J. (2017). The gateway to cellular metabolism, cell growth, and disease. *Cell*, *171*(1), pp. 10–3.
- Bourke, A.F.G. (2007). Kin selection and the evolutionary theory of aging. *Annu Rev Ecol Evol Syst*, *38*, pp. 103–28.
- Buffenstein, R., & Jarvis, J.U.M. (2002). The naked mole rat: A new record for the oldest living rodent. *Sci Aging Knowl Environ*, *2002*(21):pe7.
- Burke, M.K., King, E.G., Long, A.D., Rose, M.R., & Shahrestani, P. (2014). Genome-wide association study of extreme longevity in *Drosophila melanogaster*. *Genome Biol Evol.*, *6*(1), pp. 1–11.
- Bythell, J.C., Brown, B.E., & Kirkwood, T.B.L. (2017). Do reef corals age? *Biol Rev.*, *93*(2), pp. 1192–02.
- Charlesworth, B. (1990). Optimization models, quantitative genetics, and mutation. *Evolution*, *44*, pp. 520–38.
- Charlesworth, B. (1994). *Evolution in age-structured populations*. 2nd ed. Cambridge: Cambridge University Press.
- Childs, B.G., Durik, M., Baker, D.J., & van Deursen, J.M. (2015). Cellular senescence in aging and age-related disease: from mechanisms to therapy. *Nat Med*, *21*, pp. 1424–35.
- Childs, B.G., Gluscevic, M., Baker, D.J., Laberge, R.M., Marquess, D., Dananberg, J., & van Deursen, J.M. (2017). Senescent cells: an emerging target for diseases of ageing. *Nat Rev Drug Discov.*, *16*, pp. 718–35.
- Clark, R.I., & Walker, D.W. (2018). Role of gut microbiota in aging-related health decline: insights from invertebrate models. *Cell Mol Life Sci.*, *75*(1), pp. 93–101.
- Comfort, A. (1956). *The biology of senescence*. London: Routledhe & Kegan Paul.
- Finch, C.E. (2010). Evolution of the human life span and diseases of aging: roles of infection, inflammation, and nutrition. *Proc Natl Acad Sci USA*, *107*(suppl 1), pp. 1718–24.
- Finch, C.E. (1990). *Longevity, senescence, and the genome*. Chicago and London: The University of Chicago Press.
- Finch, C.E. (2009). Update on slow aging and negligible senescence: A mini-review. *Gerontology*, *55*(3), pp. 307–13.
- Finch, C.E. (1998). Variations in senescence and longevity include the possibility of negligible senescence. *J Gerontol A Biol Sci Med Sci.*, *53*(4):B235–9.
- Finch, C.E., & Austad, S.N. (2001). History and prospects: Symposium on organisms with slow aging. *Exp Gerontol*, *36*(4), pp. 593–7.
- Flatt, T. (2011). Survival costs of reproduction in *Drosophila*. *Exp Gerontol*, *46*(5), pp. 369–75.
- Flatt, T., & Heyland, A. (2011). *Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs*. Oxford: Oxford University Press.
- Flatt, T., & Schmidt, P.S. (2009). Integrating evolutionary and molecular genetics of aging. *Biochim Biophys Acta.*, *1790*(10), pp. 951–62.
- Dahlgren, J.P., Ehrlén, J., & Garcia, M.B. (2011). No evidence of senescence in a 300-year-old mountain herb. *J Ecol.*, *99*(6), pp. 1424–30.
- Grandison, R.C., Partridge, L., & Piper, M.D.W. (2009). Amino-acid imbalance explains extension of life span by dietary restriction in *Drosophila*. *Nature*, *462*(7276), pp. 1061–5.
- Hartmann. A., & Heinze, J. (2003). Lay eggs, live longer: division of labor and life span in a clonal ant species. *Evolution*, *57*, pp. 2424–9.
- Heinze, J., & Schrempf, A. (2008). Aging and reproduction in social insects: A mini-review. *Gerontology*, *54*, pp. 160–7.

- Highfill, C.A., Macdonald, S.J., & Reeves, G.A. (2016). Genetic analysis of variation in life span using a multiparental advanced intercross *Drosophila* mapping population. *BMC Genet., 17*(1):113.
- Ivanov, D.K., Escott-Price, V., Ziehm, M., Magwire, M.M., Mackay, T.F.C., Partridge, L., et al. (2015). Longevity GWAS using the *Drosophila* genetic reference panel. *J Gerontol A Biol Sci Med Sci., 70*(12), pp. 1470–8.
- Johnson, S.C., & Kaeberlein, M. (2016). Rapamycin in aging and disease: Maximizing efficacy while minimizing side effects. *Oncotarget, 7*(29), pp. 44876–8.
- Jones, O.R., Scheuerlein, A., Salguero-Gomez, R., Camarda, C.G., Schaible, R., Casper, B.B., et al. (2014). Diversity of ageing across the tree of life. *Nature, 505*(7482), pp. 169–73.
- Keller, L., & Genoud, M. (1997). Extraordinary life spans in ants: A test of evolutionary theories of ageing. *Nature, 389*, pp. 958–60.
- Keller, L., & Jemielity, S. (2006). Social insects as a model to study the molecular basis of ageing. *Exp Gerontol, 41*, pp. 553–6.
- Kirkwood, T.B.L., Martin, G.M., & Partridge, L. (1999). Evolution, senescence and health in old age. In: Stearns SC, editor. *Evolution in health and disease*. Oxford: Oxford University Press, p. 219–30.
- Klepsatel, P., Gáliková, M., Maio, N., Schlötterer, C., & Flatt, T. (2013). Reproductive and post-reproductive life history of wild-caught *Drosophila melanogaster* under laboratory conditions. *J Evol Biol., 26*(7), pp. 1508–20.
- Kramer, B.H., & Schaible, R. (2013). Life span evolution in eusocial workers: A theoretical approach to understanding the effects of extrinsic mortality in a hierarchical system. *PLoS One, 8*:e61813.
- Kramer, B.H., Schrempf, A., Scheuerlein, A., & Heinze, J.(2015). Ant colonies do not trade-off reproduction against maintenance. *PLoS One, 10*:e0137969.
- Kramer, B.H., van Doorn, G.S., & Weissing, F.J. (2016). Pen I. life span divergence between social insect castes: challenges and opportunities for evolutionary theories of aging. *Curr Opin Insect Sci., 16*, pp. 76–80.
- Kuhn, J.M.M., & Korb, J. (2016). Editorial overview: social insects: aging and the re-shaping of the fecundity/longevity trade-off with sociality. *Curr Opin Insect Sci., 16*, pp. vii–x.
- Kundu, P., Blacher, E., Elinav, E., & Pettersson, S. (2017). Our gut microbiome: The evolving inner self. *Cell, 171*(7), pp. 1481–93.
- Lemaitre, J.F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F. et al. (2015). Early-late life trade-offs and the evolution of ageing in the wild. *Proc R Soc Lond B., 282*(1806):20150209.
- Lemaître, J.F., & Gaillard, J.M. (2017). Reproductive senescence: new perspectives in the wild. *Biol Rev., 92*, pp. 2182–99.
- Lopez-Otin, C., Blasco, M.A., Partridge, L., Serrano, M., & Kroemer, G. (2013). The hallmarks of aging. *Cell, 153*(6), pp. 1194–217.
- Mannick, J.B., Del Giudice, G., Lattanzi, M., Valiante, N.M., Praestgaard, J., Huang, B., Lonetto, M.A., Maecker, H.T., Kovarik, J., Carson, S., et al. (2014). mTOR inhibition improves immune function in the elderly. *Sci Transl Med., 6*(268):268ra179.
- Metcalf, C.J.E. (2016). Invisible trade-offs: Van Noordwijk and de Jong and life-history evolution. *Am Nat., 187*(4):iii–v.
- Munné-Bosch, S. (2015). Senescence: Is it universal or not? *Trends Plant Sci., 20*(11), pp. 713–20.
- Noodén, L.D. (1988). Whole plant senescence. In Thiman, K.V., & Leopold, A.C. (Eds.), *Senescence and aging in plants*. Cambridge: Academic Press, p. 391–439.
- Nussey, D.H., Froy, H., Lemaitre, J.F., Gaillard, J.M., & Austad, S.N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Res Rev., 12*(1), pp. 214–25.
- Oeppen, J., Vaupel, J.W. (2002). Broken limits to life expectancy. *Science, 296*(5570), pp. 1029–31.
- Partridge, L. (1992). Measuring reproductive costs. *Trends Ecol Evol., 7*(3), pp. 99–100.
- Partridge, L., & Barton, N.H. (1996). On measuring the rate of ageing. *Proc R Soc Lond B., 263*(1375), pp. 1365–71.

- Peron, G., Gimenez, O., Charmantier, A., Gaillard, J.M., & Crochet, P.A. (2010). Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proc R Soc Lond B., 277*, pp. 2849–56.
- Petralia, R.S., Mattson, M.P., & Yao, P.J. (2014). Aging and longevity in the simplest animals and the quest for immortality. *Ageing Res Rev., 16*, pp. 66–82.
- Rodrigues, M.A., & Flatt, T. (2016). Endocrine uncoupling of the trade-off between reproduction and somatic maintenance in eusocial insects. *Curr Opin Insect Sci., 16*, pp. 1–8.
- Ruby, J.G., Smith, M., & Buffenstein, R. (2018). Naked mole-rat mortality rates defy Gompertzian laws by not increasing with age. *elife., 7*:e31157.
- Salguero-Gómez, R., Shefferson, R.P., & Hutchings, M.J. (2013). Plants do not count … or do they? New perspectives on the universality of senescence. *J Ecol., 101*(3), pp. 545–54.
- Schaible, R., Scheuerlein, A., Dańko, M.J., Gampe, J., Martínez, D.E., & Vaupel, J.W. (2015). Constant mortality and fertility over age in *Hydra*. *Proc Natl Acad Sci USA, 112*(51), pp. 15701–6.
- Schmidt, T.S.B., Raes, J., & Bork, P. (2018). The human gut microbiome: From association to modulation. *Cell, 172*(6), pp. 1198–215.
- Schrempf, A., Giehr, J., Röhrl, R., Steigleder, S., & Heinze, J. (2017). Royal Darwinian demons: enforced changes in reproductive efforts do not affect the life expectancy of ant queens. *Am Nat., 189*(4), pp. 436–42.
- Selman, C., Lingard, S., Choudhury, A.I., Batterham, R.L., Claret, M., Clements, M., et al. (2008). Evidence for life span extension and delayed age-related biomarkers in insulin receptor substrate 1 null mice. *FASEB J., 22*(3), pp. 807–18.
- Shefferson, R.P., Jones, O.R., & Salguero-Gómez, R. (2017). The evolution of senescence in the tree of life. *Cambridge: Cambridge University Press.*
- Smith, P., Willemsen, D., Popkes, M., Metge, F., Gandiwa, E., Reichard, M., & Valenzano, D.R. (2017). Regulation of life span by the gut microbiota in the short-lived African turquoise killifish. *elife., 6*:e27014.
- Sundström, J., Gulliksson, G., & Wirén, M. (2018). Synergistic effects of blood pressure-lowering drugs and statins: Systematic review and meta-analysis. *BMJ Evid Based Med., 23*(2), pp. 64–9.
- Thomas, Chang. (2012). Aging, rejuvenation, and epigenetic reprogramming: Resetting the aging clock. *Cell, 148*(1), pp. 46–57.
- Van Noordwijk, A., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *Am Nat., 128*(1), pp. 137–42.
- Vaupel, J.W. (2010). Biodemography of human ageing. *Nature, 464*(7288), pp. 536–42.
- Vaupel, J.W., Baudisch, A., Dolling, M., Roach, D.A., & Gampe, J. (2004). The case for negative senescence. *Theor Popul Biol., 65*(4), pp. 339–51.
- Vaupel, J.W., Carey, J.R., Christensen, K., Johnson, T.E., Yashin, A.I., Holm, N.V., et al. (1998). Biodemographic trajectories of longevity. *Science, 280*(5365), pp. 855–60.
- Von Wyschetzki, K., Rueppell, O., Oettler, J., & Heinze, J. (2015). Transcriptomic signatures mirror the lack of the fecundity/longevity trade-off in ant queens. *Mol Biol Evol., 32*, pp. 3173–85.
- Wang, X., Byars, S.G., & Stearns, S.C. (2013). Genetic links between post-reproductive life span and family size in Framingham. *Evol Med Pub Health*, (1), pp. 241–53.
- Warner, D.A., Miller, D.A.W., Bronikowski, A.M., & Janzen, F.J. (2016). Decades of field data reveal that turtles senesce in the wild. *Proc Natl Acad Sci USA, 113*, pp. 6502–7.
- Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution, 11*, pp. 398–411.
- Williams, P.D., & Day, T. (2003). Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution, 57*(7), pp. 1478–88.
- Wilkinson, G.S., & South, J.M. (2002). Life history, ecology and longevity in bats. *Aging Cell, 1*(2), pp. 124–31.
- Wilmoth, J.R. (2000). Demography of longevity: past, present, and future trends. *Exp Gerontol., 35*(9-10), pp. 1111–29.

Contributors and Attributions

This chapter was written by D. Wetzel with text taken from the following CC-BY resources:

- Flatt, T., Partridge, L. (2018). Horizons in the evolution of aging. *BMC Biol*, *16*(93). https://doi.org/10.1186/s12915-018-0562-z
- Andrade, R., Carrilho, F., De Sousa Lages, A., Espreguiera-Mendes, J., Mota-Pinto, A., Rebelo-Marques, A., & Ribeiro C.F. (2018). Aging hallmarks: The benefits of physical exercise. *Front. Endocrinol*, *9*(258). https://www.frontiersin.org/articles/10.3389/fendo.2018.00258/full
- Wikipedia: https://en.wikipedia.org/wiki/Senescence

CHAPTER OVERVIEW

9: The Ecology of Populations

Learning Objectives

- Define what ecologists mean by a population of organisms and the focus and scope of the science of population ecology.
- Introduce the key features of populations studied by ecologists, wildlife biologists, and conservation biologists -- such as size, density, and range -- and the field methods used to study them.
- Outline common patterns of population change, such as growth, extirpation, extinction, and cycles.
- Introduce the concepts of population regulation, density independence, and density dependence.

Summary

Populations are one of the major levels of biological organization, and "population thinking" has played a key role in ecology and evolutionary biology since Darwin. Currently, many researchers and natural resource managers are trained as population ecologists, from academics who study basic questions in evolutionary ecology to government scientists who determine catch limits for fisheries. In this chapter we define what populations are, their key features which are considered by basic and applied ecologists, and the techniques used out in the field to study populations. We'll also introduce key ecological concepts which will be elaborated on in the next chapter, including population regulation, density independence, and density dependence.

9.1: What is population ecology?

What is population ecology?

Thousands of bird species breed and reproduce in North America. Some, like the American Robin (*Turdus migratorius*), are widespread, and can be found building nests and raising their young in every state of the USA, several Canadian provinces, and many locations in Mexico. Others, like Kirtland's Warbler (*Setophaga kirtlandii)* breed almost entirely within a single state (Fig. 9.1.1); a few, like the Cozumel thrasher (*Toxostoma guttatum*) and Socorro mockingbird (*Mimus graysoni*) are found only on single small islands. Population ecologists study what determines the occurrence and abundance of species in space and time: their geographic ranges, population sizes and densities, and what factors result in them being so rare or common.

Population ecology is the science of population dynamics in space and time

Ecology is often defined as the study of the **distribution** and **abundance** of organisms. **Population ecology** is the branch of ecology that works to understand the patterns and processes of change over time or space for populations of a single species. A **species** is typically defined as a group of organisms capable of interbreeding. For some species, all of the members of the species occur in the same geographic area and could potentially meet and interbreed during their lifetimes. Most species, however, can be divided into geographically separate **populations**. Individuals within a single population are likely to interact and perhaps interbreed, while those from different populations will only come into contact if there is long-range movement between the populations (**dispersal**).

Populations can be described by their size, density, or spatial extent

One species that currently consists of a single population is the Kirtland’s warbler (*Setophaga kirtlandii*), a North American songbird. Almost all members of this species occur in the northern part of the state of Michigan in the United States (Figure 9.1.1). In contrast, the Spotted Owl (*Strix occidentalis*) is a species with many distinct populations throughout the western United States, southern Canada, and central Mexico.

Figure 9.1.1: Left: "A male Kirtland's Warbler *Setophaga kirtlandii* in a forest in Michigan, USA" by Jeol Trick is licensed under CC BY 2.0. Right: Core habitat area of Kirtland's Warbler. Source: Google Earth: https://bit.ly/3ofgDK1.

For both species and populations, patterns of distribution and abundance can be considered in several ways. These include:

1. **Size**: How many total individuals there are?
2. **Density**: How many individuals per unit of area?
3. **Dispersion**: How are individuals in a population arranged spatially relative to another? Do they occur in clumps or are they evenly spread apart?
4. **Occupancy**: Does a species or member of a population occur in a given habitat, or is it absent?
5. **Population distribution**: Where does a population occur in space?
6. **Geographic range**: What are the furthest geographic limits of where a species occurs?

In addition to static characteristics of size and distribution, populations are dynamic and fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. To study these many facets of a population's biology, ecologists use both systematic field observations to determine its current status, and mathematical tools to characterize how it responds to changes in the biotic and abiotic environments.

Population size is the number of individuals in a population

Population size is the actual number of organisms in a population. This is often of great interest to biologists – especially those working in forestry, wildlife management and conservation – and most of our basic **population models** work with population sizes. A **complete census** is one way to determine population size and entails counting each individual present within the population. This occurs in some well-studied populations, such as the Kasekela population of chimpanzees in Gombe National Park, Tanzania (Pusey et al. 2008), and the Seychelles Warbler on islands in the Indian Ocean off the coast of East Africa (Burt et al. 2016).

Although it is the most accurate methodology, counting every individual in a population can be difficult, if not impossible. In most cases ecologists can only attempt to estimate the population size (**N**) by using well-designed field studies and statistics. Indeed, some population ecologists specialize in developing mathematical and statistical models to accurately estimate population size, such as **mark-recapture models** and **camera-trapping** methods (detailed below). Often, however, we do not have good estimates of the size of a population itself, but factors that should be correlated with the population size, such as the number of animals harvested by hunters or trapped by ecologists or the density of dung found during a survey.

Data that we think correlates with actual abundance constitutes a **population index**. Index data are cheaper to collect than the data needed for formal estimates of population size such as the mark-recapture methods discussed below, but can be biased and provide an inaccurate sense of the status of a population (Stephens et al. 2015). Ideally, an index should be validated by checking its correlation with rigorous estimates of population size. For example, the abundance of large mammals such as lions, elephants and tigers is frequently indexed by the frequency of their tracks or scat. To determine the reliability of an indirect measure of population size, Belant et al. (2019) compared an index based on lion tracks to a formal estimate of population size. Unfortunately, the commonly used index of lion abundance based on their tracks overestimated abundance.

When species become **endangered** researchers often try to determine - or at least estimate - the number of individuals surviving. For example, with only approximately 4000 individuals, Kirtland’s Warbler is the rarest species breeding in the continental United States and was considered critically endangered throughout most of the 20th century. Researchers therefore worked each spring to determine as best as possible how many male warblers had established territories and were trying to attract mates.

Species that are economically important or are central players in ecosystem functioning are also often monitored intensively. Since the middle of the 20th century the abundance of Wildebeest (*Connochaetes taurinus*) in the Serengeti ecosystem of East Africa has been intensively monitored by aircraft (Figure $9.1.2$). The population was considered to be small in the 1960s when it numbered around 250,000, but by the 1990s had grown to over 1 million (Mduma et al. 1999).

Figure 9.1.2: Wildebeest in Maasai Mara. Photo by Bjørn Christian Tørrissen, http://bjornfree.com/galleries.html.

Population density is the relative abundance of an organism

While population size is a total count of individuals, **population density** is how many individuals occur in a given area of space. It is therefore a measure of **relative abundance**. For animals and trees, this is often the estimated number of animals per hectare (a hectare is 100 m by 100 m, or 2.47 acres). For plants, insects, and other smaller organisms this is often the number per square meter.

Kirtland's Warbler is a **habitat specialist** and only nests in forests dominated by a single conifer, the Jack Pine (*Pinus banksiana*). Moreover, it only nests in Jack Pines of a certain age (5-20 years) and density (>3000 pines per hectare; Donner et al. 2018). When conditions are optimal, there is usually one breeding pair of warblers per 70 hectares, or 1.4 pairs per 100 hectares (Densities are usually reported for standard areas such as 1 square meter, 100 hectares, etc.).

Estimates of population density are often much easier to obtain than estimates of total population size. Population density can be converted to a rough estimate population size through simple multiplication. If there are 1.4 pairs per hectare of good habitat, and there are 2800 hectares of habitat, we can calculate the number of pairs as 1.4 x 2000 = 2800 pairs. Two things are key to this calculation, however: first, the estimate of density is accurate, and second, the estimate of the amount of good habitat is accurate.

Recently, great progress in estimating animal density has been made using camera traps (Fig. 9.1.3). These are especially useful for studying rare and nocturnal animals, such as predators. For example, lions (*Panthera leo*) are considered vulnerable to extinction and are most threatened in West Africa, where they are restricted to a few small national parks. In western-most West Africa lions occur only in Niokolo-Koba National Park in south-eastern Senegal (Henschel et al. 2014). Mamadou Kane used camera traps to estimate the density of lions in Niokolo-Koba (Kane et al. 2015). While the entire park is 9130 km^2, Kane sampled an area of approximately 285.4 square kilometers within the highest quality lion habitat of the park. Kane estimated that there are about 3 lions per 100 square kilometers in this high-quality habitat (100 square kilometers is an area 10 km by 10 km). Three lions per 100 km^2 equals 0.03 per km^2. We can therefore estimate the total abundance in the study area as 0.03 x 285.4 = 8.6 lions.

Figure 9.1.3: "A camera trap, for taking pictures of game on trails" by Hustvedt is licensed under CC BY-SA 3.0. This model is for hunting. Motion detector on top, lens in the middle, flash on the bottom, with a little LCD for showing how many pictures taken/left on the left.

Occupancy reports the presence or absence of a population

Occupancy is simply whether a given species or member of a population occurs in a habitat patch, fragment, or area. Often it can be very difficult to count the number of individuals or determine their density; instead of asking a question like "*How many owls are there in this forest?*" it's relatively easier to ask "*Are there* any *owls present in this forest?*" It can be very time-consuming to do counts or determine density, which can limit researchers' ability to study multiple sites or locations. Focusing on determining just the presence or absence of a population in a habitat often allows researchers to study a larger area.

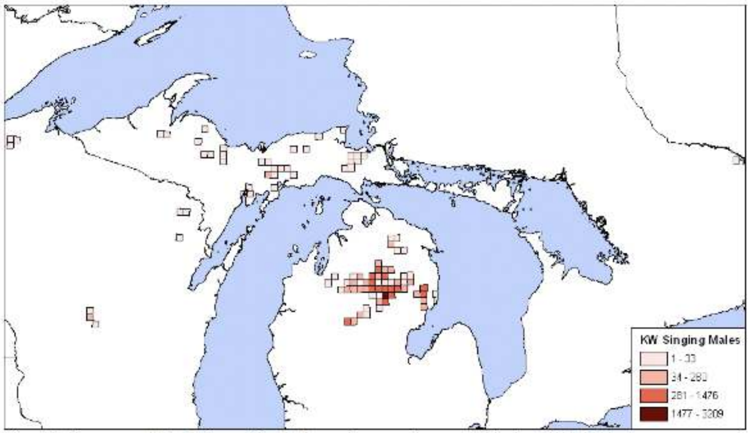


Figure 9.1.4: Frequency of Kirtland's warbler singing males counted per township from 2000-2011. *Source: U.S. Fish and Wildlife Service.*

Kirtland's Warbler is currently increasing its **population size** and is being found in stands of Jack Pine outside of the state of Michigan (Figure 9.1.4). Since the warbler's population is increasing, researchers are more interested in doing **occupancy surveys** to determine which patches of forest warblers are occurring in rather than determining exactly how many warblers are in these forests (Richards 2008).

Camera traps and occupancy studies can be used to determine if a species has become locally extinct. Giodano, Tumenta and Iongh (2017) carried out a camera-trap based occupancy study of Waza National Park in Cameroon. While they confirmed the occupancy of lions in the park, no leopards (*Panthera pardus*) were photographed. Since lions and leopards are typically similarly difficult to detect and lions were detected, they concluded that there were no longer any leopards occupying the park.

Individuals within a population can have characteristics patterns of dispersion

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species **dispersion patterns** (or distribution patterns) summarize the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the population live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as **uniform**, **random**, and **clumped** dispersion patterns, respectively (Figure 9.1.5). **Uniform dispersion** can occur in plants and is thought to result from competition for below-ground resources such as water, or secretion of substances inhibiting the growth of nearby individuals, a phenomenon called **allelopathy**. In animals like penguins that nest in large colonies, uniform dispersion can occur due to territorial behavior. An example of **random dispersion** occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion pattern of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

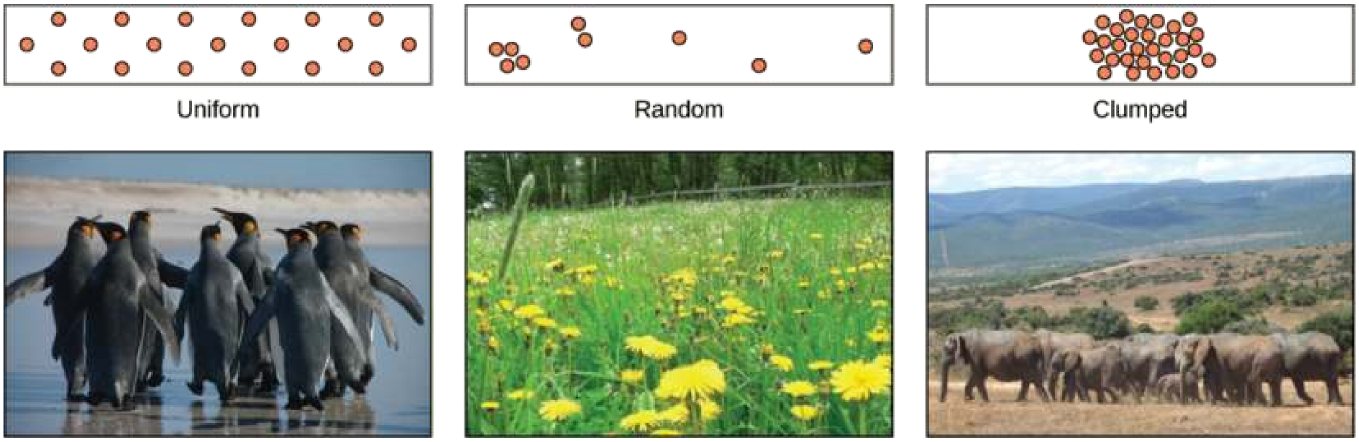


Figure 9.1.5: Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood).

Populations distributions are limited to suitable habitats

In ecology, a **niche** is the match of a species to a specific environmental condition. It describes how an organism or population responds to the distribution of environmental resources (abiotic components of the environment) and predators, pathogens, and competitors (biotic components of the environment). **Habitat** refers to the array of resources, physical and biotic factors that are present in an area, such as to support the survival and reproduction of a particular species. The geographic range of a species can be viewed as a spatial reflection of its niche, along with characteristics of the geographic template and the species that influence its potential to colonize. The **fundamental geographic range** of a species is the area it occupies in which environmental conditions are favorable, without restriction from barriers to disperse or colonize (Lomolino et al 2009). A species will be confined to its **realized geographic range** when confronting biotic interactions or abiotic barriers that limit dispersal, a more narrow subset of its larger fundamental geographic range.

An early study on ecological niches conducted by Joseph H. Connell analyzed the environmental factors that limit the range of a barnacle (*Chthamalus stellatus*) on Scotland's Isle of Cumbrae (Connell 1961) (Figure 9.1.7. In his experiments, Connell described the dominant features of *C. stellatus* niches and provided explanation for their distribution on intertidal zone of the rocky coast of the Isle. Connell described the upper portion of C. stellatus's range as limited by the barnacle's ability to resist dehydration during periods of low tide. The lower portion of the range was limited by interspecific interactions, namely competition with a cohabiting barnacle species and predation by a snail (Connell 1961). By removing the competing *B. balanoides*, Connell showed that *C. stellatus* was able to extend the lower edge of its realized niche in the absence of competition. These experiments demonstrate how biotic and abiotic factors limit the distribution of an organism.

Figure 9.1.7: *Chthamalus stellatus*, photographed near the upper shoreline, Lundy Island, UK. Max shell length about 10mm. *Source: MichaelMaggs and is published with a CC-BY-SA 3.0 license.*

The area occupied by a species can be considered at different scales

Population distribution is the geographic area where a particular population of a species occurs. This area of occupancy is determined by the local availability of appropriate habitat. Some species are **habitat generalists** (species that can thrive in a wide variety of environmental conditions; see Chapter 13) and their populations spread out almost continuously across a landscape. American Robins, for example, can breed in parks, urbanized areas, farms, and the edges of forest. Other species are **habitat specialists** and only occur in specific places where a certain type of ecosystem occurs. Aquatic species also often occur in isolated populations because their habitat is necessarily bounded by the extent of the lake, wetland, or waterway they occur in.

The Northern Spotted Owl is a **subspecies** of spotted owl that is a **habitat specialist** that only occurs in **old-growth forests** in the Pacific Northwest of North America (British Columbia, Washington, Oregon, California). While much of the Pacific Northwest is still forested, most forests are less than 100 years old and don't have the large, old trees that the owls nest in. The extent of each population of owls is therefore limited by the size of each patch of old growth forest.

A species' **geographic range** is the total geographic area occupied by a species. Bald Eagles can be found breeding in almost every state of the USA and most provinces of Canada. Its geographic range therefore encompasses almost all of North America north of Mexico. In contrast, Golden Eagles breed almost exclusively in western Canada, the western United States, and Mexico. The Golden Eagle's range therefore is restricted to the western part of the continent and Mexico.

As noted above, Kirtland's warblers are habitat specialists, which means that the species only reside in the Jack Pine Forests of northern Michigan and a few adjacent states and Canadian provinces. Subsequently, this phenomenon is referred to by biologists as a restricted range. A restricted range species refers to a species in which the range is so small, there is basically a single population. This results in the population distribution and geographic range is essentially the same.

Vocab Alert!

A term that can sometimes be confused with geographic range is **home range**. Geographic range refers to the entire spatial area a species can be found in, while a **home range** refers to an area utilized and perhaps defended by a single organism.

A species' current geographic range is often very different from its **historical range**. Factors such as habitat loss, hunting, and climate change can all reduce the distribution of populations and the species' overall geographic range. For example, lions previously ranged broadly over Africa, Western Asia, the Middle East and India (Figure 9.1.7).

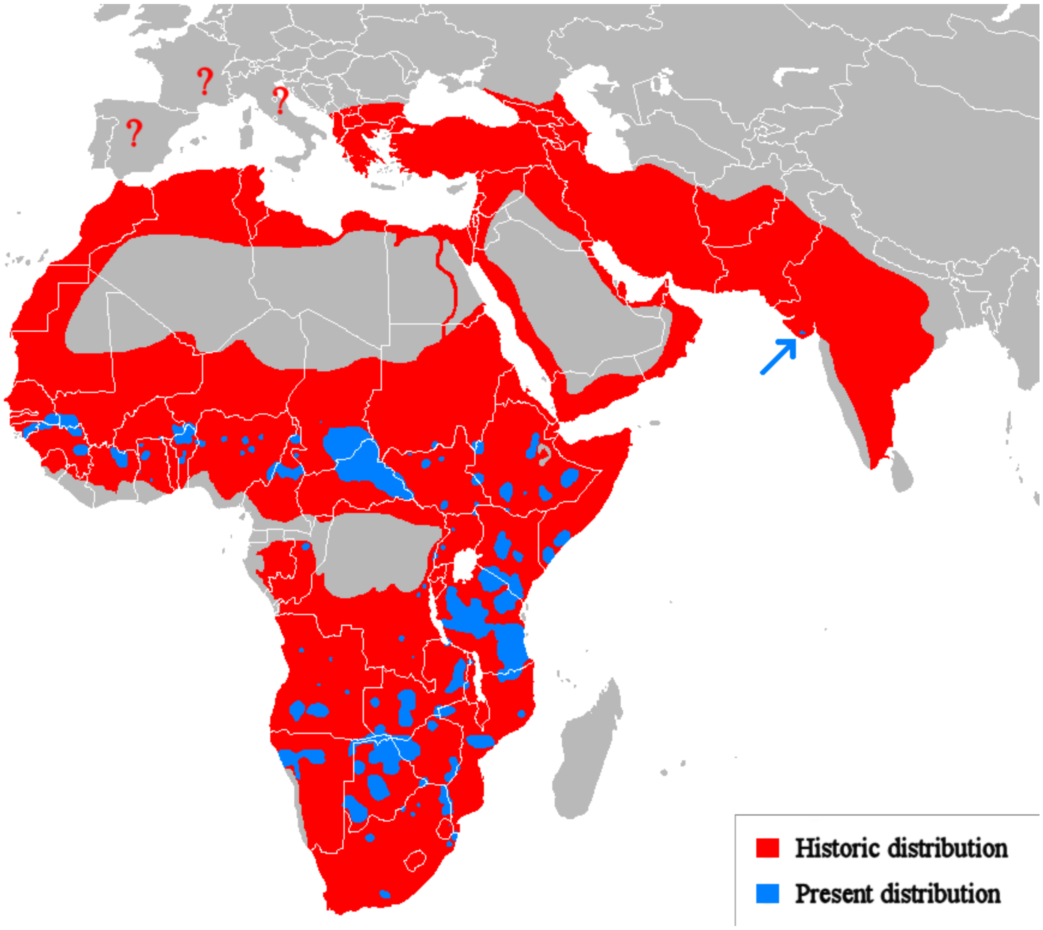


Figure 9.1.7: Historical (red) and present (blue) distribution of lions (*Panthera leo*). *Source: Tommyknocker (Wikipedia), based on a map created by 'The African Lion Environmental Research Trust (ALERT).*

Contributors and Attributions

This chapter was written by N. Brouwer with text taken from the following CC-BY resources:

- **Ecological niche by Wikipedia, the free encyclopedia**
- **OpenStax Biology 2e** section 45.1 Population Demography

9.2: Population Ecology Research Methods

Population ecology research methods

Quadrat-based methods are frequently used by plant ecologists

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a **quadrat** may be used (Figure 9.2.1). A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m^2 quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m^2 might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.

Figure 9.2.1: A scientist uses a quadrat to measure population size and density. *Source: NPS Sonoran Desert Network.*

Distance sampling methods estimate the density of organisms

Other techniques for sampling populations to estimate density or abundance are distance sampling methods. The main methods are based on **line transects** or **point transects** (Buckland et al 1993, Buckland et al 2003). In this method of sampling, the data collected are the distances of the objects being surveyed from these randomly placed lines or points, and the objective is to estimate the average density of the objects within a region (Everitt 2002). When using line transects, the observer randomly places a straight line or follows some pre-planned route through the habitat of the population of interest, then walks the line or route. Whenever the researcher observes an object of interest (e.g., an animal of the type being surveyed), they record the observation, the distance from their current position to the object (r), as well as the angle of the detection to the transect line (θ). The distance of the object to the transect can then be calculated using trigonometry as $x = r * \sin(\theta)$. These distances x are the detection distances that will be analyzed in further modeling aspects of the population (e.g., population distribution in space).

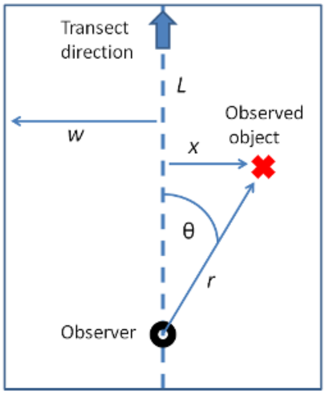


Figure 9.2.2: Basic distance sampling survey approach using line transects. A field observer detects an object and records distance r and angle θ to the transect line. This allows the calculation of object distance to the transect (x). All x from the survey are used to model how detectability decreases with distance from the transect, which allows estimation of total population density in the surveyed area. (Elmidae)

Distance-based methods are frequently used for animals with observers making their observations while walking, riding in trucks, or in low-flying aircraft. They can also be used for tasks such as surveying for very rare trees (Kissa and Sheil 2012) or plants.

Mark-recapture methods estimate the abundance of animals

For mobile organisms, such as mammals, birds, or fish, a technique called **mark and recapture** is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked (Figure 9.2.3).

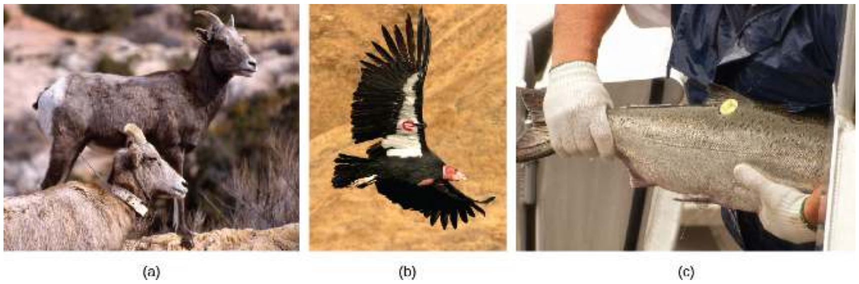


Figure 9.2.3: Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar).

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can determine the population size (N) using the following equation:

$$\frac{(\text{number marked first catch}) * (\text{total number of second catch})}{\text{number marked second catch}} = N \tag{9.2.1}$$

Using our example data,

$$\frac{80 * 100}{20} = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

A common issue with mark-recapture methods is that the process of capturing and marking the animals changes their behavior. This is known generally as a **trap response**. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates; this is known as **trap shyness**. Alternatively, animals may preferentially become **trap-happy** and be more likely to be re-trapped (especially if a food reward is offered), resulting in an underestimate of population size. In some cases, individuals may be harmed by the capture and marking technique, reducing their survival. Advanced mathematical techniques exist for dealing with trap shyness and trap happiness; if mark-recapture methods cause harm to animals, however, the method should not be used.

A variety of other techniques have been developed to collect mark-recapture and similar data, including the electronic tracking of animals tagged with radio or GPS transmitters. Techniques also exist for using trapping-only data such as hunting or commercial fishing operations to estimate the size and health of populations and communities.

? Mark-Recapture Practice Exercise 9.2.1

1) You marked 50 whales at the beginning of the breeding season in 2022 and, during a re-sighting survey at the end of the breeding season, counted 100 whales, 2 of which were tagged. What is your estimate of the total breeding population size in 2022?

2) Do you have any concerns about the validity of your answer?

3) After conducting your mark-recapture study, you find out that female gray whales migrate before male gray whales do, so not all whales would have returned to the breeding grounds when you marked individuals at the start of the season. Using the mark-recapture equation, briefly describe how this impacts the accuracy of your population estimate.

Answer

1) N = (M * S)/R = (50*100)/2 = 2500 whales estimated as the total breeding population size in 2022

2) Two is a very small sample size of re-sightings, making it difficult to ensure accuracy. Far more whales were counted at the end, suggesting that the effort may have been varied throughout the study. Also, sighting whales is difficult due to long diving periods, potentially leading to some whales not being counted, despite being present.

3) M/N = R/S but in this scenario, because N at the time of marking was not the actual size of the population, the R/S ratio at the end of the season will be smaller than predicted (since S will be larger than expected because not all of those individuals were there at the start of the season). As a result, M/N and N will be underestimated.

Contributors and Attributions

This chapter was written by N. Brouwer with text taken from the following CC-BY resources:

- **Distance sampling by Wikipedia, the free encyclopedia**
- **OpenStax Biology 2e** Section 45.1 Population Demography

9.3: Population Dynamics and Regulation

How do populations change?

Changes in population size over time and the processes that cause these to occur are called **population dynamics**. How populations change in abundance over time is a major concern of **population ecology**, **wildlife ecology**, and **conservation biology**, and is related to questions asked in **evolutionary biology**. The **processes** and **mechanisms** that drive population change are varied and include **intraspecific competition** with members of the same population, **interspecific competition** between species, the availability of food or other resources, extreme weather, inbreeding, predators or parasites.

Populations are dynamic and frequently change size, density, or spatial extent

We can consider changes in populations from multiple angles. For example, Kirtland's Warbler (S*etophaga kirtlandii*) in North America is currently:

1. Increasing in the overall number of individuals (**population size**).
2. Increasing in the number of occupied habitat patches (**occupancy**).
3. Increasing in the geographic area it occurs in (**population distribution** and **species range**).

Importantly, since the warbler prefers a certain density of Jack Pine, its density within an occupied habitat also changes. Jack Pine stands are naturally prone to burning in **forest fires**, and are also logged for timber. As the density of trees changes due to these disturbances, the density of warblers changes. After a fire or logging there are few if any mature pine trees and therefore few warblers. Approximately five years after seedlings have sprouted and grown up to be the proper size, the density of warblers can increase. When pine forests get too old habitat conditions are not ideal for the warbler and their abundance declines.

Many studies of population growth focus on changes in population size

Though there are many dimensions to **spatial** and **temporal** population dynamics, discussions of population dynamics often center on changes in population size over time. Changes in population size are often displayed in a **time series graph** with time on the **x-axis** (usually in years) and population size (N) on the y-axis. General patterns of population dynamics in terms of population size include:

1. **Growth**: Growing larger than the current size (Snail kites: Figure $9.3.1$ Panel A)
2. **Decline**: Decreasing in abundance (Elk: Figure $9.3.1$ Panel B)
3. **Stability**: Staying approximately the same size over time (Wolves: Figure $9.3.1$ Panel C)
4. **Recovery**: Stability or growth following a period of decline. (Impala: Figure $9.3.1$ Panel D).
5. **Extirpation (local extinction):** Decline of one or more populations of a species to 0 (Kirtland's Warbler, Figure $9.3.1$ Panel A).
6. **Extinction**: Decline of all members of a species to 0 (Northern White Rhino, Figure $9.3.1$ Panel B).
7. **Cycles**: repeated patterns of growth followed by decline (Lynx: Figure $9.3.1$ Panel C)

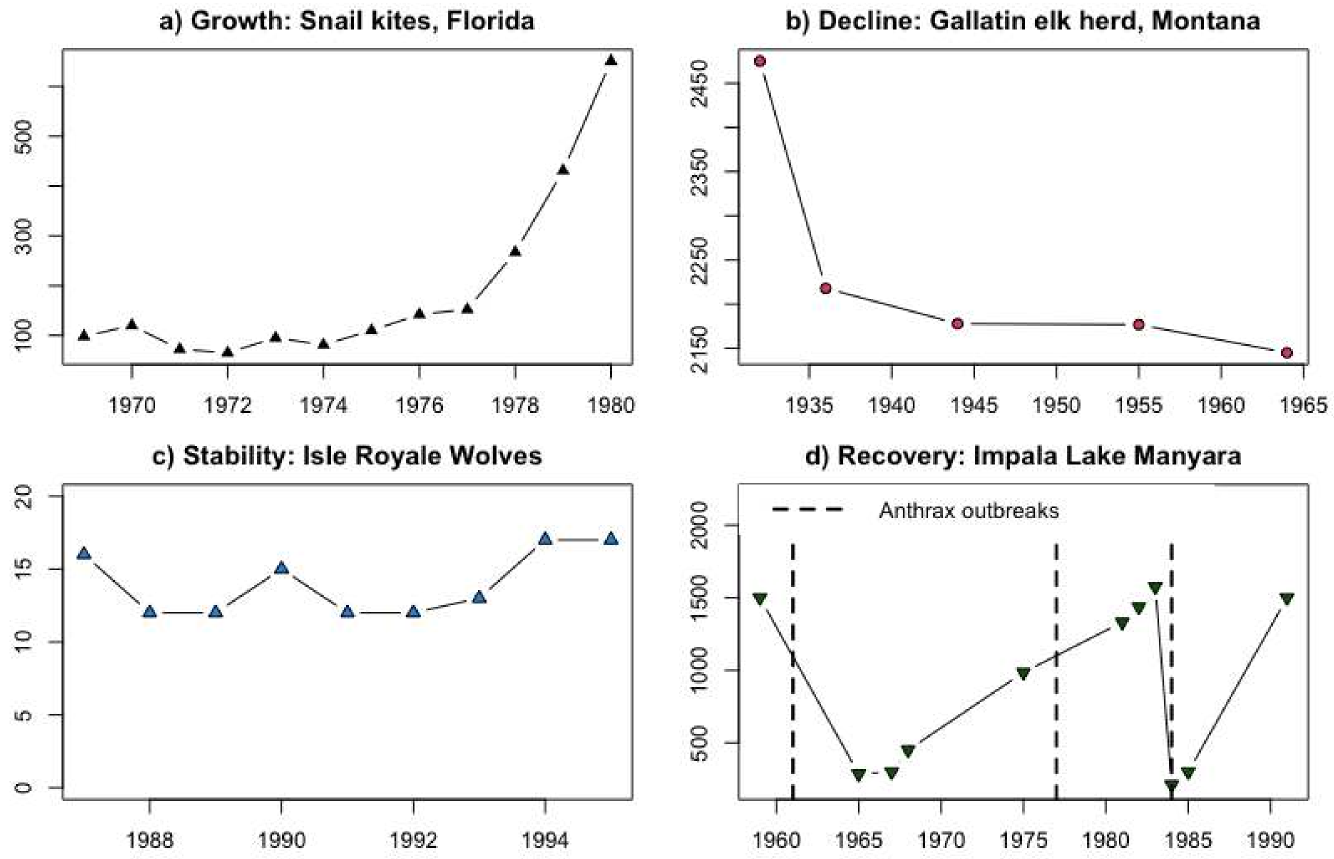


Figure 9.3.1: Common patterns of population change. The x-axis in all panels is the year and the y-axis is the number of individuals. a) Growth in a Florida Snail Kite (*Rostrhamus sociabilis*) population from 1970s to 1980s (Sykes 1983); b) Decline of the Gallatin, Montana herd of elk (*Cervus canadensis*) from the 1920s to 1960s (Peek et al. 1967); c) Stability of the Isle Royale, Michigan pack of wolves (*Canis lupus*) in the 1980s and 1990s (Peterson et al. 1998); d) Recovery after population crashes in the Lake Manyara National Park, Tanzania herd of impala (Prins and Weyerhaeuser 1987).

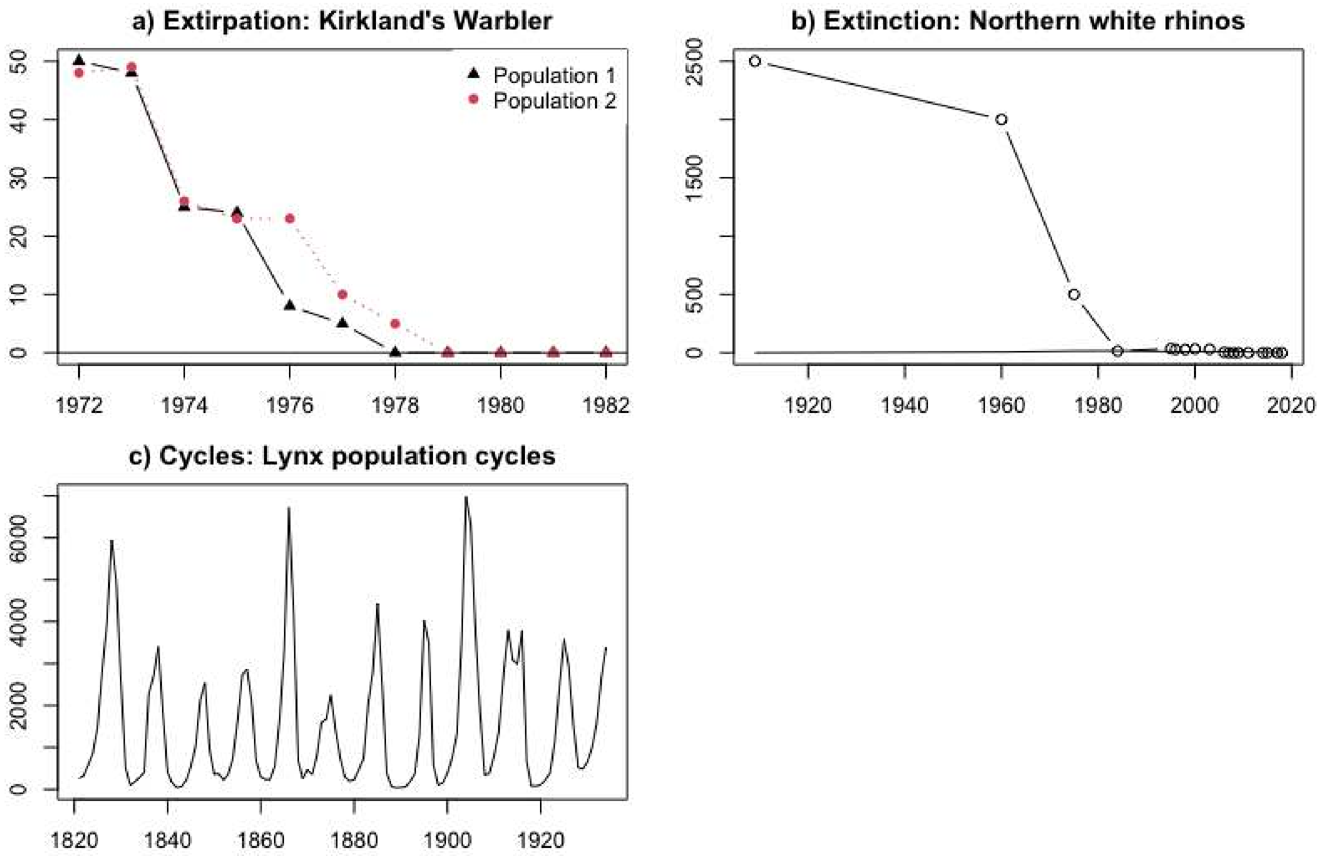


Figure $9.3.2$: Common patterns of population change. The x-axis in all panels is the year. a) Decline to extirpation (local extinction) of Kirtland's Warbler in two populations (Probst 1986). The y-axis is the number of singing males; b) Decline to global extinction of the Northern White Rhinoceros (*Ceratotherium simum cottoni*), one of two subspecies of White Rhinos (Smith 2001, Emslie 2012). The y-axis is the total number of rhinos in the wild. c) Repeated cycling of the Canada lynx (*Lynx canadensis*; Campbell and Walker 1977). The y-axis is the number of lynx trapped, an index of population size.

Over the course of many years, a single population can display many of these dynamics. For example, Kirtland's Warbler populations were monitored by determining the number of males defending territories in their summer breeding habitat in the Great Lakes region North America, primarily Michigan. There were about 500 males with territories in the 1950s (Figure $9.3.3$). The following changes occurred over the next 50 years after the species began being protected by the Endangered Species Act (Kepler et al. 1996):

1. **Decline** over the course of the 1960s to ~200 territories.
2. A period of **stability** at ~200 territories from 1975 to 1990.
3. Steady **growth** to >2500 from 1990 through 2020.

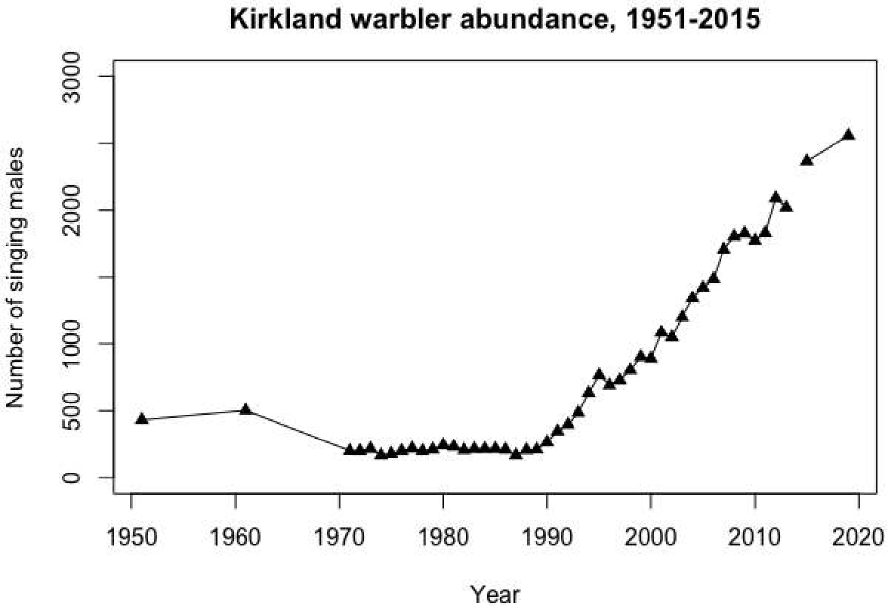


Figure 9.3.3: Number of singing Kirtland's Warbler (*Setophaga kirtlandii*) males, 1950 to 2020.

Models can be used to understand and predict population dynamics

Researchers who study population dynamics often use **mathematical models** to describe and predict population dynamics and understand what factors are driving those changes. For example, if there are 2500 Kirtland's Warblers in Michigan this year, can we predict how many will be around next year, or 10 years from now? Due to its small population size the Kirtland's Warbler was listed as an Endangered Species in 1967. In 2019 it was de-listed and now is considered "Near-threatened." Ecologists are very interested in using models to predict how large the Kirtland's Warbler population will be in the future, and what factors cause it to increase and decrease (Brown et al. 2019). In the next chapter we will explore the conceptual and mathematical tools ecologists use to understand population dynamics and predict their future trajectories.

Biotic interactions and abiotic conditions limit the sizes of populations

Population dynamics can be regulated in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-Dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Figure 9.3.4 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals (Croll et al. 1982). Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence (Walker et al. 2009). The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

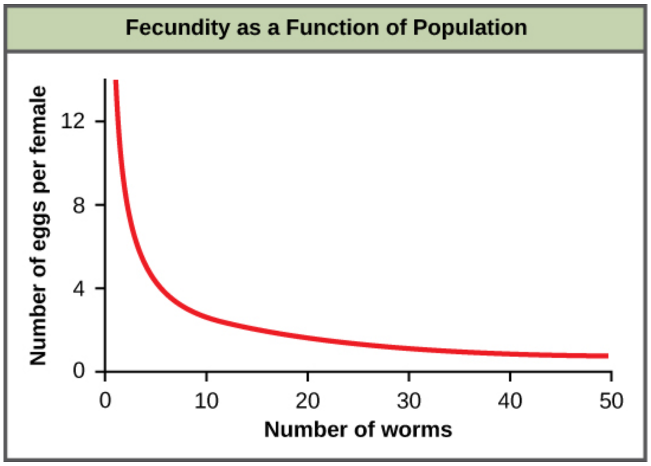


Figure 9.3.4: In this population of roundworms *Ascaris lumbricoides*, fecundity (number of eggs) decreases with population density (Croll et al. 1982).

Density-Independent Regulation and Interaction with Density-Dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Contributors and Attributions

This chapter was written by N. Brouwer with text taken from the following CC-BY resources:

- OpenStax Biology 2e section 45.4 Population Dynamics and Regulation

---

9.4: Scientist Spotlight - Jessie Isabelle Price

In November 2021, Oxford University Press (OUP) made headlines when the company announced its 2021 Word of the Year - Vax. Given the coronavirus pandemic, words like “vax” and “vaccine” have dominated our language and everyday lives, so this comes as no surprise. In a report on the language of vaccines, OUP states that the origin of “vaccine” relates to the pioneering work of 18th century British physician Edward Jenner. *Vacca* is the Latin word for cow, and through his work with inoculation, “Jenner conceived the Latin expression *variolae vaccinae* as a name for cowpox” (OUP 2021). At first, the word “vaccine” only described inoculation against cowpox, but its usage was expanded to include multiple variations of the word in reference to immunization against other diseases. But surely, one Englishman could not be the end-all-be-all, sole champion of vaccination? Cue Jessie Isabelle Price.

Born in Montrose, Pennsylvania in 1930, Price was raised by a single mother and attended predominantly white public schools. After graduating from high school and being accepted into Cornell, she deferred for a year to prepare herself academically (Gillmer 2018). Price wanted to become a physician, but could not afford additional costs that the program required. Instead, she graduated with a Bachelors of Science in microbiology in 1953 and by 1959, Price had earned a Masters and PhD in bacteriology, pathology, and parasitology. Work from her dissertation, in which she studied *Pasteurella anatipestifer* infection in Pekin ducklings, was published in the journal *Avian Diseases*. Following her graduate studies, Price remained at Cornell as a research scientist focusing on “the identification and control of bacterial diseases in commercial white Pekin Ducklings.” (Gillmer 2018)

Although her career stretched beyond her time at the Cornell Duck Disease Research Laboratory, some of her most impactful work originated from her time there. For example, farmers internationally were losing ducklings due to respiratory disease, and Price discovered that they were dying of duck hepatitis, *Pasteurella multocida*, and *Escherichia coli* (Warren 1999). Not only did she uncover the source of this avian mortality, Price developed two vaccines that saved the poultry industry money, but more importantly prevented potential disease outbreaks in other bird species. Despite this monumental achievement, if asked about the history of vaccines, Jenner (or Fauci) is typically the only name that comes to mind.

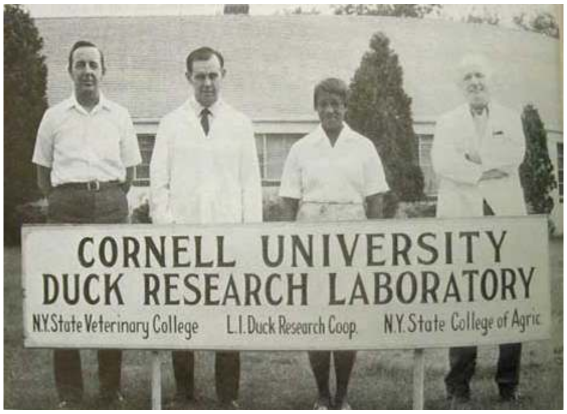


Figure 9.4.1: “Cornell University’s Duck Research Laboratory” provided by Cornell University is licensed under CC0 1.0.

References

“Doctor to Long Island Ducks.” *Ebony Magazine.* (September 1964). pp. 76-82. <https://books.google.co.uk/books?id=JaT6tBKGK3sC&lpg=PA1&pg=PA76#v=onepage&q&f=false>. Accessed December 28, 2021.

Gilllmer, Sophia. (2018). Jessie Isabelle Price (1930-2015). *BlackPast*. <https://www.blackpast.org/african-american-history/price-jessie-isabelle-1930-2015/>. Accessed November 9, 2021.

Oxford University Press. (2021). Word of the Year 2021: Vax. <https://languages.oup.com/word-of-the-year/2021/>. Accessed December 28, 2021.

Warren, Wini. (1999). Jessie Isabelle Price. Black Women Scientists in the United States. *Indiana University Press, Bloomington, Indiana, USA*, pp. 237-243.

CHAPTER OVERVIEW

10: Population modeling

Learning Objectives

- Review the basic arithmetic and algebra needed to think quantitatively about populations using mathematical models.
- Unpack the concept of the demographic rates of a population, including survival, birth rate, immigration, and emigration, and how these rates can be used to determine the growth rate of a population.
- Introduce two key patterns of population growth: exponential and logistic growth.
- Show how information on population growth can be used to project change in a population into the future.
- Detail a classic tool used by human demographers and ecologists to study population change: life tables.

Summary

Central to population ecology is the mathematical concept -- and biological reality -- of exponential population growth. The centrality of exponential growth in ecology and evolution was recognized by Darwin and plays a key role today in applied ecological decisions such as the management of invasive species, harvest limits for hunted species, and the management of endangered species. To appreciate the ecology of populations fully we therefore need to do some math. In this section, we will gently ramp up the skills and concepts we need to use math to think quantitatively about how populations change and can be effectively managed and preserved. First, we'll review the basic math we'll use throughout the chapter. Second, we'll build up the ecological concepts of demographic rates such as survival and birthrate and how they are represented mathematically. These demographic rates will then be combined into a mathematical model of population growth that shows how populations change over time due to survival and reproduction. Third, we'll show how once you have determined a population growth rate, you can predict how a population will change over time and demonstrate that it will grow exponentially. Fourth, we'll lay out a classic mathematical tool used both by human demographers and population ecologists: life tables.

10.1: Prelude - Learning the Math of Population Models

Math and mathematical models in ecology

The processes of population changes in space and time are called **population dynamics**. Over time, a population or species may expand its geographic range, colonize a new isolated habitat patch like an island, or disappear from areas where it occurred previously (**extirpation**). Even if a population or species is only found in the same locations as previously, its population size may increase or decrease, become stable, or cycle regularly.

Ecologists frequently use **mathematical models to describe** population dynamics. These models can be used to describe the trajectory of population growth when resources are abundant, its maximum size when resources are limited, or how rapidly in space it expands into new territory. Mathematical models can be intimidating at first, but you can start learning how they work - and how to use them yourself - with the basic tools of arithmetic and algebra most people learn in high school.

Basic mathematical models can be built using algebra

The term **mathematical model** perhaps sounds fancy, but in many of their forms these are just equations manipulated using standard algebra to allow us to think about how things change. In this book we'll use models for helping us think about things like populations change over time, what impact predators have on a population of its prey, and how two species using the same resource can coexist.

Here are some examples of the level of math needed to get started working with ecological models. Elsewhere we'll investigate the applications of math in ecological modeling. Prior to studying ecology, many individuals become familiar with the equation:

$$y = M * x + B$$

This equation expresses a relationship between the **variables** x and y. In biology, we'd call this a **mathematical model** and it allows us to predict x and y for particular unknowns, such as: x is the number of birds in a population this year and y is the number of next year. Or, x could be the size of a plant and y is the number of seeds it produces.

A mathematical model contains both **variables** and **parameters**. In models like ours above, x and y can be just about anything that varies between organisms or can be measured in nature: height, weight, number of species, size of a habitat, length of a river, the concentration of a toxin. In contrast, M and B are **parameters** that are generally fixed for a given situation.

Solving the variable y given x + B

Using the above equation, if I tell you $M = 1.2$ and $B = 10$, can you calculate what y is when $x = 10$? We can plug the values $M = 1.2$ and $B = 10$ into the equation:

$$y = 1.2 * x$$

We can then calculate y if $x = 10$. All the values added to the equation give us this:

$$y = 1.2 * 10 + 10$$

We then do the multiplication:

$$y = 12 + 10$$

The last step of addition tells us:

$$y = 22$$

Solving for an unknown parameter

What if I told you $y = 220$, $x = 100$, and $B = 10$; how would you calculate what M was? We could start like this with our known parameter ($B = 10$) and our values for x and y:

$$220 = M * 100 + 10$$

We then do some algebra. First deal with the 10 by subtracting it from both sides:

$$220 - 10 = M * 100 + 10 - 10$$

On the left, 220 - 10 = 210, and on the right 10 - 0 = 0, so this gives us:

$210 = M * 100$

Now divide both sides by 100.

$$\frac{210}{100} = \frac{M * 100}{100}$$

Which gives us:

$$\frac{210}{100} = M * 1$$

because 100/100 = 1.

Then divide 210 by 100:

$2.1 = M$

Not too bad? The math behind basic models in ecology is often not much more involved than this. If you can work through the steps above, you can work through the population models discussed in this book.

Using mathematical models for prediction

A common use of mathematical models in ecology is **prediction**. For example, you can often predict the number of seeds produced by a plant using an equation like this:

$(\text{number of seeds}) = M * (\text{plant size}) + B$

Which is the same $y = M * x + B$ equation we just used, where y = *number of seeds* and x = *plant size*.

If M = 10, B = 15, and *plant size* = 30 cm tall, how many seeds would be produced?

As before we can first add the values for the parameters M and B to to model:

$(\text{number of seeds}) = 10 * (\text{plant size}) + 15$

We then plug in our particular plant size of 30 cm and do the math. First multiplication:

$(\text{number of seeds}) = 10 * 30 + 15$

Then addition:

$(\text{number of seeds}) = 300 + 15$

$(\text{number of seeds}) = 315$

So, if the equation *(number of seeds) = 10 * (plant size) + 15* is accurate, a plant that is 30 cm tall would produce 315 seeds.

Basic population models

Population dynamics can be described with mathematical models

Populations change due to processes such as the deaths of current members of the population and the birth of new members (offspring). Discussions of population dynamics typically begin by writing out an equation which describes all of the key processes that impact population change, such as births and deaths. Most organisms live in seasonal environments, and we frequently consider changes in populations over the course of a single year, which we'll call a one-year **time step**.

Let's start building up some basic equations to describe changes in populations (**population dynamics**), calling the number of organisms right now N_{Now} and the number next year $N_{Next\ \text{year}}$ (The little "Now" and "Next year" are called **subscripts**).

We can write out how a population change like this:

$$N_{(\text{Next year})} = N_{(\text{Now})} - N_{(\text{Died this year})} + N_{(\text{Born this year})} \tag{10.1.1}$$

When we write equations like this, we always need to remember that often represent an *idealized* situation; rarely can we know how large a population currently is (N_{Now}), and it's *much* harder to determine exactly how many died or were born in a given year (We'll come back to these difficulties and their resolution in the next section on **demographic models**).

In addition to births and deaths, populations can also increase due to the arrival of individuals from different populations (**immigration)**, and decrease due to the exit of current members (**emigration)**. We therefore expand our idealized population equation to be:

$$N_{(\text{Next year})} = N_{(\text{Now})} - N_{(\text{Died this year})} + N_{(\text{Born this year})} - N_{(\text{Immigrant})} + N_{(\text{Emigrant})} \tag{10.1.2}$$

To make these equations more compact we often write using a more clearly expressed notation, where a subscript of "*t*" = a certain time, and "*t+1*" equals the following time period. Often this time step is one year, but it could be any period of time relevant to the biology of an organism or is convenient to the researcher. For example, many insects grow rapidly and some go through multiple generations in a single summer, and a relevant time step could therefore be months or even weeks.

Using subscripts we can rewrite our equation as:

$$N_{t+1} = N_t - N_{(\text{Died t})} + N_{(\text{Born t})} - N_{(\text{Immigrant t})} + N_{(\text{Emigrant t})} \tag{10.1.3}$$

where

$$N_{t+1} = N_{(\text{Next year})} \tag{10.1.4}$$

and

$$N_t = N_{(\text{Now})} \tag{10.1.5}$$

Often in textbooks births and deaths are given their own symbols, *B* and *D*, as are immigration (*I*) and emigration (*E*). You'll therefore see this equation:

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

or often just

$$N_{t+1} = N_t - D + B - I + E$$

with subscripts only on the N's.

Notation Alert!

Different authors and textbooks unfortunately use different notation, so it's important that everyone is clear what all their symbols mean, and that readers carefully determine what the symbols mean. In this case, it needs to be emphasized that *N*, *D*, *B*, *I*, and *E all* represent absolute numbers of individuals - they are meant to represent counts of organisms, not rates. For example, just as N_t is a count of all the individuals in the population and must be a whole number like 1000, *B* is a count of the number of births and must be a whole number like 5000. In contrast, a rate would be the number of births per individual of that population. In this case the birth rate would be *B/N* = 5000/1000 = 5. Later we will use rates, like births per year, to build demographic models.

It is useful to remember that when you're working with addition and subtraction you can move terms around in the equation and not alter the math. So our previous equation can be changed to this by **reordering** terms:

$$N_{t+1} = N_t - D + B - I + E$$

Similarly, we can add **parentheses** to help us organize things without changing the meaning. In the equation below, the number of births (B) and deaths (D) are grouped because these are opposing processes; similarly we group E (emigration) and I (immigration). Again, this does nothing to change the meaning.

$$N_{t+1} = N_t + (B - D) + (E - I) \tag{10.1.6}$$

I can state the fact that these two equations are identical with an **equality** like this:

$$N_t + B - D + E - I = N_t + {(B - D)} + {(E - I)}$$

Immigration and emigration are hard to study

In the prior example, immigration and emigration were ignored. This is because immigration and emigration are *very* difficult to study in a population. Most populations are demographically **open** to immigration to some degree, especially animal populations. An **open population** is one that regularly receives immigrants from a nearby population. Only populations that occur on oceanic islands that are distant from the mainland or occur in other isolated chunks of habitat are likely to be **closed** and receive few or no immigrants.

Many habitats do have fairly rare rates of immigration, such as most islands, lakes, and isolated **fragments** of habitat that are surrounded by inhospitable conditions such as human structures. For example, Abuko Nature Preserve in The Gambia, West Africa is surrounded on all sides by the suburbs of the capital, Banjul. Except for some birds, all animals found in Abuko were born there, will live their whole lives there, and never leave. It's possible that a brave monkey may run off, but it would have to travel a considerable distance to reach the next nearest fragment of forest. For plants, most seeds will fall onto the forest floor of the preserve except those eaten by birds. These birds may happen to fly to one of the nearest forest fragments and defecate there, but it's unlikely.

Definition: Migrant

It should be noted that for human populations the general term **migrant** is often used to describe people moving to a different country. In ecology, the terms **migrant** and **migration** are often reserved for species that undergo seasonal movements between habitats.

Figure 10.1.1 : Abuko Nature Preserve, The Gambia, West Africa. Surrounding the core forest (dark green) is more open scrub habitat (dark brown). The preserve is entirely surrounded by residences. *Source: Google Earth: https://bit.ly/abuko00*

When habitats are isolated like this, **dispersal events** are rare enough that they can be ignored for many ecological purposes. It should be noted, however, that while rare dispersal between populations doesn't have much impact on population size, it can still have an impact on **population genetics** and evolution. Population geneticists and evolutionary biologists therefore are often interested in dispersal events that a population ecologists might ignore. A population may therefore be more or less demographically closed, but **genetically open**.

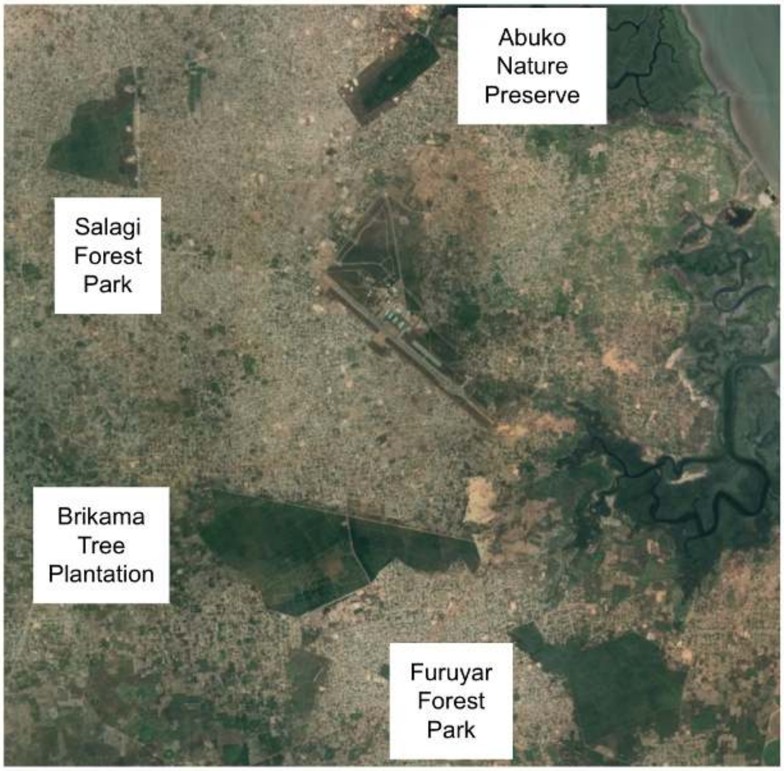


Figure 10.1.2: Forests nearest to Abuko Nature Preserve, The Gambia, West Africa. Most of the terrain between the forests is either residences or agricultural land. *Source: Google Earth: https://bit.ly/abuko1*

Ignoring immigration and emigration simplifies population models

Research on populations where immigration and emigration are minimal - or can justifiably be ignored - is convenient. This allows us to simplify our model of population dynamics from

$$N_{t+1} = N_t + B - D + E - I$$

to one without E and I:

$$N_{t+1} = N_t + B - D \tag{10.1.7}$$

We can therefore mathematically define a closed population as one where $E = 0$ and $I = 0$, and an open population as one where $E > 0$ or $I > 0$.

Moving forward, almost all of our population and other ecological models will ignore immigration and emigration. We will therefore be studying closed populations. Again, few populations are truly closed! Leaving E and I out of a model does not mean they never happen, just that they are not key players in the processes we are interested in or we are comfortable ignoring them.

While we have used a lot of symbols and equations, what we have done above presents two key creative steps in ecological modeling which are not necessarily reliant on math:

1. **Brainstorming** and writing out *all* of the key processes that can impact a population (B, D, E, I)
2. **Simplifying** the model by applying reasonable assumptions to make it easier to collect relevant data.

While math is important to the process, using your ecological imagination and intuition to determine what processes the equations should represent is just as important.

We often frame population dynamics in terms of the amount of change

Often our equation of population dynamics gets converted from focusing on the number of individuals

$$(N_t, N_{t+1}) \tag{10.1.8}$$

to the *change* in the number of individuals over time due to births and deaths. We therefore define population change as

$\Delta N = B - D$

Where is the Greek letter, Delta, which is used throughout science to mean "change."

Derivation Dance

For the curious: we can arrive at the equation $\Delta N = B - D$ via some algebra by subtracting

$$N_t \tag{10.1.9}$$

from both sides of our equation.

Our equation was:

$$N_{t+1} = N_t + B - D \tag{10.1.10}$$

We can subtract

$$N_t \tag{10.1.11}$$

from both sides:

$$N_{t+1} - N_t = N_t + B - D - N_t \tag{10.1.12}$$

Now let's rearrange terms for simplicity:

$$N_{t+1} - N_t = B - D + N_t - N_t \tag{10.1.13}$$

$$N_t - N_t = 0 \tag{10.1.14}$$

, so we simplify:

$$N_{t+1} - N_t = B - D \tag{10.1.15}$$

$$N_{t+1} - N_t \tag{10.1.16}$$

is usually written as ΔN, where is the Greek letter, Delta, which is used throughout science to mean "change".

Looking at the equation $|DeltaN = B - D$, we can ask, "*What does it mean if…*"

1. ***B* = *D*** (*B* is the same as *D*)?
2. ***B* > *D*** (*B* is *greater* than *D*)?
3. ***B* < *D*** (*B* is *less* than *D*)?

If *B* = *D*, the number of births is balanced out by deaths and the population has not experienced a net change in size $\Delta N = 0$. When *B* > *D*, births exceed deaths, ΔN is positive and the population gets bigger. When *B* < *D*, Δ is negative and the population gets smaller.

This all may look fairly simple if math comes easily to you, but is actually kind of profound for ecological research: you can ignore how large a population actually is and still know about its population dynamics by keeping track of just births and deaths. Conversely, if you know how much a population has changed in size, you can know whether there were more births than deaths, or if deaths exceed births. As noted before, tracking individual births and deaths is hard, so gaining insights into the net number of births and deaths just from changes in population sizes is very useful. Indeed, a whole branch of population modeling is based on this (Morris and Doak 2002).

10.2: Demographic rates

Population dynamics are often described in terms of demographic rates

Population ecologists often collect data on **demographic rates**: **birth rates** and **death rates** (or the converse of death rate, **survival rate**). Sometimes ecologists call these **vital rates**. Formally these are called **per capita** rates because they refer to the frequency of an event per individual of the population, such as births per person. Another common way to calculate rates, though not in ecology, is **per annum.** This is the frequency of something per *year*. A model set up in terms of demographic rates is called a **demographic model**.

> **Study Hint**
>
> While reading about mathematical models, write out the equations and make sure you understand each step of the arithmetic and algebra.

The most direct way to collect this information is if you know *all* of the individuals in a population (N) and you can count the number of individuals that are born and which subsequently survive until they are old enough to breed. Often we call this the **birth rate**, but this is not totally correct. It should really be called the "*birth and survival until the next census period*" rate.

We'll stick with convention and call it the **birth rate** and define it like this:

$$b = (\text{birth rate}) = \frac{(\text{number of babies})}{(\text{number of adults})}$$

or more succinctly:

$$b = \frac{B_t}{N_t} \tag{10.2.1}$$

That is, the per capita birth rate b is equal to the number of births in year t (B_t) divided by the number of adults (N_t) in the population. b is a fraction, and can take on values as low as zero. $b = 0$ indicates that no offspring were born, or that all offspring died before they could reproduce. $b = 2$ indicates that two offspring were born for each adult.

Once we define b as the ratio of births to total population size, we can use algebra to set up an equation for the prediction of the actual number of births:

$$B_t = b * N_t$$

That is, the number of organisms born and entering the population at time t (B_t) is equal to the number of organisms in the population (N_t) times the number of offspring produced per organism. Stated another way, the total number born (B_t) are often expressed as a proportion (b_t) of the number alive now (N_t).

For example, at the beginning of 1996 there were 249 elephants in the Addo Elephant National Park in South Africa (Whitehouse & Hall-Martin 2000). Over the last several decades the average birth rate was 0.0693. We can therefore use our birthrate equation to predict the number of births in 1996:

$$B_{1996} = b * N_{1996} = 0.0693 * 249 = 17.25$$

Indeed, there were 17 elephants born that year.

Figure 10.2.1: Elephants in Addo Elephant National Park. "Elephants at the Hapoor Dam in the park" by NJR ZA is licensed by CC BY-SA 3.0.

The per capita death rate d can be similarly defined:

$$d = \frac{D_t}{N_t} \tag{10.2.2}$$

and therefore if we know the death rate and the current population size we can predict the number that will die over the next time period:

$$D_t = d * N_t$$

The mean death rate in Addo was 0.0175; 248 elephants * 0.01750 = 4.3 predicted deaths. This is slightly fewer than the 5 that actually occurred.

So far we've only been doing some minor algebraic rearrangement of these demographic rates, but seeing how this done will help us understand how to formulate demographic models for population dynamics.

Now that we're thinking in terms of rates, we can rewrite our main population dynamics equation, which was

$$N_{t+1} = N_t - D_t + B_t$$

in terms of demographic rates, like this:

$$N_{t+1} = N_t - d * N_t + b * N_t$$

What this means is that if we can estimate d and b, we can estimate population change without having to count up the total number of deaths and births.

In Addo Elephant National Park extensive data collection allowed researchers in the 1990s to account for all births, deaths, and surviving animals. However, if they had been unable to conduct a full population survey in 1997 they could've predicted the size of the population as

$$N_{1997} = N_{1996} - d * N_{1996} + b * N_{1996} = 249 - 0.0175 * 249 + 0.0693 * 249$$

This yields an estimated population size in 1997 of 262; the actual population size was 261.

Math Review

If we want, we can **factor out** the N_t from the previous equation and get an equation like this:

$$N_{t+1} = N_t + N_t * (b - d)$$

Ecologists usually calculate survival rates, not death rates

In our equations, D_t represents the *total* number of organisms that died in a given year *t*. The number that survived is therefore $N_t - D_t$.

When studying population change ecologists typically work in terms of **survival rates**, often written as ϕ, the Greek letter “Phi.” The survival rate can be thought of as either a frequency or a probability. If you have 100 organisms and 50 survive to the next year, the survival rate is 0.50. Similarly, if a single organism has a 50% chance of survival over the next year, the survival rate is 0.50.

The number of deaths in a population plus the number of survivors sums to the total current population size. We therefore can use our death rate d and survival rate ϕ and write:

$$N_t = \phi * N_t + d * N_t$$

Note that in this equation we only have N_t, and not dealing right now with N_{t+1}.

We can do some algebra and move $d * N_t$ using subtraction to the left of the equals sign:

$$N_t - d * N_t = \phi * N_t$$

and see that the population size (N_t) minus those which died $(d * Nt)$ equals the number of survivors $(\phi * N_t)$.

Why all the fuss?

The previous equations aren't very profound - we're just accounting for the fate of all of the organisms currently in the population. Functioning population models, though, often rely on many basic mathematical manipulations in order to be set up, and we're taking the time to build up our intuition about how all the various pieces of these models work.

Another useful demonstration is this: we can also start as we just did with $N_t = \phi * N_t + d * N_t$ and divide both sides by N_t:

$$\frac{N_t}{N_t} = \frac{\phi * N_t + d * N_t}{N_t}$$

We can distribute the N_t on the right to give us

$$\frac{N_t}{N_t} = \frac{\phi * N_t}{N_t} + \frac{d * N_t}{N_t}$$

Nt/Nt cancels out on the left and the right. This gives us

$$1 = \phi + d$$

and by re-arrangement

$$1 - d = \phi$$

What does $1 = \phi + d$ mean? Again, mathematically it's a simple statement: the proportion which lived and the proportion which died over a single time step must total 1. However, keeping this manipulation in mind allows us to write out a demographic equation with some very useful features.

Let's put all of these pieces together. We'll start again with our key demographic equation using rates:

$$N_{t+1} = N_t - d * N_t + b * N_t$$

Next, to make this clearer we'll put related terms next to each other:

$$N_{t+1} = (N_t - d * N_t) + b * N_t$$

Now factor out N_t from the stuff in the parentheses:

$$N_{t+1} = N_t * (1 - d) + b * N_t$$

As we just showed, $1=\phi+d$ and so our term $(1-d)$ can be replaced like this: $1-d=\phi$.

Therefore, we get:

$$N_{t+1}=\phi * N_t+b * N_t$$

This means that the number of individuals in the future (N_{t+1}) is comprised of those that survived $(\phi * N_t)$ and their offspring $(b * N_t)$.

In Addo Elephant National Park mean mortality was 0.0175. Mean survival is therefore 1-0.0175 = 0.9825. We therefore predict population size in the future as $N_{t+1}=0.9825 * N_t+0.06927 * N_t$

We've now distilled down our demographic equation to predict future population size using the present population size N_t, survival ϕ and birth rate b. While it's taken a fair bit of working with the equation, we've now reached an important breakthrough: creating a population model without determining population size at all!

Math Review

If we want to be fancy we can do a bit of algebra and factor out the N_t from the previous equation:

$$N_{t+1}=N_t *(\phi+b)$$

Let's take stock of what we've done. So far we've gone from our initial population models that show up in most biology textbooks but isn't really used by working ecologists:

$$N_{t+1}=N_t+B_t-D_t+E_t-I_t$$

and then simplified it by ignoring immigration I and emigration E, or found a population where they don't apply or can comfortably be ignored. This gives us:

$$N_{t+1}=N_t+B_t-D_t$$

Tracking total B and D is really hard -- harder than even N_t -- so we've done some simple thinking about population processes and some algebra to get:

$$N_{t+1}=\phi * N_t+b * N_t$$

where $\phi$and b are usually estimated from a subset of the population. If we are confident that our survival and birth rate estimates are good, we can predict population size in the future. However, we're still relying on estimates of population size N_t which are still costly. For example, estimating the population sizes of large animals that live in open habitats such as polar bears and elephants often requires using aircraft. For animals that live in forests it can be very difficult to determine population sizes except over small areas. In the case of plants, populations are often so large that population size can only be determined for small, isolated populations. Luckily, there are some mathematical tools we can use to build meaningful population models that don't require population sizes to be estimated. To set this type of model up we'll introduce a core concept in ecology: the population growth rate.

Population dynamics are frequently described using the population growth rate

Population ecologists are frequently interested in both the absolute number of organisms (e.g. N_t, N_{t+1}) and also the **rate of population change over time**, usually referred to as the **population growth rate**. The Greek letter “L” called “lambda” (λ) is used to represent this rate.

If you have been following a population closely over time and have complete censuses you can calculate (λ) directly using the size (N_t) of the population at one time point and at a previous time point N_{t+1}:

$$\frac{N_{t+1}}{N_t}=\lambda \tag{10.2.3}$$

λ is therefore the **ratio** between two population sizes.

In situations where population sizes have been estimated, λ can be calculated directly from these data and used in subsequent models. In other cases, demographic rates (e.g. phi and b) are used to calculate it.

Case study: Calculating lambda (λ) for Kirtland's Warbler:

The Kirtland’s warbler has a small geographic range and is a habitat specialist. It therefore occurs in very specific habitats, so the approximate total number of individuals could be monitored relatively easily. In 2011 there were 1828 Kirkland’s warbler males, and in 2012 there were 2090. We can therefore set up our equation with $N_t = 1828$ and $N_{t+1} = 2090$. Lambda (λ) is therefore

$$\lambda = \frac{N_{t+1}}{N_t} = \frac{N_{2012}}{N_{2011}} = \frac{2090}{1828} = 1.14 \tag{10.2.4}$$

Note that $N_{t+1} > N_t$, and therefore $\lambda > 1$.

While the warbler population grew from 2011 to 2012, the next year in 2013 only 2020 singing males were counted. Therefore

$$\lambda = \frac{N_{t+1}}{N_t} = \frac{N_{2013}}{N_{2012}} = \frac{2020}{2090} = 0.967$$

Note that $N_{t+1} < N_t$, and that $\lambda < 1$.

Once we have estimates for ϕ, we can make predictions about future population sizes and **project** population dynamics into the future. For as many years as possible, we can calculate N_{t+1}/N_t; this isn’t always possible because of gaps in the data, e.g. we can’t calculate N_{2014}/N_{2013} because no data was collected in 2014.

Figure 10.2.2: Male Kirtland's Wabler. "Kirtland" by Bjamoros is licensed under CC BY-SA 3.0.

The value of lambda summarizes population dynamics

The minimum value λ can take on is 0. When $\lambda > 1$ a population grows, while if $\lambda < 1$ a population shrinks. If $\lambda = 1$ the population isn’t changing. $\lambda = 0$ means that both adult survival ϕ and reproduction b are 0. If $\lambda = 0$ the population goes extinct.

Below is a plot of the population **time series** next to a **histogram** of all of the values calculated from the time series. The time series starts in the 1970s on the left when researchers began conducting counts of all singing male Kirthland's Warblers each year. For each pair of years, λ was calculated to make the histogram.

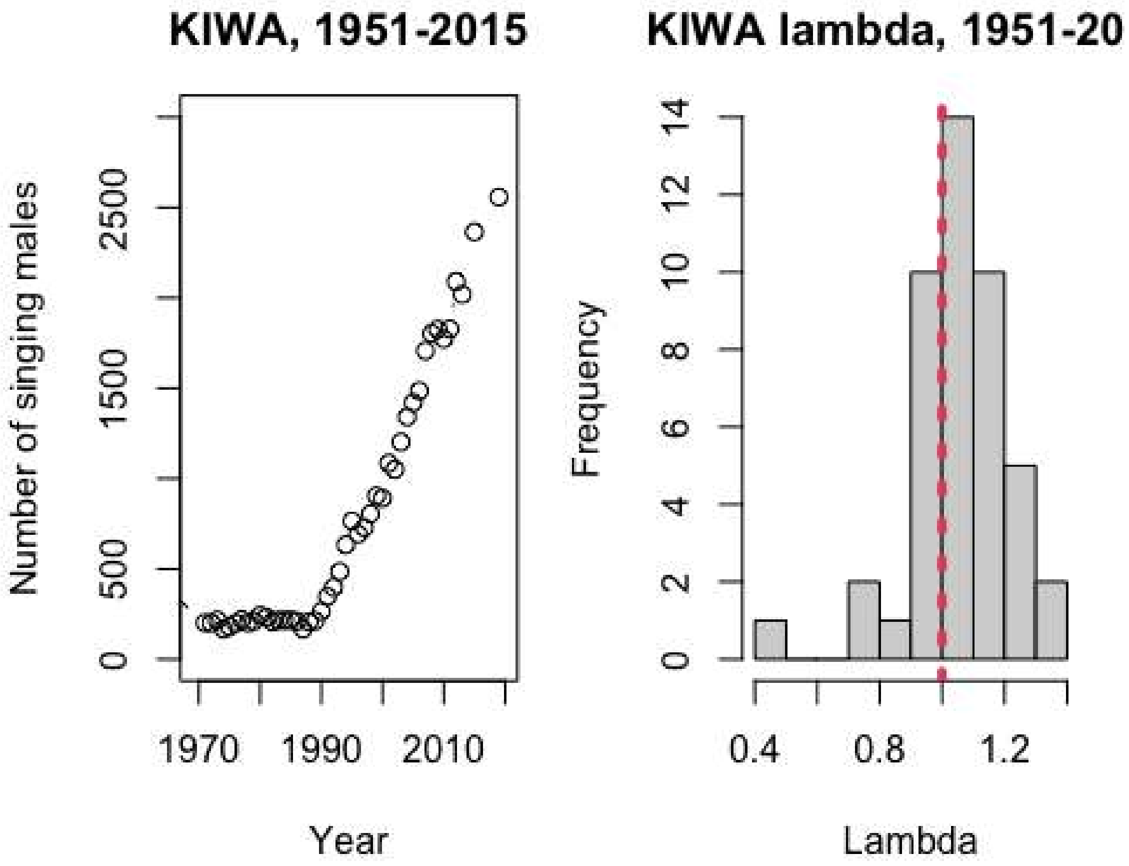


Figure 10.2.3: A time series (left) of the number of male Kirtland's warblers recorded and a histogram (right) of all population growth rates (λ) calculated from the time series. The histogram shows us the **distribution** of observed lambda values over the ~50 year time series when KIWA males were counted every year.

Exercise 10.2.1

What do you notice in the KIWA Lambda histogram? Why is the red line plotted and what is happening to the population at the red line?

Answer

The red line 1.0 is plotted because when $\lambda = 1$, a population is staying the same size because deaths are being balanced out by births.

Population growth rates can be calculated from demographic rates

As noted previously, it is often very difficult – if not impossible – to determine actual population sizes. For KIWA, researchers worked very hard to determine the number of males that were singing each year, but they were never completely sure if they found all of them. KIWA population is currently growing, and researchers are no longer collecting population size data, which allows allocation of research money to answer other questions, such as the expansion of the species' range into Wisconsin and Canada.

While still very challenging, it's often easier to determine **demographic rates** for a subset of the population, such as survival and reproduction, rather than population size. Several studies have captured KIWA males, marked them with **bird bands** and attempted to re-capture them each year to estimate survival rates (ϕ). This approach for calculating survival using mark-recapture data is similar to the one discussed in the previous chapter for calculating population size. Researchers have also found nests and determined how many baby KIWA are born per nest, and what the survival rate is for those birds until they are one year old and can breed. This gives an estimate of b.

Figure 10.2.4: Adult Male Kirtland's Warbler being banded. Source: Source: Hanna (2015): Kirtland's Warbler Banded as Nestling in Wisconsin Confirmed in Bahamas A Field Update. Photo by J. Trick. https://www.fws.gov/midwest/GreenBay...April2015.html

With these estimates we can calculate population growth rate (λ) without knowing population size as:

$$\frac{N_{t+1}}{N_t} = \phi + b$$

We then define N_{t+1}/N_t as λ and so have

$$\lambda = \phi + b \tag{10.2.5}$$

Derivation Dance

To show that λ can be defined with demographic rates as $\lambda = \phi + b$ we start with our previous demographic equation:

$$N_{t+1} = \phi * N_t + b * N_t$$

We can then divide both sides by Nt

$$N_{t+1}/N_t = \phi * N_t + b * N_t/N_t$$

We can distribute the division of N_t like this

$$N_{t+1}/N_t = \phi * N_t/N_t + b * N_t/N_t$$

This cancels out N_t entirely from the right-hand side

$$N_{t+1}/N_t = \phi + b$$

We then define N_{t+1}/N_t as before as

$$\lambda = \phi + b$$

λ represents a combination of both survival (ϕ) of adults from one year to the next plus how many offspring are produced per adult and survive to reproduce themselves (b). We now have a quantity we are very interested in, the population growth rate (λ), in terms of parameters that aren't too hard to calculate: the survival rate and birth rate (ϕ and b). This means we can understand population dynamics without needing to conduct a complete census and count every single organism -- just as long as we can track survival and reproduction on a representative subset of the population.

Alternative Derivation

We could also do our math this way. We can start with

$$N_{t+1} = \phi * N_t + b * N_t$$

and factor out N_t on the right to be:

$$N_{t+1} = N_t * (\phi + b)$$

We then divide both sides by N_t

$$N_{t+1}/N_t = N_t + b/Nt$$

This again gives us

$$\frac{N_{t+1}}{N_t} = \phi + b$$

which we write as

$$\lambda = \phi + b$$

Case study: Calculating Kirthland's Warbler with demographic data

We can estimate for any species if we have estimates of its adult survival rate and its birth rate. Survival for Kirtland's Warbler (KIWA) is around 67%, or 0.67. This means on average that if we have 100 adult KIWA nesting in a forest, we'd expect to see 67 of them again next year. Equivalently, we can say that an adult bird has a probability of surviving of 0.67.

The birth rate (b) is tricky to estimate for a number of reasons. Recall that b should really be called the "born and *survives* to reproduce" rate. Incorporating both the number of baby KIWA that hatch from eggs and their probability of surviving for one year until they can reproduce, the birth rate (b) is about 0.74.

Population growth rate is therefore

$$\lambda = 0.67 + 0.74$$
$$= 1.3$$

Since λ >1 we'd predict that the population of KIWA will be growing. We aren't actually counting all the birds, however.

10.3: Scientist Spotlight - Erin Satterthwaite

Relative to the offspring of other species, humans enter the world utterly defenseless. Emerging from a 9-month gestation period, we arrive completely dependent upon our caregivers. In contrast, newly hatched (or birthed) marine larvae are amazingly independent. Swimming, something humans may never learn in their lifetime, is an elementary skill required for the survival of mobile *and* sessile marine organisms.

Sessile means, “permanently attached or established : not free to move about” (Merriam-Webster n.d.). Something does not add up here. Sessile organisms move? Yes, when they are in the midst of the larval life stage. Both sessile and mobile marine animals, including species of fish, sponge, crab, sea star, worm, and snail experience this microscopic phase. According to Dr. Erin Satterthwaite, a marine ecologist with California Sea Grant at Scripps Institution of Oceanography , dispersal of marine young “is one of the primary determinants of recruitment of new individuals into populations and can be an important driver of population dynamics,” (Drake et al. 2018). In other words, larval movement affects how larvae settle into new populations. In turn, population size and structure influence how those populations interact with the environment and the rest of their community (Khan Academy n.d.). Dr. Satterthwaite and her colleagues found that when larvae swam toward shore (as opposed to not swimming toward shore), there was “a substantial increase in nearshore larval supply,” which meant that there would be more young available to settle into suitable habitat (Drake et al. 2018). This demonstrated that larval behavior may be an important factor shaping marine population dynamics. Overall, in order to understand and conserve marine animals, we need to better understand where they are born from, where they end up, and how they got there.

Dr. Satterthwaite’s favorite part of being a marine ecologist has been exploring nature and sharing its wonders with others. As a first-generation college and graduate student, her “path has been a winding journey,” and she “has had to rely on others for support and guidance.” For Dr. Satterthwaite, it has been this sense of community and relationships she has built along the way that has been the best part of her career.

Figure 10.3.1 : A photo of Dr. Erin Satterthwaite contributed to Project Biodiversify by Dr. Satterthwaite.

References

Scientist Spotlight inspiration from Project Biodiversify

Drake, P.T., Edwards, C.A., Morgan, S.G., & Satterthwaite, E.V. (2018). Shoreward swimming boosts modeled nearshore larval supply and pelagic connectivity in a coastal upwelling region. <https://www.sciencedirect.com/science/article/pii/S0924796317304955>. Accessed October 5, 2021.

Khan Academy. n.d. <https://www.khanacademy.org/science/biology/ecology/population-ecology/a/population-size-density-and-dispersal>. Accessed October 5, 2021.

Merriam-Webster. n.d. <https://www.merriam-webster.com/dictionary/sessile>. Accessed October 5, 2021.

10.4: Overview of Population Growth Models

Skills to Develop:

By the end of this section, you will be able to do the following:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain long-accepted models are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, which represents an **exponential growth**, and then population growth decreases as resources become depleted, indicating a logistic growth.

The best example of exponential growth is seen in bacteria. Bacteria reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is the accelerating **population growth rate**—the number of organisms added in each reproductive generation—that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, *N*, is plotted over time, a **J-shaped growth curve** is produced (Figure $10.4.1$).

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate (*D*)** (number organisms that die during a particular time interval) is subtracted from the **birth rate (*B*)** (number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N}{\Delta T} = B - D$$

where $\Delta N =$ Change in number, $\Delta T =$ = Change in time, B = birth rate and D = death rate

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "*N*") and *D* (death rate) = *dN* (the per capita death rate "d" multiplied by the number of individuals "*N*"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value "*r*" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as **zero population growth**. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its **biotic potential, or r_{max}**, thus changing the equation to:

$$\frac{dN}{dT} = r_{max}N$$

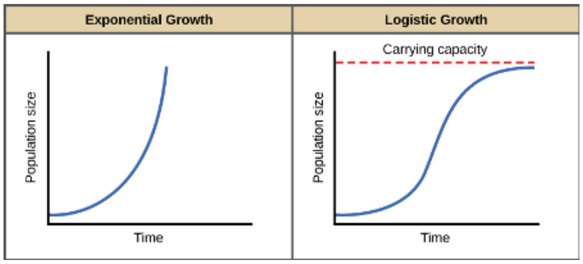


Figure $10.4.1$: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 10.3.1). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity, or *K***.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – *N*" indicates how many individuals may be added to a population at a given stage, and "*K* – *N*" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\frac{dN}{dT} = r_{max}\frac{dN}{dT} = r_{max} * N * \frac{K-N}{K}$$

Notice that when *N* is very small, $(K-N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when *N* is large, $(K-N)/K$ comes close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity *K*. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K-N)/K$ is negative).

A graph of this equation yields an **S-shaped curve** (Figure $10.4.1$), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = “within”; -specific = “species”). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment’s carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure $10.4.2a$). Its growth levels off as the population depletes the nutrients. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure $10.4.2b$). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

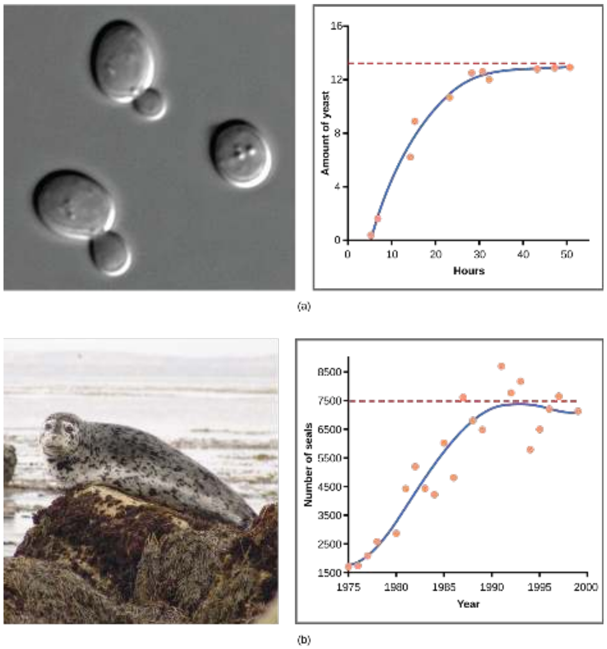


Figure $10.4.2$: (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

? Exercise $10.4.1$

If the major food source of the seals (Figure $10.4.2b$) declines due to pollution or overfishing, which of the following would likely occur?

a. The carrying capacity of seals would decrease, as would the seal population.
b. The carrying capacity of seals would decrease, but the seal population would remain the same.
c. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
d. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Answer

a. The carrying capacity of seals would decrease, as would the seal population.

Contributors and Attribution:

This material is edited from the following sources

- OpenStax Biology 2e section 45.3 Environmental Limits to Population Growth

---

10.5: Geometric and Exponential Growth

INTRODUCTION

We will begin by developing a population model in **discrete time**. That is, we will treat time as if it moved in steps, rather than continuously. This allows us to use difference equations rather than differential equations, and thereby avoid the calculus. This assumption is realistic for many populations that have seasonal, synchronous reproduction. Strictly speaking, the discrete-time model represents **geometric population growth**. Later in the chapter, we will develop a continuous-time model, properly called an **exponential** model.

Model Development

To begin, we can write a very simple equation expressing the relationship between population size and the four demographic processes. Let:

- N_t represent the size or density of the population at some arbitrary time t (we will ignore the distinction between population size and population density)
- N_{t+1} represent population size one arbitrary time-unit later
- B_t represent the total number of births in the interval from time t to time $t+1$
- D_t represent the total number of deaths in the same time interval
- I_t represent the total number of immigrants in the same time interval
- E_t represent the total number of emigrants in the same time interval

Then we can write

$$N_{t+1}=N_t+B_t-D_t+I_t-E_t$$

For simplicity, this exercise ignores immigration and emigration. Our equation becomes

$$N_{t+1}=N_t+B_t-D_t$$

This equation is easy to understand but inconvenient for modeling. The problem lies in the use of "raw" birth and death rates (B_t and B_t). We have no obvious, biologically reasonable starting assumptions about these numbers. However, if we switch from *raw* birth and death rates to *per capita* birth and death rates, we can do some fruitful modeling.

Geometric (Discrete-Time) Model of Population Growth

A **per capita** rate is a rate per individual; that is, the per capita birth rate is the number of births per individual in the population per unit time, and the per capita death rate is the number of deaths per individual in the population per unit time. Per capita birth rate is easy to understand, and seems a reasonable thing to model because reproduction (giving birth) is something individuals rather than whole populations do. Per capita death rate may seem strange at first; after all, an individual can die only once. But remember, this rate is calculated per unit time. You can think of per capita birth and death rates as *each individual's probability of giving birth or dying in a given unit of time*.

Keeping in mind that per capita rates are per individual rates, we can translate the raw rates B_t and D_t into per capita rates, which we will represent with lower-case letters (b_t and d_t) to distinguish them from the raw numbers. To calculate per capita rates, we divide the raw numbers by the population size. Thus,

$$b_t=B_t/N_t \text{ and } d_t=D_t/N_t$$

Conversely,

$$B_t = b_t N_t \text{ and } D_t = d_t N_t$$

Now we can rewrite our model in terms of per capita rates:

$$N_{t+1} = N_t + b_t N_t - d_t N_t$$

Perhaps this seems to have gotten us nowhere, but it turns out to be a very informative model if we make one further assumption. Let us assume, just to see what happens, that per capita rates of birth and death remain constant over time. In other words, let us assume that average number of births per unit time per individual in the population and the average risk of dying per unit time remain unchanged over some period of time. What will happen to population size?

Because we assume *constant* per capita birth and death rates, we can make one further minor modification to our equation by leaving off the time subscripts on *b* and *d*:

$$N_{t+1} = N_t + bN_t - dN_t \tag{10.5.1}$$

At this point, you're probably thinking that this assumption is unrealistic—that per capita rates of birth and death *are* likely to change over time for a variety of reasons. You are quite correct, but the model is still useful for three reasons:

- It provides a starting point for a more complex and realistic model in which per capita rates of birth and death do change over time.
- It is a good *heuristic model*—that is, it can lead to insights and learning despite its lack of realism.
- Many populations *do* in fact grow as predicted by this model, under certain conditions and for limited periods of time.

Method to the madness?

You may also wonder why we use this complex model (Equation 1) rather than the simpler forms of the geometric and exponential models presented in most textbooks (and developed here beginning with Equation 2). We prefer Equation 1 for three reasons:

- It emphasizes the roles of per capita birth and death rates rather than the more abstract quantities r_d or λ (explained later).
- It allows you to manipulate per capita birth and death rates directly and separately, and discover that neither alone, but rather the difference between them, determines population growth rate.
- It allows you to discover that the per capita rate of population growth $\Delta N_t / N_t$ is a constant, which you can then relate to r_d (and r if desired).

Because per capita birth and death rates do not change in response to the size (or density) of the population, this model is said to be **density-independent**.

We can further simplify Equation 1 by factoring N_t out of the birth and death terms:

$$N_{t+1} = N_t + (b-d)N_t$$

The term (*b* – *d*) is so important in population biology that it is given its own symbol, r_d. Thus $r_d = b - d$, and is called the **geometric rate of increase**. Substituting r_d for (*b* – *d*) gives us

$$N_{t+1} = N_t + r_d * N_t \tag{10.5.2}$$

To further define r_d, we can calculate the amount of change in population size, ΔN_t, by subtracting N_t from both sides of Equation 2:

$$\Delta N_t = N_{t+1} - N_t = r_d N_t$$

Because $\Delta N_t = N_{t+1} - N_t$, we can simply write

$$\Delta N_t = r_d N_t \tag{10.5.3}$$

In words, the amount of change in population size is proportional to the population size, and the constant of proportionality is r_d.

We can convert this to per capita rate of change in population size if we divide both sides by N_t:

$$\frac{\Delta N_t}{N_t} = r_d \tag{10.5.4}$$

In other words, the parameter r_d represents the (discrete-time) per capita rate of change in the size of the population.

Notation note

A common source of confusion when learning about ecological is the fact that different books and other resources will use slightly different notation and alternative -- but mathematically equivalent -- ways to set up equations (**parametrizations**). For example, the source material for this chapter used R instead of r_d.

Moving on, we can simplify Equation 2 ($N_{t+1} = N_t + r_d N_t$) even further by factoring N_t out of the terms on the right-hand side, to get

$$N_{t+1} = (1 + r_d)N_t$$

The quantity $(1 + r_d)$ is often given its own symbol, λ (lambda), and its own name: the **finite rate of increase**. Substituting λ, we can write

$$N_{t+1} = \lambda N_t \tag{10.5.5}$$

The quantity λ can be very useful in analyzing real population data. Some additional algebra will show us how.

If we divide both sides of Equation 5 by N_t, we get

$$\frac{N_{t+1}}{N_t} = \lambda \tag{10.5.6}$$

In words, λ is the ratio of the population size at one time to its size one time-unit earlier. We can calculate λ from population counts at successive times, even if we do not know per capita rates of birth and death.

In Equations 2 and 5, we showed how to calculate the size of the population one time unit into the future. What if you wanted to know how big the population will be at some distant future time? You could carry out the one-time-step calculations many times, until you arrived at the desired answer. But there is also a shortcut. Population size at time 1 is $\lambda^1 N_0$, at time 2 it is $\lambda^2 N_0$, and at time 3 it is $\lambda^3 N_0$. In general, we can write

$$N_t = \lambda^t N_0 \tag{10.5.7}$$

Notation note

N_0 is called "N-naught." In population ecology it is often used to denote an initial population size.

Doubling time

The previous expression may strike you as rather abstract. One way to understand its impact is to use Equation 7 to calculate **doubling time** (t_{double})—that is, the time required for the population to double in size. If we plug the doubling time into Equation 7, we get

$$N_{t_{double}} = \lambda^{t_{double}} N_0$$

We can derive doubling time by exploiting the fact that the population at time t_{double} is, by definition, twice the population at time 0:

$$N_{t_{double}} = 2N_0$$

Substituting $2N_0$ for N_t double gives us

$$2N_0 = \lambda^{t_{double}} N_0$$

If we divide both sides by N_0, we get

$$2 = \lambda^{t_{double}}$$

Taking the logarithm of both sides gives us

$$ln(N_0) = t_{double} ln(\lambda)$$

Dividing both sides by $ln(\lambda)$, we get

$$\frac{ln(2)}{ln(\lambda)} = t_{double} \tag{10.5.8}$$

What does this mean? Suppose r_d = 0.1 individuals/individual/year. Therefore, $\lambda = 1 + r_d = 1.1$. This implies that the population increases by 10% per year, which doesn't sound like much. But, if you plug this value of λ into Equation 8, you'll find that the population doubles in about 7.27 years, which seems more impressive.

You may be wondering how a population that grows in discrete intervals of a year can double in a non-integer number of years. It can't, of course. This calculation really means that the population will not quite double in 7 years, and will more than double in 8 years.

Exponential (Continuous-Time) Model of Population Growth

Population growth can also be modeled in continuous time, which is more realistic for populations that reproduce continuously, rather than seasonally. Continuous-time models also allow use of the calculus, which provides many powerful analytical tools. Here, we will eschew the calculus, and simply present some results.

Most textbooks begin with the continuous-time analog of Equation 3:

$$dN/dt = rN \tag{10.5.9}$$

The left-hand side of Equation 9 represents the **instantaneous** rate of change in population size, which is different from the rate of change over some discrete time interval, $\Delta N/N$, that we looked at in Equation 7. Therefore, we use a lowercase r instead of r_d to distinguish the continuous-time exponential model from the discrete-time geometric model. The symbol r is called the **instantaneous rate of increase** or the **intrinsic rate of increase**. The parameters r and r_d are *not* equal, although they are related, as we will show below.

As we did with the discrete-time model, we can calculate the per capita rate of population growth by dividing both sides of Equation 9 by N:

$$\frac{dN/dt}{N} = r \tag{10.5.10}$$

You can use the calculus to operate on Equation 10 and calculate the size of the population at any time. We will spare you the derivation, but the resulting equation is

$$N_t = N_0 e^{rt} \tag{10.5.11}$$

where e is the root of the natural logarithms $(e \approx 2.71828)$.

You can derive the relationship between r and r_d as follows. Suppose we start two populations with the same initial number of individuals, N_0, and both grow at the same rate. However, one grows in continuous time and the other grows in discrete time. Because they grow at the same rate, at some later time, t, they will have reached the same size, N_t. If we write the discrete-time population on the left and the continuous-time population on the right we can derive as follows:

$$N_t = N_t$$

$$N_0\lambda^t = N_0e^{rt}$$

$$\lambda^t = e^{rt}$$

$$ln(\lambda^t) = ln(e^{rt})$$

$$tln(\lambda) = rtln(e)$$

$$ln(\lambda) = rln(e)$$

The natural log of e is 1, so

$$ln(\lambda) = r * 1$$

$$\lambda = e^r$$

So, we can convert back and forth between continuous-and-discrete time models. Remember that $\lambda = 1 + r_d$.

Suppose we have a population growing in continuous time with some value of *r*, and a population growing in discrete time with the same value of *R*, i.e., $r = r_d$. Which will grow faster? As we did with the geometric model, we can derive the doubling time for the exponential model (Gotelli 2001). We begin with Equation 11, and plug in t_double:

$$N_{t_{double}} = N_0e^{rt_{double}}$$

Substituting $2N_0$ for $N_{t_{double}}$, we get

$$2N_0 = N_0e^{rt_{double}}$$

Dividing both sides by N_0 gives us

$$2 = e^{rt_{double}}$$

and taking the natural logarithm of both sides yields

$$ln(2) = ln(e^{rt_{double}})$$

$$ln(2) = rt_{double}$$

Finally, we divide both sides by r, and rearrange, to get

$$t_{double} = \frac{ln(2)}{r}$$

Parallel to our earlier example, let us suppose $r = 0.01$ individuals/individual/year. As before, this implies a 10% annual increase in the population, but now this increase occurs continuously rather than in discrete time intervals. How long does it take for this population to double? Plugging in the value 0.1 for r yields a doubling time of 6.93 years, somewhat faster than indicated by the geometric model.

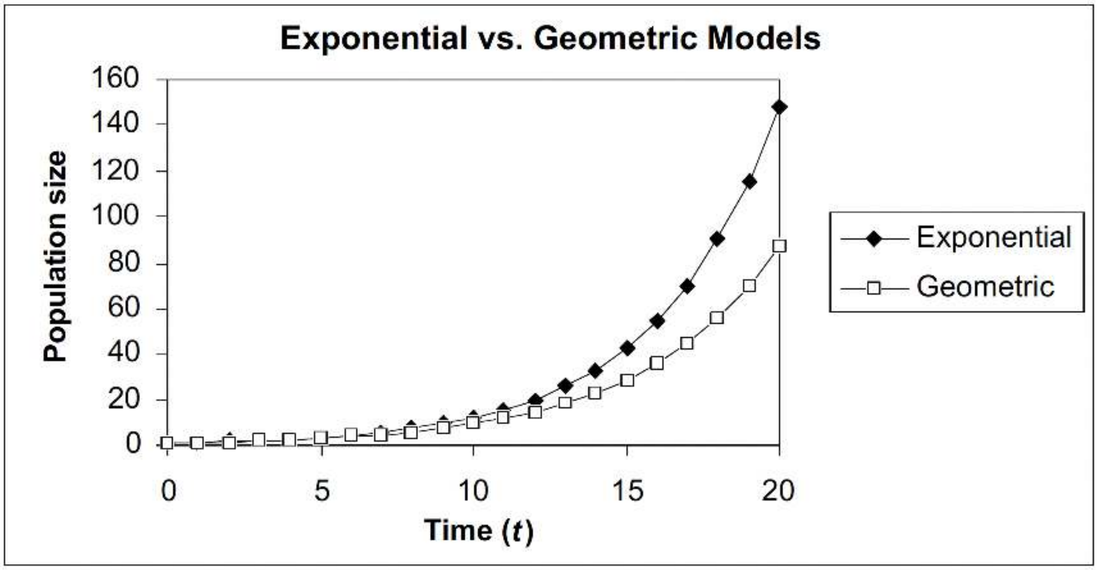


Figure 10.5.1 : Exponential growth models have a faster growth rate than geometric models, so the population size of exponentially growing populations outpaces geometrically growing populations over time.

EXPLORE THIS MODEL

Before moving on to the next section, explore this Exponential Growth Shiny App developed by Dr. Aaron Howard to better understand how changes to the initial population size (N) and the population growth rate (r) impact population size over time.

References

Donovan, T.M., & Welden, C. (2002). Spreadsheet exercises in ecology and evolution. *Sinauer Associates, Inc. Sunderland, MA, USA.*

Gotelli, N.J. (2001). *A Primer of Ecology*, 3rd Edition. Sinauer Associates, Sunderland, MA.

10.5.1: Logistic population growth

INTRODUCTION

This material in this chapter has been adapted from Donovan and Welden (2002).

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

As in the previous section on Geometric and Exponential Growth, we begin with a model of population dynamics in discrete time, with explicit parameters for per capita rates of birth and death.

In the previous section, we developed the following geometric model of population dynamics:

$$N_{t+1} = N_t + b * N_t - d * N_t$$

where

N_t =population at time t

N_{t+1} = population at one time unit later

b= per capita birth rate

d = per capita birth rate

As you discovered in the earlier exercise, this model produces geometric population growth (the discrete-time analog of exponential growth) if b and d are held constant and $b > d$ However, the assumption that per capita rates of birth and death remain constant is unrealistic, so we will now develop a model in which these rates change. Specifically, we will consider only one cause of changes in per capita birth and death rates: the size of the population itself. In other words, we will assume that environmental conditions, food supply, and so on remain constant; only the size of the population itself changes. These additions result in the **logistic growth** model.

Because per capita rates of birth and death *do* change in response to population size or density, logistic models are **density-dependent**, in contrast to geometric and exponential models, which are density-independent. As the population grows, less food and water, fewer nesting and hiding sites, and fewer resources in general are available to each individual, affecting both an individual's rate of reproduction and its risk of death. Our model will thus include **intraspecific competition** (competition among members of the same species) for resources. These models are used to inform practical decisions in the management of fisheries and game animal populations and are used to predict the growth of the human population. Later exercises will develop models of interspecific (between two species) competition and predator-prey dynamics.

Logistic growth models include an **equilibrium population size** in this model. In other words, populations grow until they reach a stable size. The population is at equilibrium when *total* deaths equal *total* births and when *per capita* rates of birth and death are equal. This equilibrium populations size is so important in population biology, it is given its own name—the **carrying capacity**. The carrying capacity is defined as the largest population that can be supported indefinitely, given the resources available in the environment. This carrying capacity is represented by the parameter K.

$$\frac{dN}{dt} = rN\frac{(K - N_t)}{K}$$

If we begin with a very small population, the term $\frac{(K-N_t)}{K}$ is very nearly equal to $\frac{(K)}{K}$ or 1. The model will then behave like a geometric model, and the population will grow, provided $r > 1$. The population will grow slowly at first, because the parameter r is also being multiplied by a number N_t that is nearly equal to zero, but it will grow faster and faster, at least for a while. At some point, however, population growth will begin to slow because the term $\frac{(K-N_t)}{K}$ is getting smaller and smaller as N_t gets larger and closer to K.

At the other extreme, imagine a population that starts out at a size very close to its carrying capacity, K. The term $\frac{(K-N_t)}{K}$ becomes nearly equal to zero, and population growth is extremely slow. When $N_t = K$, the population stops growing altogether.

EXPLORE THIS MODEL

Before moving on to the next section, explore the Logistic growth Shiny App developed by Dr. Aaron Howard to better understand how changes to the initial population size N, carrying capacity K, and the population growth rate r impact population size over time.

References

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. *Sinauer Associates, Inc. Sunderland, MA, USA.*

10.6: Projecting population growth

Predicting changes in population size using lambda

Once we have a value for and the current size of the population from a complete census, we can estimate the future size of the population.

Recall that we arrived at lambda previously by setting up this equation

$$N_{t+1}/N_t = \lambda = \phi + b$$

Where is ϕ the survival rate of adults, and b is the number of offspring produced per adult that live to reproduce themselves.

We can rearrange this equation for making projections like this:

$$N_{t+1} = \lambda * N_t$$

Derivation Dance

$N_{t+1}/N_t = \lambda$ indicates that our concept of lambda is based on the ratio of two population sizes. Let's start with this:

$$N_{t+1}/N_t = \lambda$$

Now multiple both sizes by N_t

$$N_{t+1}/N_t * N_t = \lambda * N_t$$

N_t cancels out from the left side and we get

$$N_{t+1} = \lambda * N_t$$

This tells us that the population size next year (N_{t+1}) can be calculated as $\lambda * (current.population.size)$.

Case Study: Projecting the number of Kirtland's Warblers

In 1990 it was estimated that there were 265 KIWA males with territories. If \[\lambda] = 1.3 as we calculated earlier, we'd predict that in 1991 the population size would be

$$N_{1991} = \lambda * N_{1990}$$

$$N_{1991} = 1.3 * 265 = 344.5$$

So we'd predict there to be 344 or 345 birds in 1991 (you can't have 0.5 of an organism. Indeed, researchers observed 347 birds.

We can repeat this using our estimate for 1991 to estimate 1992 and so on. When you plug the output of an equation (eg N_{1991}=344) back into itself repeatedly this is called **recursion.**

The equation

$$N_{t+1} = \lambda * N_t$$

is therefore sometimes referred to as a **recursion equation**. (Similar terms are **iterate** and **iteratively**.)

Exponential population growth

If you take the population size of 344 KIWA from our last calculation and plug it back into the population growth equation like this to estimate the number of warblers in the next year, 1992:

$$N_{1992} = 1.3 * 344 = 447.2$$

The estimated population the following year will be about 447 KIWA males. In reality, there were 497 males counted, so our projection is a bit low

If you repeat this process of plugging the results of one calculation into the next calculation 8 more times (for 10 total years of population change) we can project the population size for a decade. Note the convex, upward curvature of the line. This upward, accelerating curve is an **exponential growth curve**. Exponential growth occurs when something increases by multiplication. This is in contrast to **arithmetic growth**, which occurs when something increases by addition.

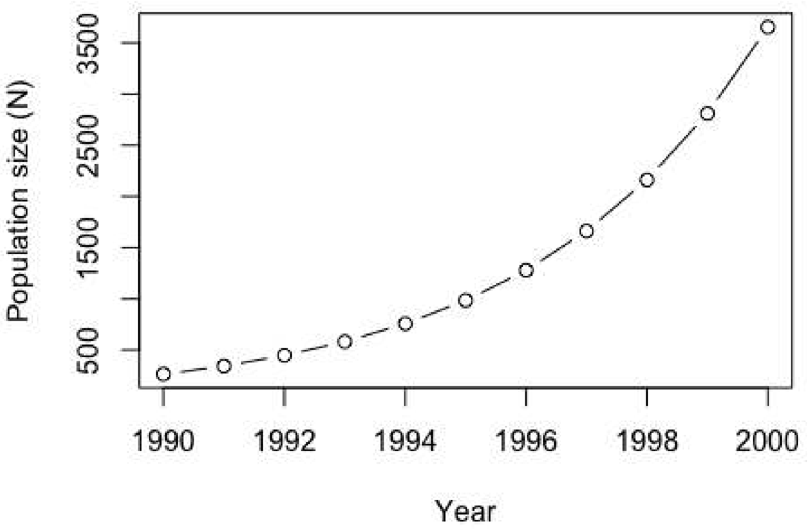


Figure 10.6.1: Exponential growth increases by multiplication and accelerates the population size over time without limit.

Many things in the world change arithmetically. For example, if you are being paid by the hour to do a job and don't have to work an entire day, the amount you earn increases arithmetically. Some populations can grow arithmetically if individuals from other populations are being **introduced** intentionally to the population. For example, the Peregrine falcon (*Falco peregrinus*) has a geographic range that encompases the entire world. However, due to the impacts of pesticides such as DDT the falcon was almost extirpated from many places in the United States. In addition to banning DDT, falcon populations were restored by taking young falcons from large populations and introducing them to smaller populations. If 10 falcons were introduced each year to a population, the fixed number of new individuals results in arithmetic contribution to growth.

In contrast to the fixed increases of arithmetic growth, exponential growth occurs multiplicatively - that is, by multiplying the current population size by a growth rate. If a population of falcons has 100 birds and a growth rate of 1.10, then it's population size the next year is 100*1.10 = 110. The next year if the growth rate is still 1.10 the population would be 110*1.10 = 121. Therefore the first time step the change in population size (delta N) was 10 individuals (110-100 = 10), while over the second time step delta N was 11 individuals (121-110 = 11). If we projected a third year the population would be 121*1.10 = 133.1. Delta N is therefore increasing each year from 10, to 11, to about 12. This is why we use the term "*accelerating*" to describe this type of growth: each year the amount of change increases.

Figure 10.6.2: Male peregrine falcon (*Falco peregrinus*) in Humber Bay Park West in Toronto. "*Falco peregrinus*" by Сапсан is licensed under CC BY-SA 3.0.

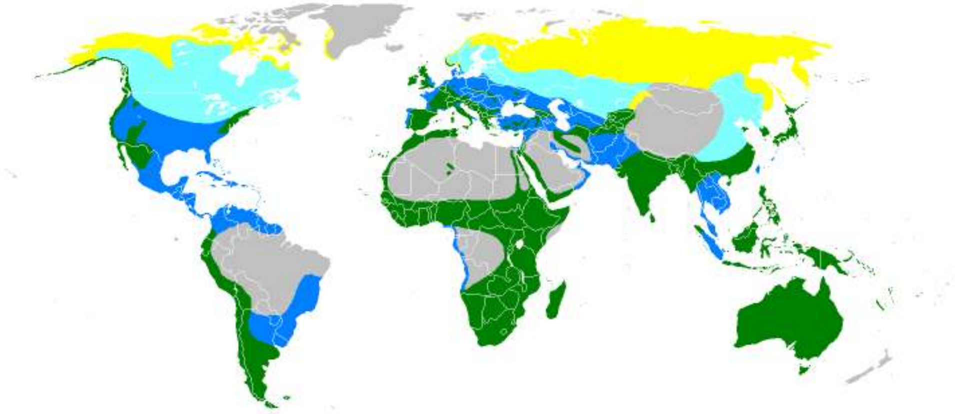


Figure 10.6.3: The peregrine falcon's range covers most of the world, besides some areas of Africa, the Arabian Peninsula, South America, Greenland, and Asia. The birds' large home range allows for alternative options from limiting factors. "Range map for *Falco peregrinus* (including *F. (p.) pelegrinoides,* the Barbary falcon)" by MPF is licensed under CC BY-SA 3.0.

Case study: The Montserrat Oriole

The Montserrat Oriole (*Icterus oberi*) is a relative of the Baltimore Oriole (*Icterus galbula*). While the Baltimore Oriole occurs throughout eastern and central North America, the Montserrat Oriole lives only on the Caribbean island of Montserrat. Montserrat is a small volcanic island that is only about 10 miles long and 7 miles wide and lies east of Puerto Rico and north of Barbados. Since the Montserrat Oriole only occurs on the island of Montserrat. It therefore is an entirely closed population. The Montserrat Oriole is therefore called a single-island **endemic species**, like the Cozumel Thrasher.

Figure 10.6.4: The red box identifies Montserrat. "Location of Montserrat" by TUBS is licensed under CC BY-SA 3.0 / adapted from original.

Figure 10.6.5: The Montserrat Oriole is only present on the island of Montserrat in a closed population. "Male Montserrat Oriole (*Icterus oberi*), London Zoo" by Neil Phillips is licensed under CC BY 2.0.

Volcanic activity in the 1990s on Montserrat has destroyed its forest habitat and rained ash down across the island, destroying nests and killing the birds' insect prey. N was therefore negative due to a low number of births of new birds and a high death rate of members of the existing population due to starvation. The species is therefore threatened with **extinction** - death of all members of the population. Biologists have become very interested in determining how many orioles are left on the island and what is happening with the population.

The Montserrat Oriole population size is small, but researchers have never been able to determine how many there are. What they have done, however, is marked a subset of adult orioles with **bird bands** and re-captured them each year to estimate survival rates. They have also found some nests and determined how many baby orioles are born per nest, and what the survival rate is for those birds until they are one year old and can breed. This gives an estimate of b.

Survival for the Montserrat Oriole is currently around 70%, or 0.70. This means that if there were 100 birds banded, 70 of them survived to the following year. Alternatively, we can think of this in terms of probability: a single bird banded this year has a 70% chance of surviving to the next year to be re-captured.

The birth rate is tricky to estimate for a number of reasons; incorporating both the number of Orioles that hatch from eggs and their probability of surviving for one year until they can reproduce, the birth rate (b) is about 0.42. The population growth rate is therefore

$$\lambda = 0.70 + 0.42$$

$$\lambda = 1.12$$

Since λ >1 we'd predict that the population of Orioles will be growing. As before, we aren't actually counting all the birds, but instead using demographic rates to estimate lambda.

In 2012 it was estimated that there might be as few as 300 Orioles on the island. If $\lambda = 1.12$ as we calculated above, we'd predict that in 2013 the population size would be

$$N_{2013} = \lambda * N_{2012}$$

$$N_{2013} = 1.12 * 300 = 336$$

In 2001 a second, very small population of Montserrat Orioles was found very near to the crater of the volcano on the island. Researchers haven't studied this population much, but they estimate that there were about 100 birds in 2020.

Figure $10.6.6$: Green spots on the island of Montserrat identify habitats. "Range map of Montserrat Oriole (*Icterus oberi*)" by Cephas is licensed under CC BY-SA 4.0.

If you start with 100 Orioles and you estimate that for this population is 1.10 you can start with this equation

$$N_{t+1} = \lambda * Nt$$

We can make this more specific with subscripts:

$$N_{2021} = \lambda * N_{2020}$$

then plug in the values $lambda = 1.10$ and N = 100

$$N_{2021} = 1.1 * 100$$

and get the project population the following year

$$N_{2021} = 110$$

So, if you have 100 orioles in 2020 you'd expect to have 2021 next year.

Exponential population growth of Orioles

If you take the population size of 110 orioles from our last calculation and plug it back into the population growth equation you can estimate the number of orioles in next year, 2022:

$$N_{2022} = 1.1 * 110$$

the estimated population the following year will be 121 orioles.

$$N_{2022} = 121$$

If you repeat this 8 more times (for 10 total years of population change since 2020) you will see a graph like the one below. Note the slight, convex, upward curvature of the line.

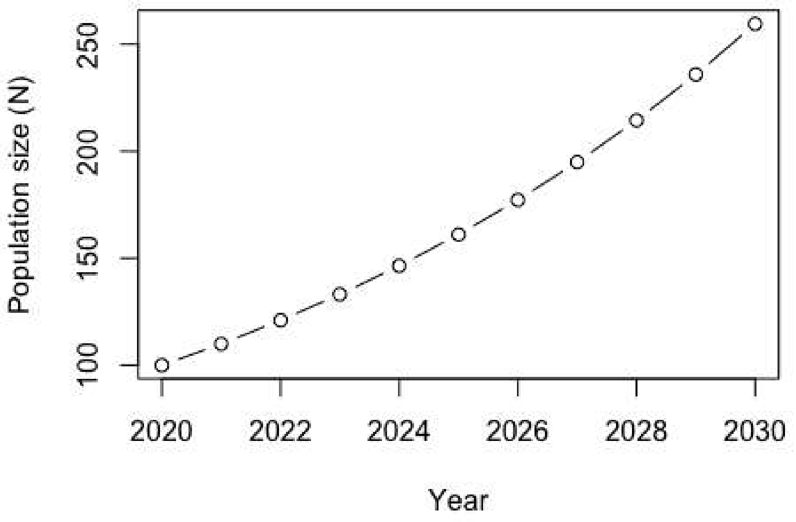


Figure 10.6.7: Exponential growth models can be used to graph the predicted population sizes of species.

Contributors and Attributions

This chapter was written by NL Brouwer (University of Pittsburgh)

10.7: Life Tables

This material in this chapter has been adapted from Donovan and Welden (2002).

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

Objectives

- Use age or stage-specific abundance data to calculate a variety of life table parameters.
- Discover how patterns of survivorship relate to the classic three types of survivorship curves.
- Learn how patterns of survivorship relate to life expectancy.
- Explore how patterns of survivorship and fecundity affect the rate of population growth.

10.7.1: Introduction

A life table is a record of survival and reproductive rates in a population, broken out by age, size, or developmental stage (e.g., egg, hatchling, juvenile, adult). Ecologists and demographers (scientists who study human population dynamics) have found life tables useful in understanding patterns and causes of mortality, predicting the future growth or decline of populations, and managing populations of endangered species.

Predicting the growth and decline of human populations is one very important application of life tables. As you might expect, whether the population of a country or region increases or decreases depends in part on how many children each person has and the age at which people die. But it may surprise you to learn that population growth or decline also depends on the age at which they have their children.

Another use of life tables is in species conservation efforts, such as in the case of the loggerhead sea turtle of the southeastern United States (Crouse et al., 1987). Generally speaking, the loggerhead population is declining and mortality among loggerhead eggs and hatchlings is very high. These facts led conservation biologists to advocate for the protection of nesting beaches. When these measures proved ineffective in halting the population decline, compiling and analyzing a life table for loggerheads indicated that reducing mortality of older turtles would have a greater probability of reversing the population decline. Therefore, management efforts shifted to persuading fishermen to install turtle exclusion devices on their nets to prevent older turtles from drowning.

10.7.2: **Life Table Varieties**

Life tables come in two varieties: cohort and static. A **cohort life table** follows the survival and reproduction of all members of a cohort from birth to death. A cohort is the set of all individuals born, hatched, or recruited into a population during a defined time interval. Cohorts are frequently defined on an annual basis (e.g., all individuals born in 1978), but other time intervals can be used as well.

A **static life table** records the number of living individuals of each age in a population and their reproductive output. The two varieties have distinct advantages and disadvantages, some of which we discuss below.

Life tables (whether cohort or static) that classify individuals by age are called **age-based life tables**. Such life tables treat age the same way we normally do: that is, individuals that have lived less than one full year are assigned age zero; those that have lived one year or more but less than two years are assigned age one; and so on. Life tables represent age by the letter *x*, and use *x* as a subscript to refer to survivorship, fecundity, and so on, for each age.

Size-based and **stage-based life tables** classify individuals by size or developmental stage, rather than by age. Size-based and stage-based tables are often more useful or more practical for studying organisms that are difficult to classify by age, or whose ecological roles depend more on size or stage than on age.

10.7.2.1: Cohort Life Tables

To build a cohort life table for, let’s say, humans born in the United States during the year 1900, we would record how many individuals were born during the year 1900, and how many survived to the *beginning* of 1901, 1902, etc., until there were no more survivors. This record is called the **survivorship schedule**.

We must also record the **fecundity schedule**—the number of offspring born to individuals of each age. The total number of offspring is usually divided by the number of individuals in the age, giving the average number of offspring per individual, or per capita fecundity.

Many life tables count only females and their female offspring; for animals with two sexes and equal numbers of males and females of each age, the resulting numbers are the same as if males and females were both counted. For most plants, hermaphroditic animals, and many other organisms, distinctions between the sexes are nonexistent or more complex, and life table calculations may have to be adjusted.

10.7.2.2: Static Life Tables

A static life table is similar to a cohort life table but introduces a few complications. For many organisms, especially mobile animals with long life spans, it can be difficult or impossible to follow all the members of a cohort throughout their lives. In such cases, population biologists often count how many individuals of each age are alive *at a given time*. That is, they count how many members of the population are currently in the 0–1- year-old class, the 1–2-year-old class, etc.

These counts can be used as if they were counts of survivors in a cohort, and all the calculations described below for a cohort life table can be performed using them. In doing this, however, the researcher must bear in mind that she or he is assuming that age-specific survivorship and fertility rates have remained constant since the oldest members of the population were born. This is usually not the case and can lead to some strange results, such as negative mortality rates. These are often resolved by averaging across several ages, or by making additional assumptions.

10.7.3: **Life Table Parameters**

Survivorship and fecundity schedules are the raw data of any life table. From them we can calculate a variety of other quantities, including age-specific rates of survival, mortality, fecundity, survivorship curves, life expectancy, generation time, net reproductive rate, and intrinsic rate of increase. Which of these quantities you calculate will depend on your goals in constructing the life table.

Key Parameters

x and n_x When conducting a study, these are the data generally collected on populations. We then calculate the rest of the life table from these data.

- x The first column, represents the age classes. This column could represent days, minutes, or life stages (eggs, juveniles, adults, etc.).
- n_x The number of individuals from the original cohort that are alive at the specified age, age class, or life stage (x).

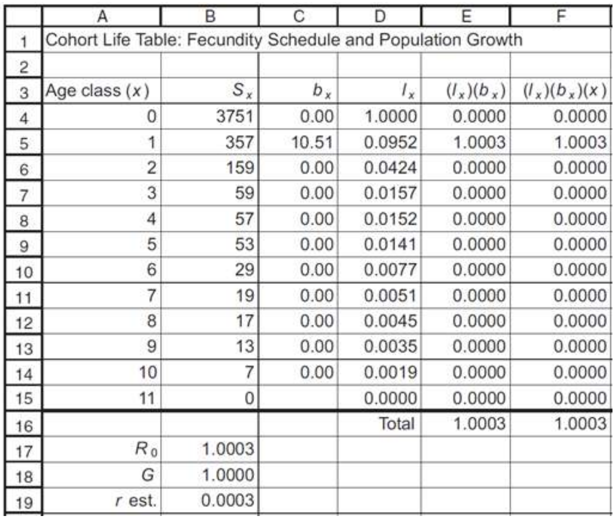
From information on the number of individuals at each age, we can calculate a variety of survival and mortality rates.

- d_x The difference between the number of individuals alive for any age class (n_x) and the next older age class (n_{x+1}) is the number of individuals that have died during that time intervals. d_x is a measure of age-specific mortality.
- q_x The number of individuals that died during any given time interval (d_x) divided by the number alive at the beginning of that interval (n_x) provides an age-specific mortality rate.
- s_xThe age-specific survival rate for age interval x is the proportion of individuals that survive during any given time interval.
- l_x The number of individuals surviving to any given life stage as a proportion of the original cohort size. l_x represents the probability at birth of surviving to any given life stage.

Calculating life expectancy E_x requires calculating two additional parameters, L_x and T_x .

- L_x The number of individuals that are alive in the middle of the first age class – 0.5 years old, or 1.5 years old.
- T_x The total years lived into the future by individuals in age class x. This value is calculated by summing the values of Lx cumulatively from age x to the end of the life table. The number of time units left for all individuals to live from age x onward – obtained by summing all values of L_x .
- E_x The life expectancy for an individual of age x is age-specific life expectancy divided by number of individuals at age x. Life expectancy represents the average additional length of times than an individual will live once it has reached age x.

A typical life table is shown in Figure 1. If we were to build a cohort life table for a population born during the year 1900, we would record how many individuals were born during the year 1900, and how many survived to the *beginning* of 1901, 1902, etc., until there were no more survivors. This record is called the **survivorship schedule**. We would also record the **fecundity schedule**: the number of offspring born to members of each age class. The total number of offspring is usually divided by the number of individuals in the age class, giving the average number of offspring per individual, which is represented by b_x.



	A	B	C	D	E	F
1	Cohort Life Table: Fecundity Schedule and Population Growth					
2						
3	Age class (x)	S_x	b_x	l_x	$(l_x)(b_x)$	$(l_x)(b_x)(x)$
4	0	3751	0.00	1.0000	0.0000	0.0000
5	1	357	10.51	0.0952	1.0003	1.0003
6	2	159	0.00	0.0424	0.0000	0.0000
7	3	59	0.00	0.0157	0.0000	0.0000
8	4	57	0.00	0.0152	0.0000	0.0000
9	5	53	0.00	0.0141	0.0000	0.0000
10	6	29	0.00	0.0077	0.0000	0.0000
11	7	19	0.00	0.0051	0.0000	0.0000
12	8	17	0.00	0.0045	0.0000	0.0000
13	9	13	0.00	0.0035	0.0000	0.0000
14	10	7	0.00	0.0019	0.0000	0.0000
15	11	0		0.0000	0.0000	0.0000
16				Total	1.0003	1.0003
17	R_0	1.0003				
18	G	1.0000				
19	r est.	0.0003				

Figure 10.7.1: A cohort of 3751 individuals tracked over time. The number alive at the beginning of each year is given in Column B, and the average number of offspring per female is given in Column C. Columns D through G are calculated from information in columns A through C.

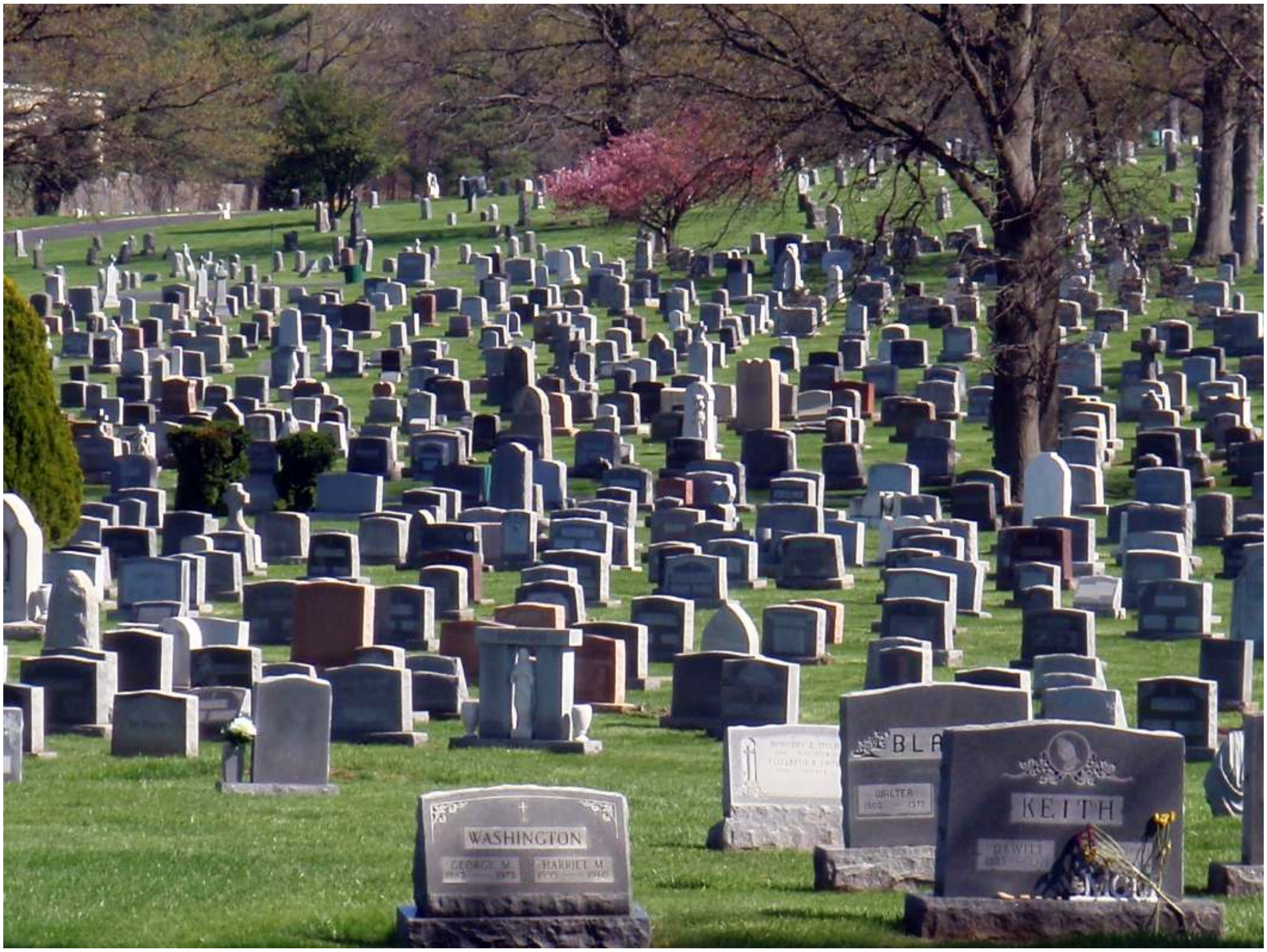


Figure $10.7.2$: "Mt. Olivet Cemetery" was taken by Daniel Lobo and is licensed under Creative Commons Attribution 2.0 Generic.

Calculating Key Parameters

Standardized Survival Schedule (l_x). Because we want to compare cohorts of different initial sizes, we standardize all cohorts to their initial size at time zero, n_0. We do this by dividing each n_x by n_0. This proportion of original numbers surviving to the beginning of each interval is denoted l_x, and calculated as

$$l_x = \frac{n_x}{n_0} \tag{10.7.1}$$

We can also think of l_x as the probability that an individual survives from birth to the beginning of age x. Because we begin with *all* the individuals born during the year (or other interval), l_x always begins at a value of one (i.e., n_0/n_0), and can only decrease with time. At the last age, k, n_k is zero.

Age-Specific Survivorship (S_x). Standardized survivorship, l_x, gives us the probability of an individual surviving from birth to the beginning of age x. But what if we want to know the probability that an individual who has already survived to age x will survive to age $x+1$? We calculate this age-specific survivorship as $S_x = l_{x+1}/l+x$, or equivalently,

$$S_x = \frac{n_{x+1}}{n_x} \tag{10.7.2}$$

Life Expectancy (E_x)**.** You may have heard another demographic statistic, life expectancy, mentioned in discussions of human populations. Life expectancy is how much longer an individual of a given age can be expected to live beyond its present age. Life expectancy is calculated in three steps.

First, we compute the proportion of survivors at the mid-point of each time interval (L_x—note the capital L here); that is,

$$L_x = \frac{n_x + n_{x+1}}{2} \tag{10.7.3}$$

Second, we sum all the L_x values from the age of interest (n) up to the oldest age, k:

$$T_x = \sum_{n=1}^{\infty} (L_x) \tag{10.7.4}$$

Finally, we calculate life expectancy as

$$E_x = \frac{T_x}{n_x} \tag{10.7.5}$$

Life expectancy is age-specific—it is the expected number of time-intervals remaining to members of a given age. The statistic most often quoted (usually without qualification) is the life expectancy at birth (E_0).

10.7.4: Survivorship Curves

There are three classic survivorship curves, called Type I, Type II, and Type III (Figure 2). To understand survivorship curves you can use survivorship schedules (*Sx*) to calculate and graph **standardized survivorship** (l_x), **age-specific survivorship** (g_x), and **life expectancy** (e_x).

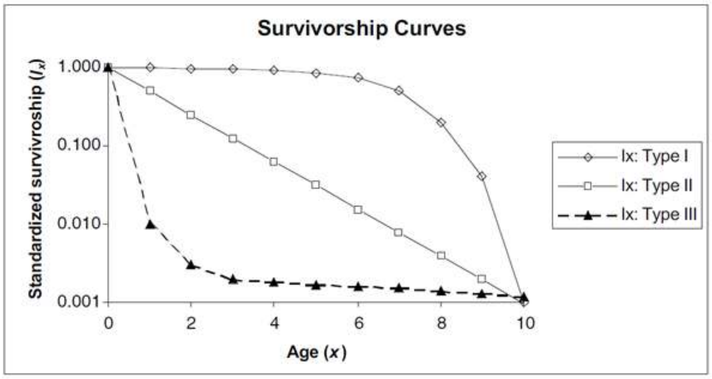


Figure 10.7.3: Hypothetical survivorship curves. Note that the *y*-axis has a logarithmic scale. Type 1 organisms have high survivorship throughout life until old age sets in, and then survivorship declines dramatically to 0. Humans are type 1 organisms. Type III organisms, in contrast, have very low survivorship early in life, and few individuals live to old age.

Population Growth or Decline

We frequently want to know whether a population can be expected to grow, shrink, or remain stable, given its current age-specific rates of survival and fecundity. We can determine this by computing the **net reproductive rate** (R_0). To predict long-term changes in population size, we must use this net reproductive rate to estimate the intrinsic rate of increase (r).

Net Reproductive Rate (*R*$_0$) We calculate net reproductive rate (R_0) by multiplying the standardized survivorship of each age (l_x) by its fecundity ((b_x)), and summing these products:

$$R_0 = \sum_{x=0}^{k} l_x b_x \tag{10.7.6}$$

The net reproductive rate is the lifetime reproductive potential of the average female, adjusted for survival. Assuming survival and fertility schedules remain constant over time, if $R_0 > 1$, then the population will grow exponentially. If $R_0 < 1$, the population will shrink exponentially, and if $R_0 = 1$, the population size will not change over time. You may be tempted to conclude the $R_0 = r$, the intrinsic rate of increase of the exponential model. However, this is not quite correct, because r measures population change in absolute units of time (e.g., years) whereas R_0 measures population change in terms of generation time. To convert R_0 into r, we must first calculate generation time G, and then adjust R_0.

Generation Time. Generation time is calculated as

$$G = \frac{\sum_{x=0}^{k} l_x b_x x}{\sum_{x=0}^{k} l_x b_x} \tag{10.7.7}$$

For organisms that live only one year, the numerator and denominator will be equal, and generation time will equal to one year. For all longer-lived organisms, generation time will be greater than one year, but exactly how much greater will depend on the survival and fertility schedules. A long-lived species that reproduces at an early age may have a shorter generation time than a shorter-lived one that delays reproduction.

Intrinsic Rate of Increase. We can use our knowledge of exponential population growth and our value of R_0 to estimate the intrinsic rate of increase (r) (Gotelli 2001). The size of an exponentially growing population at some arbitrary time t is $N_t = N_0 e^{rt}$, where e is the base of the natural logarithms and r is the intrinsic rate of increase. If we consider the growth of such a population from time zero through one generation time, G, it is

$$N_G = N_0 e^r G$$

Dividing both sides by N_0 gives us

$$\frac{N_G}{N_0} = e^r G$$

We can think of N_G / N_0 as roughly equivalent to R_0; both are estimates of the rate of population growth over the period of one generation.

Substituting R_0 into the equation gives us

$$R_0 \approx e^r G$$

Taking the natural logarithm of both sides gives us

$$ln(R_0) \approx rG$$

and dividing through by G gives us an estimate of r:

$$r \approx \frac{ln(R_0)}{G}$$

Finally, we can use our estimate of *r* (uncorrected or corrected) to predict the size of the population in the future. This kind of analysis is done for human populations to predict the effects of changes in medical care and birth control programs. If we assume that all age groups are roughly equivalent in size, a similar analysis can be done for endangered species to determine what intervention may be most effective in promoting population growth. The same analysis can be applied to pest species to determine what intervention may be most effective in reducing population size.

Reproductive Value

The idea that different individuals have different "value" in terms of their contribution to future generations is called their *reproductive value* (Fisher 1930). As Caswell (2001) states, "The amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced all enter into the **reproductive value** of an age-class."

The reproductive value of an individual of age x is designated at V_x, and is the number of offspring that an individual is expected to produce over its remaining life span (after adjusting for the growth rate of the population). Biologists are often interested in knowing the "value" of the different individuals from a practical standpoint because knowing something about the reproductive value can suggest which individuals should be harvested, killed, transplanted, etc. from a conservation or management perspective.

The reproductive value of different ages is strongly tied to an organism's life history. Typically, reproductive value is low at birth, increases to a peak near the age of first reproduction, and then declines (Caswell 2001).

Life History Table Practice 10.7.1

x	n_x	d_x	q_x	S_x
age	individuals alive at start of age x	age-specific mortality	age-specific mortality rate	age-specific survival rate
---	---	$n_x - n_{x+1}$	$\frac{d_x}{n_x} \quad (10.7.8)$	$\frac{n_{x+1}}{n_x} \quad (10.7.9)$
0	125	?	?	?
1	58	?	?	?
2	32	?	?	?
3	16	?	?	?
4	4	?	?	?
5	0	?	?	?

Answer

x	n_x	d_x	q_x	S_x
age	individuals alive at start of age x	age-specific mortality	age-specific mortality rate	age-specific survival rate
---	---	$n_x - n_{x+1}$	$\frac{d_x}{n_x} \quad (10.7.10)$	$\frac{n_{x+1}}{n_x} \quad (10.7.11)$
0	125	67	0.54	0.46
1	58	26	0.45	0.55
2	32	16	0.5	0.5
3	16	12	0.75	0.25
4	4	4	1.00	0

5	0	---	---	---

Life History Table Practice 10.7.2

x	n_x	I_x	L_x	T_x	E_x	b_x
age	individuals alive at start	proportion surviving at start of age x	# surviving	years left to live	life expectancy	average # of female offspring per female
---	---	$\frac{n_x}{n_0}$ (10.7.12)	$\frac{n_x+n_{x+1}}{2}$ (10.7.13)	$\sum_{n=1}^{\infty}(L_x)$ (10.7.14)	$\frac{T_x}{n_x}$ (10.7.15)	---
0	125	?	?	?	?	0
1	58	?	?	?	?	2
2	32	?	?	?	?	3
3	16	?	?	?	?	2
4	4	?	?	?	?	0
5	0	?	?	?	?	0

Answer

x	n_x	I_x	L_x	T_x	E_x	b_x
age	individuals alive at start	proportion surviving at start of age x	# surviving	years left to live	life expectancy	average # of female offspring per female
---	---	$\frac{n_x}{n_0}$ (10.7.16)	$\frac{n_x+n_{x+1}}{2}$ (10.7.17)	$\sum_{n=1}^{\infty}(L_x)$ (10.7.18)	$\frac{T_x}{n_x}$ (10.7.19)	
0	125	1.00	91.5	172.5	1.38	0
1	58	0.46	45	81	1.40	2
2	32	0.25	24	36	1.13	3
3	16	0.13	10	12	0.75	2
4	4	0.03	2	2	0.5	0
5	0	0	0	0	0	0

10.7.5: References

Caswell, H. (2001). *Matrix Population Models*, 2nd Ed. Sinauer Associates, Sunderland, MA.

Connell, J.H. (1970). A predator-prey system in the marine intertidal region. I. *Balanus glandula. Ecological Monographs, 40*: 49–78. (Reprinted in *Ecology: Individuals, Populations and Communities*, 2nd edition, M. Begon, J. L. Harper and C. R. Townsend.. (1990) Blackwell Scientific Publications, Oxford.)

Crouse, D.T., Crowder, L.B., & Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology, 68,* pp. 1412–1423.

Deevey, E.S., Jr. (1947). Life tables for natural populations of animals. *The Quarterly Review of Biology, 22,* pp. 283–314. (Reprinted in *Readings in Population and Community Ecology*, W.E. Hazen (ed.). 1970, W.B. Saunders, Philadelphia.)

Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Gotelli, N.J. (2001). *A Primer of Ecology*, 3rd Edition. Sinauer Associates, Sunderland, MA.

10.8: Population Models Practice Exercises

Put your knowledge and comprehension to the test with these practice problems! Some of these questions may require you to use a calculator and draw out models while you practice. Be sure to complete all questions included in each section before you click "Answer" for that section because the answers for all the questions in that section will be revealed together.

General Population Growth Equation 10.8.1

Your ecology class starts the semester out with a student population of 42. By the end of the semester, two students dropped out of the college, one student dropped the class, one student died on a fieldtrip, and five students joined the course late. What is the class population at the end of the semester?

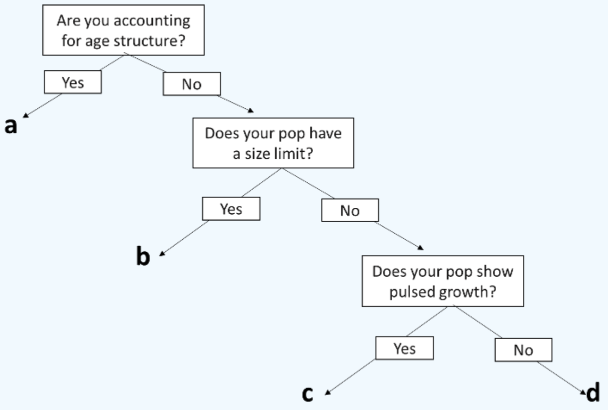
$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

Answer

N_t = 42 + (0-1) + (5-3) = 43 students

Choosing the Right Model 10.8.2

Which type of model (exponential, logistic, geometric, Leslie Matrix) belongs at each point in this figure?



Answer

a) Leslie Matrix Model

b) Logistic Model

c) Geometric Model

d) Exponential Model

Reading Results 10.8.3

How does the population change under the following conditions (increase, decrease, or remain stable)?

1) $\lambda = 1.02$

2) $R_0 = 1$

3) N > K

4) r = -0.10

Answer

1) increase

2) remains stable

3) decrease (population overshoots carrying capacity)

4) decrease

? Geometric Model 10.8.4

Given N_t (population size at initial time) = 500, B = 300, and D = 350, calculate λ.

1) Is this population increasing, decreasing, or stable?

2) What will the population be in 10 years? What about in 30 years?

Answer

1) N_{t+1} = N_t + B –D = 500 + 300 – 350 = 450

λ = N_{t+1} / N_t = 450/500 = 9/10 = 0.9

Since λ < 1, the population is decreasing.

2) N_{t+1} = N_0 λ t

N_{10} = 500*(0.9)10 = 174

N_{30} = 500*(0.9)30 = 21

? Exponential Model 10.8.5

A new species you are studying has continuous reproduction in a newly invaded habitat. The species' population is still growing without limit.

1) If the initial population size is 3000, and the growth rate is 0.02, what is the expected population in 25 years? How about in 50 years?

2) If at t_0, the population size is 500, and r = 0.035, how many years until the population reaches 4,000 individuals?

Answer

1) N_t = N_0 e t r

N_0 = 3000, r = 0.02

N_{25} = 3000*e(25)(0.02) = 4,946

N_{50} = 3000*e(50)(0.02) = 8,154

2) Population doubling time = 70/3.5 = 20: 20 years to reach 1000 individuals, 40 years to reach 2000 individuals, 60 years to reach 4000 individuals.

CHAPTER OVERVIEW

11: Behavioral Ecology

Learning Objectives

- Explain Tinbergen’s levels of analysis and be able to formulate questions that would be addressed at each level of analysis.
- Use concepts from optimal foraging models to explain foraging behavior, and compare and contrast solitary versus group foraging.
- Explain the costs and benefits of migration, and describe how these movements are studied by ecologists.
- Describe the variety forms and functions of animal communication.
- Explain direct and indirect and use Hamilton’s rule to assess when kin selection could be acting in a population.

Summary

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures. Behavioral ecology seeks to address questions associated with the proximate causes, ontogeny, survival value, and phylogeny of a behavior. The field of behavioral ecology includes a variety of disciplines, including the study of how organisms find food, how they move about the environment, and how they communicate with each other. This field is also interested in studying the evolution of social behaviors and social systems.

11.1: Proximate and Ultimate Causes of Behavior

Behavioral ecology

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures (**Figure 11.1.1**). Behavioral ecology emerged after Nikolaas Tinbergen outlined four questions to address when studying animal behaviors (**Figure 11.1.2**) that focused on two levels of answers: What are the ultimate (evolutionary) explanations of behavior, and what are the proximate (physiological or developmental) explanations of behavior?

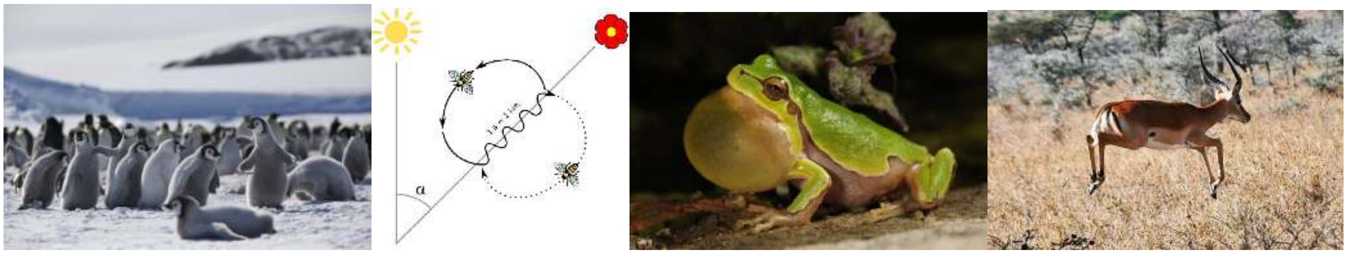
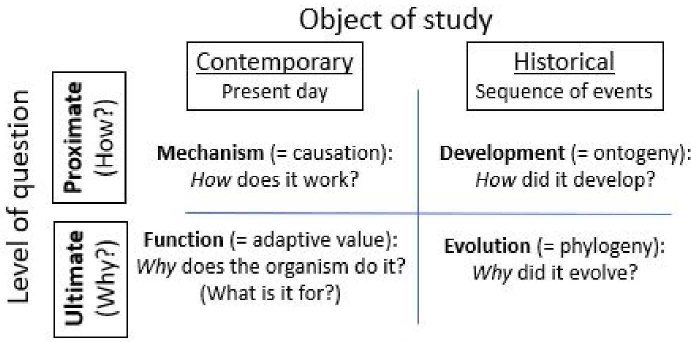


Figure 11.1.1: The study of behavioral ecology focuses on the ways organisms behaviorally interact with their physical and social environment. Here we see penguins huddling in the Antarctic (Ian Duffy), the bee waggle dance communicating information (Emmanuel Boutet), a frog with inflated vocal sac (Benny Trapp), and a stotting gazelle (Rick Wilhelmsen).

Tinbergen's four questions are complementary categories of explanations for animal behaviour. These are also commonly referred to as levels of analysis.[1] It suggests that an integrative understanding of behaviour must include: **ultimate (evolutionary) explanations**, in particular the behaviour (1) **adaptive function** and (2) **phylogenetic** history; and the **proximate explanations**, in particular the (3) underlying **physiological mechanisms** and (4) **ontogenetic/developmental history**.[2]

When asked about the purpose of sight in humans and animals, even elementary-school children can answer that animals have vision to help them find food and avoid danger (function/adaptation). Biologists have three additional explanations: sight is caused by a particular series of evolutionary steps (phylogeny), the mechanics of the eye (mechanism/causation), and even the process of an individual's development (ontogeny).



Object of study

Level of question	Contemporary Present day	Historical Sequence of events
Proximate (How?)	**Mechanism** (= causation): *How* does it work?	**Development** (= ontogeny): *How* did it develop?
Ultimate (Why?)	**Function** (= adaptive value): *Why* does the organism do it? (What is it for?)	**Evolution** (= phylogeny): *Why* did it evolve?

Figure 11.1.2: Summary of Tinbergen's four questions (Dan Wetzel).

Evolutionary (ultimate) explanations

1. Function (adaptation)

Darwin's theory of evolution by natural selection is the only scientific explanation for why an animal's behavior is usually well adapted for survival and reproduction in its environment. However, claiming that a particular mechanism is well suited to the present environment is different from claiming that this mechanism was selected for in the past due to its history of being adaptive.[4] The literature conceptualizes the relationship between function and evolution in two ways. On the one hand, function and evolution are often presented as separate and distinct explanations of behaviour.[4]

On the other hand, the common definition of adaptation, a central concept in evolution, is a trait that was functional to the reproductive success of the organism and that is thus now present due to being selected for; that is, function and evolution are inseparable. However a trait can have a current function that is adaptive without being an adaptation in this sense, if for instance the environment has changed. Imagine an environment in which having a small body suddenly conferred benefit on an organism when previously body size had had no effect on survival.[4]

A small body's function in the environment would then be adaptive, but it wouldn't become an adaptation until enough generations had passed in which small bodies were advantageous to reproduction for small bodies to be selected for. Given this, it is best to understand that presently functional traits might not all have been produced by natural selection.[4] The term "function" is preferable to "adaptation," because adaptation is often construed as implying that it was selected for due to past function.

2. Phylogeny (evolution)

Evolution captures both the history of an organism via its phylogeny, and the history of natural selection working on function to produce adaptations.[5] There are several reasons why natural selection may fail to achieve optimal design. One entails random processes such as mutation and environmental events acting on small populations. Another entails the constraints resulting from early evolutionary development. Each organism harbors traits, both anatomical and behavioral, of previous phylogenetic stages, since many traits are retained as populations evolve.

Reconstructing the phylogeny of a species often makes it possible to understand the "uniqueness" of recent characteristics: Earlier phylogenetic stages and (pre-) conditions which persist often also determine the form of more modern characteristics. For instance, the vertebrate eye (including the human eye) has a blind spot, whereas octopus eyes do not. In those two lineages, the eye was originally constructed one way or the other. Once the vertebrate eye was constructed, there were no intermediate forms that were both adaptive and would have enabled it to evolve without a blind spot.

Proximate explanations

3. Mechanism (causation)

In examining living organisms, biologists are confronted with diverse levels of complexity (e.g. chemical, physiological, psychological, social). They therefore investigate causal and functional relations within and between these levels. A biochemist might examine, for instance, the influence of social and ecological conditions on the release of certain neurotransmitters and hormones, and the effects of such releases on behaviour, e.g. stress during birth has a tocolytic (contraction-suppressing) effect.

Some prominent classes of causal mechanisms include:

- The brain: Broca's area, a small section of the human brain, has a critical role in linguistic capability.
- Hormones: chemicals used to communicate among cells of an individual organism. Testosterone, for instance, stimulates aggressive behaviour in a number of species.
- Pheromones: chemicals used to communicate among members of the same species. Some species (e.g., dogs and some moths) use pheromones to attract mates.

4. Ontogeny

Ontogeny is the process of development of an individual organism from the zygote through the embryo to the adult form.

In the latter half of the twentieth century, social scientists debated whether human behaviour was the product of nature (genes) or nurture (environment in the developmental period, including culture). Many forms of developmental learning have a critical period, for instance, for imprinting among geese and language acquisition among humans. In such cases, genes determine the timing of the environmental impact.

Causal relationships

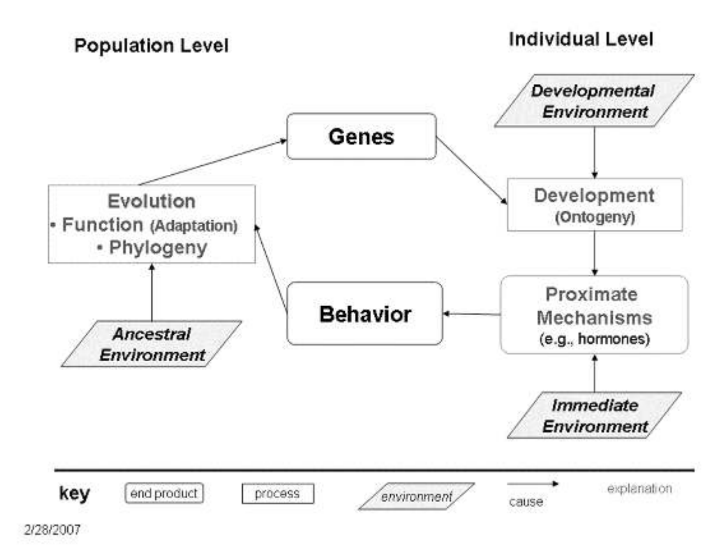


Figure 11.1.3: Diagrammatic explanation of behavioral ecology: the interaction between an organisms behavior, its genes, the environment, and evolutionary forces (credit: W. Pete Welch, available in the public domain; adopted from Tinbergen, 1963).

The figure shows the causal relationships among the categories of explanations. The left-hand side represents the evolutionary explanations at the species level; the right-hand side represents the proximate explanations at the individual level. In the middle are those processes' end products—genes (i.e., genome) and behaviour, both of which can be analyzed at both levels.

Evolution, which is determined by both function and phylogeny, results in the genes of a population. The genes of an individual interact with its developmental environment, resulting in mechanisms, such as a nervous system. A mechanism (which is also an end-product in its own right) interacts with the individual's immediate environment, resulting in its behaviour.

Here we return to the population level. Over many generations, the success of the species' behaviour in its ancestral environment—or more technically, the environment of evolutionary adaptedness may result in evolution as measured by a change in its genes.

In sum, there are two processes—one at the population level and one at the individual level—which are influenced by environments in three time periods.

Examples

Let's look at a couple of examples of explaining a trait or behavior using Tinbergen's four questions:

Visual perception

- Function: to find food and avoid danger.
- Phylogeny: the vertebrate eye initially developed with a blind spot, but the lack of adaptive intermediate forms prevented the loss of the blind spot.
- Causation: the lens of the eye focuses light on the retina.
- Development: neurons need the stimulation of light to wire the eye to the brain (Moore, 2001:98–99).

Sleep (Bode & Kuula, 2021):[7]

- Function: energy restoration, metabolic regulation, thermoregulation, boosting immune system, detoxification, brain maturation, circuit reorganization, synaptic optimization, avoiding danger.
- Phylogeny: sleep exists in invertebrates, lower vertebrates, and higher vertebrates. NREM and REM sleep exist in eutheria, marsupialiformes, and also evolved in birds.

- Mechanisms: mechanisms regulate wakefulness, sleep onset, and sleep. Specific mechanisms involve neurotransmitters, genes, neural structures, and the circadian rhythm.
- Ontogeny: sleep manifests differently in babies, infants, children, adolescents, adults, and older adults. Differences include the stages of sleep, sleep duration, and sex differences.

References

1. MacDougall-Shackleton, S.A. (2011-07-27). "The levels of analysis revisited". *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1574), pp. 2076–2085. doi:10.1098/rstb.2010.0363. PMC 3130367. PMID 21690126.
2. Daly, M., & Wilson, M. (1983). *Sex, evolution, and behaviour*. Brooks-Cole.
3. p411 in Tinbergen, Niko. (1963). "On Aims and Methods in Ethology," Zeitschrift für Tierpsychologie, 20: 410–433.
4. Nikolaas Tinbergen, ethology, Cartwright 2000:10; Buss 2004:12)
5. "Phylogeny" often emphasizes the evolutionary genealogical relationships among species (Alcock 2001:492; Mayr, 2001:289) as distinct from the categories of explanations. Although the categories are more relevant in a conceptual discussion, the traditional term is retained here.
6. Bode, Adam; Kuula, Liisa (September 2021). "Romantic Love and Sleep Variations: Potential Proximate Mechanisms and Evolutionary Functions". *Biology*, *10*(9), pp. 923. doi:10.3390/biology10090923.

Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) from the following sources:

- Wikipedia, Behavioral ecology
- Wikipedia, Tinbergen's four questions.

11.2: Foraging Ecology

Foraging

Figure 11.2.1: Grizzly bear (*Ursus arctos horribilis*) mother and cubs foraging in Denali National Park, Alaska.

Foraging is searching for wild food resources. It affects an animal's fitness because it plays an important role in an animal's ability to survive and reproduce.[1] Foraging theory is a branch of behavioral ecology that studies the foraging behavior of animals in response to the environment where the animal lives.

Behavioral ecologists use economic models to understand foraging; many of these models are a type of optimal model. Thus foraging theory is discussed in terms of optimizing a payoff from a foraging decision. The payoff for many of these models is the amount of energy an animal receives per unit time, more specifically, the highest ratio of energetic gain to cost while foraging.[2] Foraging theory predicts that the decisions that maximize energy per unit time and thus deliver the highest payoff will be selected for and persist. Key words used to describe foraging behavior include *resources*, the elements necessary for survival and reproduction which have a limited supply, *predator*, any organism that consumes others, *prey*, an organism that is eaten in part or whole by another,[1] and *patches*, concentrations of resources.

Behavioral ecologists first tackled this topic in the 1960s and 1970s. Their goal was to quantify and formalize a set of models to test their null hypothesis that animals forage randomly. Important contributions to foraging theory have been made by:

- Eric Charnov, who developed the marginal value theorem to predict the behavior of foragers using patches;
- Sir John Krebs, with work on the optimal diet model in relation to tits and chickadees;
- John Goss-Custard, who first tested the optimal diet model against behavior in the field, using redshank, and then proceeded to an extensive study of foraging in the common pied oystercatcher

Factors influencing foraging behavior

Several factors affect an animal's ability to forage and acquire profitable resources.

Learning

Learning is defined as an adaptive change or modification of a behavior based on a previous experience.[3] Since an animal's environment is constantly changing, the ability to adjust foraging behavior is essential for maximization of fitness. Studies in social insects have shown that there is a significant correlation between learning and foraging performance.[3]

In nonhuman primates, young individuals learn foraging behavior from their peers and elders by watching other group members forage and by copying their behavior.[4] Observing and learning from other members of the group ensure that the younger members of the group learn what is safe to eat and become proficient foragers (Figure 11.2.2).

Figure 11.2.2: A troop of olive baboons (*Papio anubis*) foraging in Laikipia, Kenya. Young primates learn from elders in their group about proper foraging.

One measure of learning is 'foraging innovation'—an animal consuming new food, or using a new foraging technique in response to their dynamic living environment.[5] Foraging innovation is considered learning because it involves behavioral plasticity on the animal's part. The animal recognizes the need to come up with a new foraging strategy and introduce something it has never used before to maximize his or her fitness (survival). Forebrain size has been associated with learning behavior. Animals with larger brain sizes are expected to learn better.[5] A higher ability to innovate has been linked to larger forebrain sizes in North American and British Isle birds according to Lefebvre et al. (1997).[6] In this study, bird orders that contained individuals with larger forebrain sizes displayed a higher amount of foraging innovation. Examples of innovations recorded in birds include following tractors and eating frogs or other insects killed by it and using swaying trees to catch their prey.[5]

Another measure of learning is spatio-temporal learning (also called time-place learning), which refers to an individual's ability to associate the time of an event with the place of that event.[7] This type of learning has been documented in the foraging behaviors of individuals of the stingless bee species *Trigona fulviventris*.[7] Studies showed that *T. fulviventris* individuals learned the locations and times of feeding events, and arrived to those locations up to thirty minutes before the feeding event in anticipation of the food reward.[7]

Genetics

Figure 11.2.3: A European honey bee extracts nectar. According to Hunt (2007), two genes have been associated with the sugar concentration of the nectar honey bees collect.

Foraging behavior can also be influenced by genetics. The genes associated with foraging behavior have been widely studied in honeybees with reference to the following; onset of foraging behavior, task division between foragers and workers, and bias in foraging for either pollen or nectar.[5][8] Honey bee foraging activity occurs both inside and outside the hive for either pollen or nectar. Similar behavior is seen in many social wasps, such as the species *Apoica flavissima*. Studies using quantitative trait loci (QTL) mapping have associated the following loci with the matched functions; Pln-1 and Pln-4 with onset of foraging age, Pln-1 and 2 with the size of the pollen loads collected by workers, and Pln-2 and pln-3 were shown to influence the sugar concentration of the nectar collected (Figure 11.2.3).[8]

Predators and parasites

The presence of predators while a (prey) animal is foraging affects its behaviour. In general, foragers balance the risk of predation with their needs, thus deviating from the foraging behaviour that would be expected in the absence of predators.[9]

Similarly, parasitism can affect the way in which animals forage. Parasitism can affect foraging at several levels. Animals might simply avoid food items that increase their risk of being parasitized, as when the prey items are intermediate hosts of parasites. Animals might also avoid areas that would expose them to a high risk of parasitism. Finally, animals might effectively self-medicate, either prophylactically or therapeutically.[10]

Types of foraging

Foraging can be categorized into two main types. The first is solitary foraging, when animals forage by themselves. The second is group foraging.

Solitary foraging

Solitary foraging includes the variety of foraging in which animals find, capture and consume their prey alone. Individuals can manually exploit patches or they can use tools to exploit their prey. For example, Bolas spiders attack their prey by luring them with a scent identical to the female moth's sex pheromones.[11] Animals may choose to forage on their own when the resources are abundant, which can occur when the habitat is rich or when the number of conspecifics foraging are few. In these cases there may be no need for group foraging.[12] In addition, foraging alone can result in less interaction with other foragers, which can decrease the amount of competition and dominance interactions an animal deals with. It will also ensure that a solitary forager is less conspicuous to predators.[13] Solitary foraging strategies characterize many of the phocids (the true seals) such as the elephant and harbor seals. An example of an exclusive solitary forager is the South American species of the harvester ant, *Pogonomyrmex vermiculatus*.[14][15]. The theory scientists use to understand solitary foraging is called optimal foraging theory, which predicts that foragers alter their behavior (e.g., when to move to the next foraging area) to maximize energy intake. See the book section on "Optimal Foraging Theory" for more information.

Group foraging

Group foraging is when animals find, capture and consume prey in the presence of other individuals. In other words, it is foraging when success depends not only on your own foraging behaviors but the behaviors of others as well.[16] An important note here is that group foraging can emerge in two types of situations. The first situation is frequently thought of and occurs when foraging in a group is beneficial and brings greater rewards known as an aggregation economy. The second situation occurs when a group of animals forage together but it may not be in an animal's best interest to do so known as a dispersion economy. Think of a cardinal at a bird feeder for the dispersion economy. We might see a group of birds foraging at that bird feeder but it is not in the best interest of the cardinal for any of the other birds to be there too (Figure $11.2.4$). The amount of food the cardinal can get from that bird feeder depends on how much it can take from the bird feeder but also depends on how much the other birds take as well.

Figure $11.2.4$: A male northern cardinal at a bird feeder. Birds feeding at a bird feeder is an example of a dispersion economy. This is when it may not be in an animal's best interest to forage in a group.

In red harvester ants, the foraging process is divided between three different types of workers: nest patrollers, trail patrollers, and foragers. These workers can utilize many different methods of communicating while foraging in a group, such as guiding flights, scent paths, and "jostling runs", as seen in the eusocial bee *Melipona scutellaris*.[17]

Chimpanzees in the Taï Forest in Côte d'Ivoire also engage in foraging for meats when they can, which is achieved through group foraging. Positive correlation has been observed between the success of the hunt and the size of the foraging group. The chimps have also been observed implying rules with their foraging, where there is a benefit to becoming involved through allowing successful hunters first access to their kills.[22][23][24]

Cost and benefits of group foraging

Figure $11.2.5$: Female lions make foraging decisions and more specifically decisions about hunting group size with protection of their cubs and territory defense in mind.[21]

As already mentioned, group foraging brings both costs and benefits to the members of that group. Some of the benefits of group foraging include being able to capture larger prey,[21] being able to create aggregations of prey,[22] being able to capture prey that are difficult or dangerous and most importantly reduction of predation threat.[16] With regard to costs, however, group foraging results in competition for available resources by other group members. Competition for resources can be characterized by either scramble competition whereby each individual strives to get a portion of the shared resource, or by interference competition whereby the presence of competitors prevents a forager's accessibility to resources.[1] Group foraging can thus reduce an animal's foraging payoff.[16]

Group foraging may be influenced by the size of a group. In some species like lions and wild dogs, foraging success increases with an increase in group size then declines once the optimal size is exceeded. A myriad number of factors affect the group sizes in different species. For example, lionesses (female lions) do not make decisions about foraging in a vacuum (Figure $11.2.5$). They make decisions that reflect a balance between obtaining food, defending their territory and protecting their young. In fact, we see that lion foraging behavior does not maximize their energy gain. They are not behaving optimally with respect to foraging because they have to defend their territory and protect young so they hunt in small groups to reduce the risk of being caught alone.[21] Another factor that may influence group size is the cost of hunting. To understand the behavior of wild dogs and the average group size we must incorporate the distance the dogs run.[23]

References

1. Danchin, E., Giraldeau, L., & Cezilly, F. (2008). *Behavioural Ecology*. New York: Oxford University Press. ISBN 978-0-19-920629-2.
2. Hughes, R.N, ed. (1989). *Behavioural Mechanisms of Food Selection.* London & New York: Springer-Verlag, p. v. ISBN 978-0-387-51762-9
3. Raine, N.E., & Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. *Proceedings of the Royal Society B: Biological Sciences, 275*(1636), pp. 803–08. doi:10.1098/rspb.2007.1652. PMC 2596909. PMID 18198141.
4. Rapaport, L.G., & Brown, G.R. (2008). Social influences on foraging behavior in young nonhuman primates:learning what, where and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews, 17*(4), pp. 189–201. doi:10.1002/evan.20180. S2CID 86010867.
5. Dugatkin, L.A. (2004). *Principles of Animal Behavior*.
6. Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour, 53*(3), pp. 549–60. doi:10.1006/anbe.1996.0330. S2CID 53146859.
7. Murphy, C.M., & Breed, M.D. (2008). Time-place learning in a neotropical stingless bee, *Trigona fulviventris Guérin* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society, 81*(1), pp. 73–76. doi:10.2317/JKES-704.23.1. ISSN 0022-8567. S2CID 86256384.
8. Hunt, G.J., et al. (2007). Behavioral genomics of honeybee foraging and nest defense. *Naturwissenschaften, 94*(4), pp. 247–67. doi:10.1007/s00114-006-0183-1. PMC 1829419. PMID 17171388.
9. Roch, S., von Ammon, L., Geist, J., & Brinker, A. (2018). Foraging habits of invasive three-spined sticklebacks (*Gasterosteus aculeatus*) – impacts on fisheries yield in Upper Lake Constance. *Fisheries Research, 204*, pp. 172–80. doi:10.1016/j.fishres.2018.02.014.
10. Hutchings, M.R., Athanasiadou, S., Kyriazakis, I., Gordon, I.J. (2008). Can animals use foraging behaviour to combat parasites? *Proceedings of the Nutrition Society, 62*(2), pp. 361–370. doi:10.1079/PNS2003243. ISSN 1475-2719.
11. Foraging Strategies | Encyclopedia.com. *www.encyclopedia.com*. Retrieved 2021-09-26.
12. Riedman, M. (1990). *The pinnipeds: seals, sea lions, and walruses*. Berkeley: University of California Press. ISBN 978-0-520-06497-3. ISBN The pinnipeds: seals, sea lions, and walruses By Marianne Riedman 1990.
13. le Roux, Aliza; Michael I. Cherry; Lorenz Gygax (5 May 2009). "Vigilance behaviour and fitness consequences: comparing a solitary foraging and an obligate group-foraging mammal". *Behavioral Ecology and Sociobiology*. **63** (8): 1097–1107. doi:10.1007/s00265-009-0762-1. S2CID 21961356.
14. Torres-Contreras, H., Olivares-Donoso, R., & Niemeyer, H.M. (2007). Solitary foraging in the ancestral South American ant, *Pogonomyrmex vermiculatus*. Is it due to constraints in the production or perception of trail pheromones? *Journal of Chemical Ecology, 33*(2), pp. 435–40. doi:10.1007/s10886-006-9240-7. PMID 17187299. S2CID 23930353.

15. About Forest to Food. *Harvesting Nature's Bounty, One Step at a Time. 2023-06-05. Retrieved 2023-06-29.*
16. Stephens, D.W., Brown, J.S. & Ydenberg, R.C. (2007). *Foraging: Behavior and Ecology*. Chicago: University of Chicago Press.
17. Hrncir, M., Jarau, S., Zucchi, R., Barth, F.G. (2000). Recruitment behavior in stingless bees, *Melipona scutellaris* and *M. quadrifasciata*. II. Possible mechanisms of communication. *Apidologie*, *31*(1), pp. 93–113. doi:10.1051/apido:2000109.
18. Boesch, C. (1994). Cooperative hunting in wild Chimpanzees. *Animal Behaviour, 48*(3), pp. 653–67. doi:10.1006/anbe.1994.1285. S2CID 53177700
19. Gomes, C.M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long term basis. *PLOS ONE*, *4*(4): e5116. doi:10.1371/journal.pone.0005116. PMC 2663035. PMID 19352509
20. Gomes, C.M., & Boesch, C. (2011). Reciprocity and trades in wild west African chimpanzees. *Behavioral Ecology and Sociobiology*, *65*(11), pp. 2183–96. doi:10.1007/s00265-011-1227-x. S2CID 37432514.
21. Packer, C., Scheel, D., & Pusey, A.E. (1990). Why lions form groups: Food is not enough. *American Naturalist*, *136*, pp. 1–19. doi:10.1086/285079. S2CID 85145653.
22. Benoit-Bird, K., & Whitlow, W.L. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *The Journal of the Acoustical Society of America*, *125*(1), pp. 125–37. doi:10.1121/1.2967480. PMID 19173400. Archived from the original (PDF) on 2012-04-25. Retrieved 2011-11-29
23. Creel, S., & Creel, N.M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, *50*(5), pp. 1325–39. doi:10.1016/0003-3472(95)80048-4. S2CID 53180378.

Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) and Natasha Gownaris (Gettysburg College) from the following sources:

- Wikipedia, the free Encyclopedia, article on Foraging

11.3: Optimal Foraging Theory

Optimal foraging theory

Figure $11.3.1$: Worker bees forage nectar not only for themselves, but for their whole hive community. Optimal foraging theory predicts that this bee will forage in a way that will maximize its hive's net yield of energy.

Optimal foraging theory (**OFT**) is a behavioral ecology model that helps predict how an animal behaves when searching for food. Although obtaining food provides the animal with energy, searching for and capturing the food require both energy and time. To maximize fitness, an animal adopts a foraging strategy that provides the most benefit (energy) for the lowest cost, maximizing the net energy gained (Figure $11.3.1$). OFT helps predict the best strategy that an animal can use to achieve this goal.

OFT is an ecological application of the optimality model. This theory assumes that the most economically advantageous foraging pattern will be selected for in a species through natural selection.[1] When using OFT to model foraging behavior, organisms are said to be maximizing a variable known as the **currency**, such as the most food per unit time. In addition, the **constraints** of the environment are other variables that must be considered. Constraints are defined as factors that can limit the forager's ability to maximize the currency. The **optimal decision rule**, or the organism's best foraging strategy, is defined as the decision that maximizes the currency under the constraints of the environment. Identifying the optimal decision rule is the primary goal of the OFT.[2]

Building an optimal foraging model

An optimal foraging model generates quantitative predictions of how animals maximize their fitness while they forage. The model building process involves identifying the currency, constraints, and appropriate decision rule for the forager.[2][3]

Currency is defined as the unit that is optimized by the animal. It is also a hypothesis of the costs and benefits that are imposed on that animal.[4] For example, a certain forager gains energy from food, but incurs the cost of searching for the food: the time and energy spent searching could have been used instead on other endeavors, such as finding mates or protecting young. It would be in the animal's best interest to maximize its benefits at the lowest cost. Thus, the currency in this situation could be defined as net energy gain per unit time.[2] However, for a different forager, the time it takes to digest the food after eating could be a more significant cost than the time and energy spent looking for food. In this case, the currency could be defined as net energy gain per digestive turnover time instead of net energy gain per unit time.[5] Furthermore, benefits and costs can depend on a forager's community. For example, a forager living in a hive would most likely forage in a manner that would maximize efficiency for its colony rather than itself.[4] By identifying the currency, one can construct a hypothesis about which benefits and costs are important to the forager in question.

Constraints are hypotheses about the limitations that are placed on an animal.[4] These limitations can be due to features of the environment or the physiology of the animal and could limit their foraging efficiency. The time that it takes for the forager to travel from the nesting site to the foraging site is an example of a constraint. The maximum number of food items a forager is able to carry back to its nesting site is another example of a constraint. There could also be cognitive constraints on animals, such as limits to learning and memory.[2] The more constraints that one is able to identify in a given system, the more predictive power the model will have.[4]

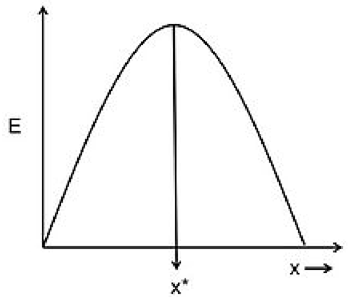


Figure 11.3.2: Energy gain per cost (E) for adopting foraging strategy x. Adapted from Parker & Smith.[34]

Given the hypotheses about the currency and the constraints, the **optimal decision rule** is the model's prediction of what the animal's best foraging strategy should be.[2] Possible examples of optimal decision rules could be the optimal number of food items that an animal should carry back to its nesting site or the optimal size of a food item that an animal should feed on. Figure 11.3.2 shows an example of how an optimal decision rule could be determined from a graphical model.[6] The curve represents the energy gain per cost (E) for adopting foraging strategy x. Energy gain per cost is the currency being optimized. The constraints of the system determine the shape of this curve. The optimal decision rule (x*) is the strategy for which the currency, energy gain per costs, is the greatest. Optimal foraging models can look very different and become very complex, depending on the nature of the currency and the number of constraints considered. However, the general principles of currency, constraints, and optimal decision rule remain the same for all models.

To test a model, one can compare the predicted strategy to the animal's actual foraging behavior. If the model fits the observed data well, then the hypotheses about the currency and constraints are supported. If the model doesn't fit the data well, then it is possible that either the currency or a particular constraint has been incorrectly identified.[4]

Different feeding systems and classes of predators

Optimal foraging theory is widely applicable to feeding systems throughout the animal kingdom. Under the OFT, *any* organism of interest can be viewed as a predator that forages prey. There are different classes of predators that organisms fall into and each class has distinct foraging and predation strategies.

- **True predators** attack large numbers of prey throughout their life. They kill their prey either immediately or shortly after the attack. They may eat all or only part of their prey. True predators include tigers, lions, whales, sharks, seed-eating birds, ants.[7
- **Grazers** eat only a portion of their prey. They harm the prey, but rarely kill it. Grazers include antelope, cattle, and mosquitoes.
- **Parasites**, like grazers, eat only a part of their prey (host), but rarely the entire organism. They spend all or large portions of their life cycle living in/on a single host. This intimate relationship is typical of tapeworms, liver flukes, and plant parasites, such as the potato blight.
- **Parasitoids** are mainly typical of wasps (order *Hymenoptera*), and some flies (order *Diptera*). Eggs are laid inside the larvae of other arthropods which hatch and consume the host from the inside, killing it. This unusual predator–host relationship is typical of about 10% of all insects.[8] Many viruses that attack single-celled organisms (such as bacteriophages) are also parasitoids; they reproduce inside a single host that is inevitably killed by the association.

The optimization of these different foraging and predation strategies can be explained by the optimal foraging theory. In each case, there are costs, benefits, and limitations that ultimately determine the optimal decision rule that the predator should follow.

The optimal diet model

One classical version of the optimal foraging theory is the **optimal diet model**, which is also known as the prey choice model or the contingency model. In this model, the predator encounters different prey items and decides whether to eat what it has or search for a more profitable prey item. The model predicts that foragers should ignore low profitability prey items when more profitable items are present and abundant.[9]

The profitability of a prey item is dependent on several ecological variables. **E** is the amount of energy (calories) that a prey item provides the predator. Handling time (**h**) is the amount of time it takes the predator to handle the food, beginning from the time the predator finds the prey item to the time the prey item is eaten. The profitability of a prey item is then defined as **E/h**. Additionally, search time (**S**) is the amount of time it takes the predator to find a prey item and is dependent on the abundance of the food and the ease of locating it.[2] In this model, the currency is energy intake per unit time and the constraints include the actual values of **E**, **h**, and **S**, as well as the fact that prey items are encountered sequentially.

Model of choice between big and small prey

Using these variables, the optimal diet model can predict how predators choose between two prey types: big **prey1** with energy value **E1** and handling time **h1**, and small **prey2** with energy value **E2** and handling time **h2**. In order to maximize its overall rate of energy gain, a predator must consider the profitability of the two prey types. If it is assumed that big prey1 is more profitable than small prey2, then **E1/h1** > **E2/h2**. Thus, if the predator encounters prey1, it should always choose to eat it, because of its higher profitability. It should never bother to go searching for prey2. However, if the animal encounters prey2, it should reject it to look for a more profitable prey1, *unless* the time it would take to find prey1 is too long and costly for it to be worth it. Thus, the animal should eat prey2 only if **E2/h2 > E1/(h1+S1)**, where **S1** is the search time for prey1. Since it is always favorable to choose to eat prey1, the choice to eat prey1 is not dependent on the abundance of prey2. But since the length of **S1** (i.e. how difficult it is to find prey1) is logically dependent on the density of prey1, the choice to eat prey2 *is* dependent on the abundance of prey1.[4]

Generalist and specialist diets

The optimal diet model also predicts that different types of animals should adopt different diets based on variations in search time. This idea is an extension of the model of prey choice that was discussed above. The equation, **E2/h2** > **E1/(h1+S1)**, can be rearranged to give: **S1** > **[(E1h2)/E2] – h1**. This rearranged form gives the threshold for how long **S1** must be for an animal to choose to eat both prey1 and prey2.[4] Animals that have **S1**'s that reach the threshold are defined as generalists. In nature, generalists include a wide range of prey items in their diet.[10] An example of a generalist is a mouse, which consumes a large variety of seeds, grains, and nuts.[11] In contrast, predators with relatively short **S1**'s are still better off choosing to eat only prey1. These types of animals are defined as specialists and have very exclusive diets in nature.[10] An example of a specialist is the koala, which solely consumes eucalyptus leaves.[12] In general, different animals across the four functional classes of predators exhibit strategies ranging across a continuum between being a generalist and a specialist. Additionally, since the choice to eat prey2 is dependent on the abundance of prey1 (as discussed earlier), if prey1 becomes so scarce that S1 reaches the threshold, then the animal should switch from exclusively eating prey1 to eating both prey1 and prey2.[4] In other words, if the food within a specialist's diet becomes very scarce, a specialist can sometimes switch to being a generalist.

Functional response curves

As previously mentioned, the amount of time it takes to search for a prey item depends on the density of the prey. Functional response curves show the rate of prey capture as a function of food density and can be used in conjunction with the optimal diet theory to predict foraging behavior of predators. There are three different types of functional response curves (Figure 11.3.3).[13]

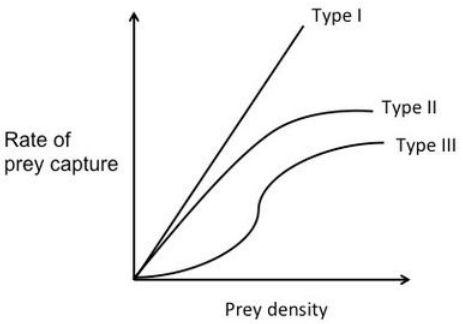


Figure 11.3.3: Three types of functional response curves. Adapted from Staddon.[13]

For a **Type I** functional response curve, the rate of prey capture increases linearly with food density. At low prey densities, the search time is long. Since the predator spends most of its time searching, it eats every prey item it finds. As prey density increases, the predator is able to capture the prey faster and faster. At a certain point, the rate of prey capture is so high, that the predator doesn't have to eat every prey item it encounters. After this point, the predator should choose only the prey items with the highest E/h.[14]

For a **Type II** functional response curve, the rate of prey capture negatively accelerates as it increases with food density.[13] This is because it assumes that the predator is limited by its capacity to process food. In other words, as the food density increases, handling time increases. At the beginning of the curve, rate of prey capture increases nearly linearly with prey density and there is almost no handling time. As prey density increases, the predator spends less and less time searching for prey and more and more time handling the prey. The rate of prey capture increases less and less, until it finally plateaus. The high number of prey basically "swamps" the predator.[14]

A **Type III** functional response curve is a sigmoid curve. The rate of prey capture increases at first with prey density at a positively accelerated rate, but then at high densities changes to the negatively accelerated form, similar to that of the Type II curve.[13] At high prey densities (the top of the curve), each new prey item is caught almost immediately. The predator is able to be choosy and doesn't eat every item it finds. So, assuming that there are two prey types with different profitabilities that are both at high abundance, the predator will choose the item with the higher **E/h**. However, at low prey densities (the bottom of the curve) the rate of prey capture increases faster than linearly. This means that as the predator feeds and the prey type with the higher **E/h** becomes less abundant, the predator will start to switch its preference to the prey type with the lower **E/h**, because that type will be relatively more abundant. This phenomenon is known as prey switching.[13]

Predator–prey interaction

Predator–prey coevolution often makes it unfavorable for a predator to consume certain prey items, since many anti-predator defenses increase handling time.[15] Examples include porcupine quills, the palatability and digestibility of the poison dart frog, crypsis, and other predator avoidance behaviors. In addition, because toxins may be present in many prey types, predators include a lot of variability in their diets to prevent any one toxin from reaching dangerous levels. Thus, it is possible that an approach focusing only on energy intake may not fully explain an animal's foraging behavior in these situations.

The marginal value theorem and optimal foraging

The **marginal value theorem** is a type of optimality model that is often applied to optimal foraging. This theorem is used to describe a situation in which an organism searching for food in a patch must decide when it is economically favorable to leave. While the animal is within a patch, it experiences the law of diminishing returns, where it becomes harder and harder to find prey as time goes on. This may be because the prey is being depleted, the prey begins to take evasive action and becomes harder to catch, or the predator starts crossing its own path more as it searches.[4] This law of diminishing returns can be shown as a curve of energy gain per time spent in a patch (Figure 11.3.4). The curve starts off with a steep slope and gradually levels off as prey becomes harder to find. Another important cost to consider is the traveling time between different patches and the nesting site. An animal loses foraging time while it travels and expends energy through its locomotion.[2]

In this model, the currency being optimized is usually net energy gain per unit time. The constraints are the travel time and the shape of the curve of diminishing returns. Graphically, the currency (net energy gain per unit time) is given by the slope of a diagonal line that starts at the beginning of traveling time and intersects the curve of diminishing returns (Figure 11.3.4). In order to maximize the currency, one wants the line with the greatest slope that still touches the curve (the tangent line). The place that this line touches the curve provides the optimal decision rule of the amount of time that the animal should spend in a patch before leaving.

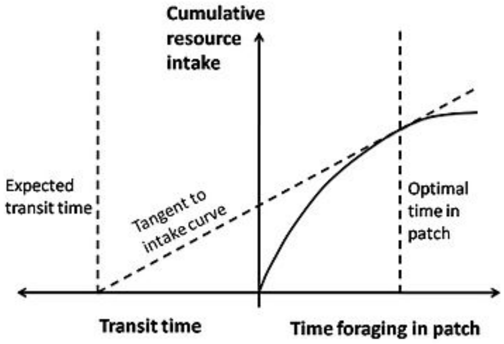


Figure 11.3.4: Marginal value theorem shown graphically.

Examples of optimal foraging models in animals

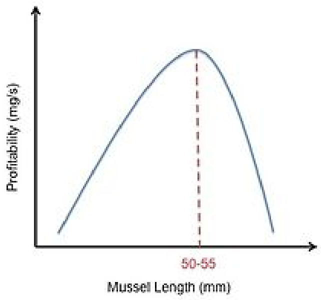


Figure $11.3.5$: Right-shifted mussel profitability curve. Adapted from Meire & Ervynck.[44]

Optimal foraging of oystercatchers

Oystercatcher mussel feeding provides an example of how the optimal diet model can be utilized. Oystercatchers forage on mussels and crack them open with their bills. The constraints on these birds are the characteristics of the different mussel sizes. While large mussels provide more energy than small mussels, large mussels are harder to crack open due to their thicker shells. This means that while large mussels have a higher energy content (**E**), they also have a longer handling time (**h**). The profitability of any mussel is calculated as **E/h**. The oystercatchers must decide which mussel size will provide enough nutrition to outweigh the cost and energy required to open it.[2] In their study, Meire and Ervynck tried to model this decision by graphing the relative profitabilities of different sized mussels. They came up with a bell-shaped curve, indicating that moderately sized mussels were the most profitable. However, they observed that if an oystercatcher rejected too many small mussels, the time it took to search for the next suitable mussel greatly increased. This observation shifted their bell-curve to the right (Figure $11.3.5$). However, while this model predicted that oystercatchers should prefer mussels of 50–55 mm, the observed data showed that oystercatchers actually prefer mussels of 30–45 mm. Meire and Ervynk then realized the preference of mussel size did not depend only on the profitability of the prey, but also on the prey density. After this was accounted for, they found a good agreement between the model's prediction and the observed data.[16]

Optimal foraging in starlings

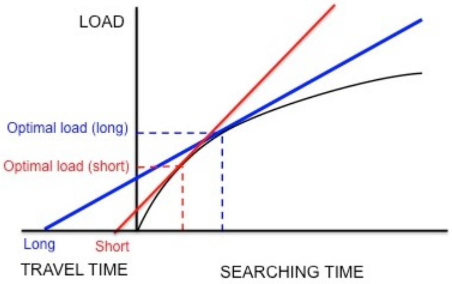


Figure $11.3.6$: If starlings are maximizing net rate of energy gain, longer traveling time results in larger optimum load. Adapted from Krebs and Davies.[4]

The foraging behavior of the European starling, *Sturnus vulgaris*, provides an example of how marginal value theorem is used to model optimal foraging. Starlings leave their nests and travel to food patches in search for larval leatherjackets to bring back to their young. The starlings must determine the optimal number of prey items to take back in one trip (i.e. the optimal load size). While the starlings forage within a patch, they experience diminishing returns: the starling is able to hold only so many leatherjackets in its bill, so the speed with which the parent picks up larvae decreases with the number of larvae that it already has in its bill. Thus, the constraints are the shape of the curve of diminishing returns and the travel time (the time it takes to make a round trip from the nest to a patch and back). In addition, the currency is hypothesized to be net energy gain per unit time.[32] Using this currency and the constraints, the optimal load can be predicted by drawing a line tangent to the curve of diminishing returns, as discussed previously (Figure $11.3.6$).

Kacelnik et al. wanted to determine if this species does indeed optimize net energy gain per unit time as hypothesized.[17] They designed an experiment in which the starlings were trained to collect mealworms from an artificial feeder at different distances from the nest. The researchers artificially generated a fixed curve of diminishing returns for the birds by dropping mealworms at successively longer and longer intervals. The birds continued to collect mealworms as they were presented, until they reached an "optimal" load and flew home. As Figure $11.3.6$ shows, if the starlings were maximizing net energy gain per unit time, a short travel time would predict a small optimal load and a long travel time would predict a larger optimal load. In agreement with these predictions, Kacelnik found that the longer the distance between the nest and the artificial feeder, the larger the load size. In addition, the observed load sizes quantitatively corresponded very closely to the model's predictions. Other models based on different currencies, such as energy gained per energy spent (i.e. energy efficiency), failed to predict the observed load sizes as accurately. Thus, Kacelnik concluded that starlings maximize net energy gain per unit time. This conclusion was not disproved in later experiments.[18][19]

References

1. Werner, E.E., & Hall, D.J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology, 55*(5), pp. 1042. doi:10.2307/1940354. JSTOR 1940354.
2. Sinervo, B. (1997). Optimal foraging theory: Constraints and cognitive processes. Archived 23 November 2015 at the Wayback Machine, pp. 105–130 in *Behavioral Ecology*. University of California, Santa Cruz.
3. Stephens, D.W., & Krebs, J.R. (1986). Foraging theory. 1st ed. Monographs in Behavior and Ecology. *Princeton University Press*. ISBN 9780691084428.[*page needed*]
4. Krebs, J.R., & Davies, N.B. (1989). *An introduction to behavioral ecology*. 4th ed. Oxford: Blackwell Scientific Publications.
5. Verlinden, C., & Wiley, R.H. (1989). The constraints of digestive rate: An alternative model of diet selection. *Evolutionary Ecology, 3*(3), pp. 264. doi:10.1007/BF02270727. S2CID 46608348.
6. Parker, G. A., & Smith, J.M. (1990). Optimality theory in evolutionary biology. *Nature, 348*(6296), pp. 27. Bibcode:1990Natur.348...27P. doi:10.1038/348027a0.
7. Cortés, E., & Gruber, S.H. (1990). Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia*, (1), pp. 204–218. doi:10.2307/1445836. JSTOR 1445836.
8. Godfray, H.C.J. (1994). *Parasitoids: Behavioral and evolutionary ecology*. Princeton University Press, Princeton.[*ISBN missing*][*page needed*]
9. Stephens, D.W., Brown, J.S., & Ydenberg, R.C. (2007). *Foraging: Behavior and ecology*. Chicago: University of Chicago Press.[*ISBN missing*][*page needed*]
10. Pulliam, H.R. (1974). On the theory of optimal diets. *American Naturalist, 108*(959), pp. 59–74. doi:10.1086/282885. JSTOR 2459736. S2CID 8420787.
11. Adler, G. H., & Wilson, M.L. (1987). Demography of a habitat generalist, the white-footed mouse, in a heterogeneous environment. *Ecology, 68*(6), pp. 1785–1796. doi:10.2307/1939870. JSTOR 1939870. PMID 29357183.
12. Shipley, L.A., Forbey, J. S., & Moore, B.D. (2009). Revisiting the dietary niche: When is a mammalian herbivore a specialist? *Integrative and Comparative Biology, 49*(3), pp. 274–290. doi:10.1093/icb/icp051. PMID 21665820.
13. Staddon, J.E.R. (1983). Foraging and behavioral ecology. Adaptive Behavior and Learning. First Edition ed. Cambridge UP. [*ISBN missing*][*page needed*]
14. Jeschke, J.M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecological Monographs, 72*, pp. 95–112. doi:10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2.
15. Boulding, E.G. (1984). Crab-resistant features of shells of burrowing bivalves: Decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology, 76*(3), pp. 201–23. doi:10.1016/0022-0981(84)90189-8.
16. Meire, P.M., & Ervynck, A. (1986). Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Animal Behaviour, 34*(5), pp. 1427. doi:10.1016/S0003-3472(86)80213-5. S2CID 53705917.
17. Kacelnik, A. (1984). Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *The Journal of Animal Ecology, 53*(1), pp. 283–299. doi:10.2307/4357. JSTOR 4357.
18. Bautista, L.M., Tinbergen, J.M., Wiersma, P., & Kacelnik, A. (1998). Optimal foraging and beyond: How starlings cope with changes in food availability. *The American Naturalist, 152*(4), pp. 221–38. doi:10.1086/286189. hdl:11370/1da2080d-6747-4072-93bc-d761276ca5c0. JSTOR 10.1086/286189. PMID 18811363. S2CID 12049476.
19. Bautista, L.M., Tinbergen, J.M., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proc. Natl. Acad. Sci. USA, 93*(3), pp. 1089–94. Bibcode:2001PNAS...98.1089B. doi:10.1073/pnas.98.3.1089. JSTOR 3054826. PMC

14713. PMID 11158599.

Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) and Natasha Gownaris (Gettysburg College) from the following sources:

- Wikipedia, the free encyclopedia

11.4: Movement Ecology

The content for this subtopic is found in an external page. Please click the link below to access this information.

Animal Migration

Nebel, S. (2010) Animal Migration. *Nature Education Knowledge* 3(10):77

11.5: Animal Communication

The content for this subtopic is found in an external page. Please click the link below to access this information.

An Introduction to Animal Communication

Gillam, E. (2011) An Introduction to Animal Communication. *Nature Education Knowledge* 3(10):70

11.6: How Does Social Behavior Evolve?

The content for this subtopic is found in an external page. Please click the link below to access this information.

How Does Social Behavior Evolve?

McGlynn, T. (2010) How Does Social Behavior Evolve? *Nature Education Knowledge* 3(10):69

11.7: How Do Social Systems Evolve

The content for this subtopic is found in an external page. Please click the link below to access this information.

Cooperation, Conflict, and the Evolution of Complex Animal Societies

Rubenstein, D. & Kealey, J. (2010) Cooperation, Conflict, and the Evolution of Complex Animal Societies. *Nature Education Knowledge* 3(10):78

Chapter summary

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures. Behavioral ecology seeks to address questions associated with the proximate causes, ontogeny, survival value, and phylogeny of a behavior. The field of behavioral ecology includes a variety of disciplines, including the study of how organisms find food, how they move about the environment, and how they communicate with each other. This field is also interested in studying the evolution of social behaviors and social systems.

CHAPTER OVERVIEW

12: Sex Strategies

Learning Objectives

- Compare and contrast the costs and benefits of asexual reproduction versus sexual reproduction, and explain hypotheses for the evolution of sexual reproduction.
- Explain the variety of ways in which sexes are determined across plants and animals.
- Describe different types of mating systems in plants and animals.
- Describe the different forms of sexual selection, and explain hypotheses for the evolution of female choice.

Summary

The paradox of sexual reproduction is that although it is ubiquitous in multicellular organisms, there are many disadvantages to reproducing sexually when we compare it to asexual reproduction. This chapter explores some of the multitude of hypotheses for why sexual reproduction exists, the variety of ways in which sexes are determined in plants and animals, and some of the variation in mating systems of sexual organisms. This chapter also focuses on sexual selection, a form of natural selection that occurs when traits that improve mating success are favored by selection, even if they cause a decrease in survival.

12.1: The paradox of sex- sexual versus asexual reproduction

The Paradox of Sex

Sexual Reproduction

Sexual reproduction is a type of reproduction that involves a complex life cycle in which a gamete (such as a sperm or egg cell) with a single set of chromosomes (haploid) combines with another to produce a zygote that develops into an organism composed of cells with two sets of chromosomes (diploid).[1] Sexual reproduction is the most common life cycle in multicellular eukaryotes, such as animals, fungi and plants. Sexual reproduction does not occur in prokaryotes (organisms without cell nuclei), but they have processes with similar effects such as bacterial conjugation, transformation and transduction, which may have been precursors to sexual reproduction in early eukaryotes.

In the production of sex cells in eukaryotes, diploid mother cells divide to produce haploid cells known as gametes in a process called meiosis that involves genetic recombination. The homologous chromosomes pair up so that their DNA sequences are aligned with each other, and this is followed by exchange of genetic information between them. Two rounds of cell division then produce four haploid gametes, each with half the number of chromosomes from each parent cell, but with the genetic information in the parental chromosomes recombined. Two haploid gametes combine into one diploid cell known as a zygote in a process called fertilization. The zygote incorporates genetic material from both gametes. Multiple cell divisions, without change of the number of chromosomes, then form a multicellular diploid phase or generation.

The evolution of sexual reproduction is considered paradoxical,[2] because asexually reproducing individuals should be able to outperform sexually reproducing individuals. This is because every offspring produced by an asexually reproducing individual can produce its own own offspring, while sexually reproducing individuals must produce two sexes: one to fertilize the opposite sex and one to produce/bear offspring. This implies that an asexual population has an intrinsic capacity to grow more rapidly with each generation.[3] This 50% cost is a fitness disadvantage of sexual reproduction.[4] The two-fold cost of sex includes this cost and the fact that any organism can only pass on 50% of its own genes to its offspring. One definite advantage of sexual reproduction is that it impedes the accumulation of genetic mutations.[5]

The first fossilized evidence of sexual reproduction in eukaryotes is from the Stenian period, about 1.05 billion years ago.[6][7]

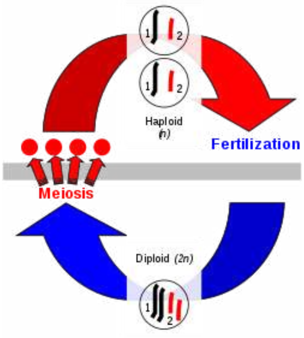


Figure 12.1.1: In the first stage of sexual reproduction, "meiosis", the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During "fertilization", haploid gametes come together to form a diploid zygote, and the original number of chromosomes is restored.

Asexual Reproduction

Asexual reproduction is a type of reproduction that does not involve the fusion of gametes or change in the number of chromosomes. The offspring that arise by asexual reproduction from either unicellular or multicellular organisms inherit the full set of genes of their single parent. Asexual reproduction is the primary form of reproduction for single-celled organisms such as archaea and bacteria. Many eukaryotic organisms including plants, animals, and fungi can also reproduce asexually.[1] In vertebrates, the most common form of asexual reproduction is parthenogenesis (described below), which is typically used as an alternative to sexual reproduction in times when reproductive opportunities are limited.[2]

While all prokaryotes reproduce without the formation and fusion of gametes, mechanisms for lateral gene transfer such as conjugation, transformation and transduction can be likened to sexual reproduction in the sense of genetic recombination in meiosis.[3]

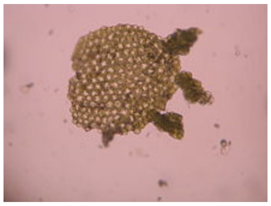


Figure 12.1.2: Asexual reproduction in liverworts: a caducous phylloid germinating.

Types of Asexual Reproduction

Fission

Prokaryotes (archaea and bacteria) reproduce asexually through binary fission, in which the parent organism divides in two to produce two genetically identical daughter organisms. Eukaryotes (such as protists and unicellular fungi) may reproduce in a functionally similar manner by mitosis; most of these are also capable of sexual reproduction.

Multiple fission at the cellular level occurs in many protists, e.g. sporozoans and algae. The nucleus of the parent cell divides several times by mitosis, producing several nuclei. The cytoplasm then separates, creating multiple daughter cells.[4][5][6]

Budding

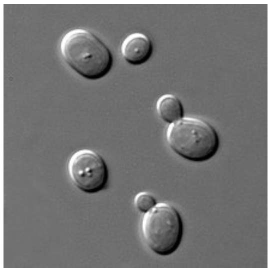


Figure 12.1.3: The yeast *Saccharomyces cerevisiae* reproducing by budding.

Some cells divide by budding (for example baker's yeast), resulting in a "mother" and a "daughter" cell that is initially smaller than the parent. Budding is also known on a multicellular level; an animal example is the hydra,[7] which reproduces by budding. The buds grow into fully matured individuals which eventually break away from the parent organism.

Internal budding is a process of asexual reproduction, favored by parasites such as *Toxoplasma gondii*. It involves an unusual process in which two (*endodyogeny*) or more (*endopolygeny*) daughter cells are produced inside a mother cell, which is then consumed by the offspring prior to their separation.[8]

Vegetative Propagation

Figure 12.1.4: Vegetative plantlets of mother-of-thousands, *Bryophyllum daigremontianum (Kalanchoe daigremontiana).*

Vegetative propagation is a type of asexual reproduction found in plants where new individuals are formed without the production of seeds or spores and thus without syngamy or meiosis.[9] Examples of vegetative reproduction include the formation of miniaturized plants called plantlets on specialized leaves, for example in kalanchoe (*Bryophyllum daigremontianum*) and many produce new plants from rhizomes or stolon (for example in strawberry). Other plants reproduce by forming bulbs or tubers (for example tulip bulbs and *Dahlia* tubers). Some plants produce adventitious shoots and may form a clonal colony. In these examples, all the individuals are clones, and the clonal population may cover a large area.[10]

Spore Formation

Many multicellular organisms form spores during their biological life cycle in a process called *sporogenesis*. Exceptions are animals and some protists, which undergo *meiosis* immediately followed by fertilization. Plants and many algae on the other hand undergo *sporic meiosis* where meiosis leads to the formation of haploid spores rather than gametes. These spores grow into multicellular individuals (called gametophytes in the case of plants) without a fertilization event. These haploid individuals give rise to gametes through mitosis. Meiosis and gamete formation therefore occur in separate generations or "phases" of the life cycle, referred to as alternation of generations. Since sexual reproduction is often more narrowly defined as the fusion of gametes (fertilization), spore formation in plant sporophytes and algae might be considered a form of asexual reproduction (agamogenesis) despite being the result of meiosis and undergoing a reduction in ploidy. However, both events (spore formation and fertilization) are necessary to complete sexual reproduction in the plant life cycle.

Fungi and some algae can also utilize true asexual spore formation, which involves mitosis giving rise to reproductive cells called mitospores that develop into a new organism after dispersal. This method of reproduction is found for example in conidial fungi and the red algae *Polysiphonia*, and involves sporogenesis without meiosis. Thus the chromosome number of the spore cell is the same as that of the parent producing the spores.

Fragmentation

Figure 12.1.5: *Linckia guildingi* "comet", a starfish regrowing from a single arm.

Fragmentation is a form of asexual reproduction where a new organism grows from a fragment of the parent. Each fragment develops into a mature, fully grown individual. Fragmentation is seen in many organisms. Animals that reproduce asexually include planarians, many annelid worms including polychaetes[11] and some oligochaetes[12], turbellarians and sea stars. Many fungi and plants reproduce asexually. Some plants have specialized structures for reproduction via fragmentation, such as *gemmae* in liverworts. Most lichens, which are a symbiotic union of a fungus and photosynthetic algae or cyanobacteria, reproduce through fragmentation to ensure that new individuals contain both symbionts.

Parthenogenesis

Parthenogenesis is a form of agamogenesis in which an unfertilized egg develops into a new individual. It has been documented in over 2,000 species.[13] Parthenogenesis occurs in the wild in many invertebrates (e.g. water fleas, rotifers, aphids, stick insects, some ants, bees and parasitic wasps) and vertebrates (mostly reptiles, amphibians, and fish). It has also been documented in domestic birds and in genetically altered lab mice.[14][15] Plants can engage in parthenogenesis as well through a process called apomixis. However this process is considered by many to not be an independent reproduction method, but instead a breakdown of the mechanisms behind sexual reproduction.[16] Parthenogenetic organisms can be split into two main categories: facultative and obligate.

The Evolution of Sex

Sexual reproduction is an adaptive feature which is common to almost all multi-cellular organisms (and also some single-cellular organisms) with many being incapable of reproducing asexually. Prior to the advent of sexual reproduction, the adaptation process whereby genes would change from one generation to the next (genetic mutation) happened very slowly and randomly. Sex evolved as an extremely efficient mechanism for producing variation, and this had the major advantage of enabling organisms to adapt to changing environments. Sex did, however, come with a cost. In reproducing asexually, no time nor energy needs to be expended in choosing a mate. And if the environment has not changed, then there may be little reason for variation, as the organism may already be well adapted. Sex, however, has evolved as the most prolific means of species branching into the tree of life. Diversification into the phylogenetic tree happens much more rapidly via sexual reproduction than it does by way of asexual reproduction.

Evolution of sexual reproduction describes how sexually reproducing animals, plants, fungi and protists could have evolved from a common ancestor that was a single-celled eukaryotic species.[1][2][3] Sexual reproduction is widespread in the Eukarya, though a few eukaryotic species have secondarily lost the ability to reproduce sexually, such as Bdelloidea, and some plants and animals routinely reproduce asexually (by apomixis and parthenogenesis) without entirely having lost sex. The evolution of sex contains two related yet distinct themes: its *origin* and its *maintenance*.

The origin of sexual reproduction can be traced to early prokaryotes, around two billion years ago (Gya), when bacteria began exchanging genes via conjugation, transformation, and transduction.[4] Though these processes are distinct from true sexual reproduction, they share some basic similarities. In eukaryotes, true sex is thought to have arisen in the Last Eukaryotic Common Ancestor (LECA), possibly via several processes of varying success, and then to have persisted (compare to "LUCA - Last Universal Common Ancestor," referring to ancestry shared by plants, animals, and bacteria).[5]

Since hypotheses for the origin of sex are difficult to verify experimentally (outside of evolutionary computation), most current work has focused on the persistence of sexual reproduction over evolutionary time. The maintenance of sexual reproduction (specifically, of its dioecious form) by natural selection in a highly competitive world has long been one of the major mysteries of biology, since both other known mechanisms of reproduction – asexual reproduction and hermaphroditism – possess apparent advantages over it. Asexual reproduction can proceed by budding, fission, or spore formation and does not involve the union of gametes, which accordingly results in a much faster rate of reproduction compared to sexual reproduction, where 50% of offspring are males and unable to produce offspring themselves. In hermaphroditic reproduction, each of the two parent organisms required for the formation of a zygote can provide either the male or the female gamete, which leads to advantages in both size and genetic variance of a population.

Sexual reproduction therefore must offer significant fitness advantages because, despite the two-fold cost of sex (see below), it dominates among multicellular forms of life, implying that the fitness of offspring produced by sexual processes outweighs the costs. Sexual reproduction derives from recombination, where parent genotypes are reorganized and shared with the offspring. This stands in contrast to single-parent asexual replication, where the offspring is always identical to the parents (barring mutation). Recombination supplies two fault-tolerance mechanisms at the molecular level: *recombinational DNA repair* (promoted during meiosis because homologous chromosomes pair at that time) and *complementation* (also known as heterosis, hybrid vigor or masking of mutations).

Figure 12.1.6: Ladybugs mating; Pollen production is an essential step in sexual reproduction of seed plants.

Historical Perspective

The issue of the evolution of sexual reproduction features in the writings of Aristotle, and modern philosophical-scientific thinking on the problem dates from at least Erasmus Darwin (1731–1802) in the 18th century. August Weismann picked up the thread in 1889, arguing that sex serves to generate genetic variation, as detailed in the majority of the explanations below. On the other hand, Charles Darwin (1809–1882) concluded that the effect of hybrid vigor (complementation) "is amply sufficient to account for the ... genesis of the two sexes". This is consistent with the repair and complementation hypothesis, described below. Since the emergence of the modern evolutionary synthesis in the 20th century, numerous biologists including W. D. Hamilton, Alexey Kondrashov, George C. Williams, Harris Bernstein, Carol Bernstein, Michael M. Cox, Frederic A. Hopf and Richard E. Michod – have suggested competing explanations for how a vast array of different living species maintain sexual reproduction.

Disadvantages of Sex and Sexual Reproduction

The paradox of the existence of sexual reproduction is that though it is ubiquitous in multicellular organisms, there are ostensibly many inherent disadvantages to reproducing sexually when weighed against the relative advantages of alternative forms of reproduction, such as asexual reproduction. Thus, because sexual reproduction abounds in complex multicellular life, there must be some significant benefit(s) to sex and sexual reproduction that compensates for these fundamental disadvantages.

Population Expansion Cost of Sex

Among the most limiting disadvantages to the evolution of sexual reproduction by natural selection is that an asexual population can grow much more rapidly than a sexual one with each generation.

For example, assume that the entire population of some theoretical species has 100 total organisms consisting of two sexes (i.e. males and females), with 50:50 male-to-female representation, and that only the females of this species can bear offspring. If all capable members of this population procreated once, a total of 50 offspring would be produced (the *F1* generation). Contrast this outcome with an asexual species, in which each and every member of an equally sized 100-organism population is capable of bearing young. If all capable members of this asexual population procreated once, a total of 100 offspring would be produced – twice as many as produced by the sexual population in a single generation.

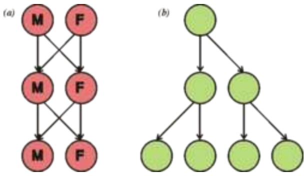


Figure 12.1.7: This diagram illustrates the *two-fold cost of sex*. If each individual were to contribute to the same number of offspring (two), *(a)* the sexual population remains the same size each generation, where the *(b)* asexual population doubles in size each generation.

This idea is sometimes referred to as the **two-fold cost of sexual reproduction**. It was first described mathematically by John Maynard Smith.[26] In his manuscript, Smith further speculated on the impact of an asexual mutant arising in a sexual population, which suppresses meiosis and allows eggs to develop into offspring genetically identical to the mother by mitotic division.[27] The mutant-asexual lineage would double its representation in the population each generation, all else being equal.

Technically the problem above is not one of sexual reproduction but of having a subset of organisms incapable of bearing offspring. Indeed, some multicellular organisms (isogamous) engage in sexual reproduction but all members of the species are capable of bearing offspring.[28] The two-fold reproductive disadvantage assumes that males contribute only genes to their offspring and sexual females waste half their reproductive potential on sons.[27] Thus, in this formulation, the principal cost of sex is that males and females must successfully copulate, which almost always involves expending energy to come together through time and space. Asexual organisms do not need to expend the energy necessary to find a mate.

Genetic Heritability Cost of Sex

A sexually reproducing organism only passes on ~50% of its own genetic material to each offspring. This is a consequence of the fact that gametes from sexually reproducing species are haploid. Again, however, this is not applicable to all sexual organisms. There are numerous species which are sexual but do not have a genetic-loss problem because they do not produce males or females. Yeast, for example, are isogamous sexual organisms which have two mating types which fuse and recombine their haploid genomes. Both sexes reproduce during the haploid and diploid stages of their life cycle and have a 100% chance of passing their genes into their offspring.[28]

Some species avoid the 50% cost of sexual reproduction, although they have "sex" (in the sense of genetic recombination). In these species (e.g., bacteria, ciliates, dinoflagellates and diatoms), "sex" and reproduction occurs separately.[29][30]

Advantages of Sex and Sexual Reproduction

The concept of sex includes two fundamental phenomena: the sexual process (fusion of genetic information of two individuals) and sexual differentiation (separation of this information into two parts). Depending on the presence or absence of these phenomena, all of the existing forms of reproduction can be classified as asexual, hermaphrodite or dioecious. The sexual process and sexual differentiation are different phenomena, and, in essence, are diametrically opposed. The first creates (increases) diversity of genotypes, and the second decreases it by half.

Reproductive advantages of the asexual forms are in quantity of the progeny, and the advantages of the hermaphrodite forms are in maximal diversity. Transition from the hermaphrodite to dioecious state leads to a loss of at least half of the diversity. So, the primary challenge is to explain the advantages given by sexual differentiation, i.e. the benefits of two separate sexes compared to hermaphrodites rather than to explain benefits of sexual forms (hermaphrodite + dioecious) over asexual ones. It has already been understood that since sexual reproduction is not associated with any clear reproductive advantages, as compared with asexual, there should be some important advantages in evolution.[6]

Advantages Due to Genetic Variation

For the advantage due to genetic variation, there are three possible reasons this might happen. First, sexual reproduction can combine the effects of two beneficial mutations in the same individual (i.e. **sex aids in the spread of advantageous traits**). Also, the necessary mutations do not have to have occurred one after another in a single line of descendants.[7] Second, sex acts to bring together currently deleterious mutations to create severely unfit individuals that are then eliminated from the population (i.e. **sex aids in the removal of deleterious genes**). However, in organisms containing only one set of chromosomes, deleterious mutations would be eliminated immediately, and therefore removal of harmful mutations is an unlikely benefit for sexual reproduction. Lastly, **sex creates new gene combinations that may be more fit** than previously existing ones, or may simply lead to reduced competition among relatives.

For the advantage due to DNA repair, there is an immediate large benefit of removing DNA damage by recombinational DNA repair during meiosis, since this removal allows greater survival of progeny with undamaged DNA. The advantage of complementation to each sexual partner is avoidance of the bad effects of their deleterious recessive genes in progeny by the masking effect of normal dominant genes contributed by the other partner.

The classes of hypotheses based on the creation of variation are further broken down below. Any number of these hypotheses may be true in any given species (they are not mutually exclusive), and different hypotheses may apply in different species. However, a research framework based on creation of variation has yet to be found that allows one to determine whether the reason for sex is universal for all sexual species, and, if not, which mechanisms are acting in each species.

On the other hand, the maintenance of sex based on DNA repair and complementation applies widely to all sexual species.

Protection from Major Genetic Mutation

In contrast to the view that sex promotes genetic variation, Heng,[8] and Gorelick and Heng[9] reviewed evidence that sex actually acts as a constraint on genetic variation. They consider that sex acts as a coarse filter, weeding out major genetic changes, such as chromosomal rearrangements, but permitting minor variation, such as changes at the nucleotide or gene level (that are often neutral) to pass through the sexual sieve.

Novel Genotypes

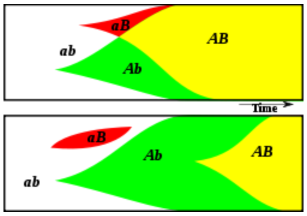


Figure 12.1.8: This diagram illustrates how sex might create novel genotypes more rapidly. Two advantageous alleles *A* and *B* occur at random. The two alleles are recombined rapidly in a sexual population (top), but in an asexual population (bottom) the two alleles must independently arise because of clonal interference.

Sex could be a method by which novel genotypes are created. Because sex combines genes from two individuals, sexually reproducing populations can more easily combine advantageous genes than can asexual populations. If, in a sexual population, two different advantageous alleles arise at different loci on a chromosome in different members of the population, a chromosome containing the two advantageous alleles can be produced within a few generations by recombination. However, should the same two alleles arise in different members of an asexual population, the only way that one chromosome can develop the other allele is to independently gain the same mutation, which would take much longer. Several studies have addressed counterarguments, and the question of whether this model is sufficiently robust to explain the predominance of sexual versus asexual reproduction remains.[10]

Ronald Fisher also suggested that sex might facilitate the spread of advantageous genes by allowing them to better escape their genetic surroundings, if they should arise on a chromosome with deleterious genes.

Supporters of these theories respond to the balance argument that the individuals produced by sexual and asexual reproduction may differ in other respects too – which may influence the persistence of sexuality. For example, in the heterogamous water fleas of the genus *Cladocera*, sexual offspring form eggs which are better able to survive the winter versus those the fleas produce asexually.

Increased Resistance to Parasites

One of the most widely discussed theories to explain the persistence of sex is that it is maintained to assist sexual individuals in resisting parasites, also known as the **Red Queen Hypothesis**.[11][10][12][13][14]

When an environment changes, previously neutral or deleterious alleles can become favorable. If the environment changed sufficiently rapidly (i.e. between generations), these changes in the environment can make sex advantageous for the individual. Such rapid changes in environment are caused by the co-evolution between hosts and parasites.

Imagine, for example that there is one gene in parasites with two alleles *p* and *P* conferring two types of parasitic ability, and one gene in hosts with two alleles *h* and *H*, conferring two types of parasite resistance, such that parasites with allele *p* can attach themselves to hosts with the allele *h*, and *P* to *H*. Such a situation will lead to cyclic changes in allele frequency – as *p* increases in frequency, *h* will be disfavored.

In reality, there will be several genes involved in the relationship between hosts and parasites. In an asexual population of hosts, offspring will only have the different parasitic resistance if a mutation arises. In a sexual population of hosts, however, offspring will have a new combination of parasitic resistance alleles.

In other words, like Lewis Carroll's Red Queen, sexual hosts are continually "running" (adapting) to "stay in one place" (resist parasites).

Evidence for this explanation for the evolution of sex is provided by comparison of the rate of molecular evolution of genes for kinases and immunoglobulins in the immune system with genes coding other proteins. The genes coding for immune system proteins evolve considerably faster.[15][16]

Further evidence for the Red Queen hypothesis was provided by observing long-term dynamics and parasite coevolution in a "mixed" (sexual and asexual) population of snails (*Potamopyrgus antipodarum*). The number of sexuals, the number of asexuals, and the rates of parasite infection for both were monitored. It was found that clones that were plentiful at the beginning of the study became more susceptible to parasites over time. As parasite infections increased, the once plentiful clones dwindled dramatically in number. Some clonal types disappeared entirely. Meanwhile, sexual snail populations remained much more stable over time.[17][18]

However, Hanley et al.[19] studied mite infestations of a parthenogenetic gecko species and its two related sexual ancestral species. Contrary to expectation based on the Red Queen hypothesis, they found that the prevalence, abundance and mean intensity of mites in sexual geckos was significantly higher than in asexuals sharing the same habitat.

In 2011, researchers used the microscopic roundworm *Caenorhabditis elegans* as a host and the pathogenic bacteria *Serratia marcescens* to generate a host-parasite coevolutionary system in a controlled environment, allowing them to conduct more than 70 evolution experiments testing the Red Queen Hypothesis. They genetically manipulated the mating system of *C. elegans*, causing populations to mate either sexually, by self-fertilization, or a mixture of both within the same population. Then they exposed those populations to the *S. marcescens* parasite. It was found that the self-fertilizing populations of *C. elegans* were rapidly driven extinct by the coevolving parasites while sex allowed populations to keep pace with their parasites, a result consistent with the Red Queen Hypothesis.[20][21] In natural populations of *C. elegans*, self-fertilization is the predominant mode of reproduction, but infrequent out-crossing events occur at a rate of about 1%.[22]

DNA Repair and Complementation

The repair and complementation hypothesis assumes that genetic recombination is fundamentally a DNA repair process, and that when it occurs during meiosis it is an adaptation for repairing the genomic DNA which is passed on to progeny. Recombinational repair is the only repair process known which can accurately remove double-strand damages in DNA, and such damages are both common in nature and ordinarily lethal if not repaired. For instance, double-strand breaks in DNA occur about 50 times per cell cycle in human cells (naturally occurring DNA damage). Recombinational repair is prevalent from the simplest viruses to the most complex multicellular eukaryotes. It is effective against many different types of genomic damage, and in particular is highly efficient at overcoming double-strand damages. Studies of the mechanism of meiotic recombination indicate that meiosis is an adaptation for repairing DNA.[34] These considerations form the basis for the first part of the repair and complementation hypothesis.

In some lines of descent from the earliest organisms, the diploid stage of the sexual cycle, which was at first transient, became the predominant stage, because it allowed complementation — the masking of deleterious recessive mutations (i.e. hybrid vigor or heterosis). Outcrossing, the second fundamental aspect of sex, is maintained by the advantage of masking mutations and the disadvantage of inbreeding (mating with a close relative) which allows expression of recessive mutations (commonly observed as inbreeding depression). This is in accord with Charles Darwin,[35] who concluded that the adaptive advantage of sex is hybrid vigor; or as he put it, "the offspring of two individuals, especially if their progenitors have been subjected to very different conditions, have a great advantage in height, weight, constitutional vigor and fertility over the self fertilized offspring from either one of the same parents."

However, outcrossing may be abandoned in favor of parthenogenesis or selfing (which retain the advantage of meiotic recombinational repair) under conditions in which the costs of mating are very high. For instance, costs of mating are high when individuals are rare in a geographic area, such as when there has been a forest fire and the individuals entering the burned area are the initial ones to arrive. At such times mates are hard to find, and this favors parthenogenic species.

In the view of the repair and complementation hypothesis, the removal of DNA damage by recombinational repair produces a new, less deleterious form of informational noise, allelic recombination, as a by-product. This lesser informational noise generates genetic variation, viewed by some as the major effect of sex.

Deleterious Mutation Clearance

Mutations can have many different effects upon an organism. It is generally believed that the majority of non-neutral mutations are deleterious, which means that they will cause a decrease in the organism's overall fitness.[36] If a mutation has a deleterious effect, it will then usually be removed from the population by the process of natural selection. Sexual reproduction is believed to be more efficient than asexual reproduction in removing those mutations from the genome.[37]

There are two main hypotheses which explain how sex may act to remove deleterious genes from the genome.

Evading Harmful Mutation Build-up

While DNA is able to recombine to modify alleles, DNA is also susceptible to mutations within the sequence that can affect an organism in a negative manner. Asexual organisms do not have the ability to recombine their genetic information to form new and differing alleles. Once a mutation occurs in the DNA or other genetic carrying sequence, there is no way for the mutation to be removed from the population until another mutation occurs that ultimately deletes the primary mutation. This is rare among organisms.

Hermann Joseph Muller introduced the idea that mutations build up in asexual reproducing organisms. Muller described this occurrence by comparing the mutations that accumulate as a ratchet. Each mutation that arises in asexually reproducing organisms turns the ratchet once. The ratchet is unable to be rotated backwards, only forwards. The next mutation that occurs turns the ratchet once more. Additional mutations in a population continually turn the ratchet and the mutations, mostly deleterious, continually accumulate without recombination.[38] These mutations are passed onto the next generation because the offspring are exact genetic clones of their parents. The genetic load of organisms and their populations will increase due to the addition of multiple deleterious mutations and decrease the overall reproductive success and fitness.

Removal of Deleterious Genes

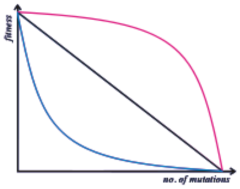


Figure 12.1.9: Diagram illustrating different relationships between numbers of mutations and fitness. Kondrashov's model requires *synergistic epistasis*, which is represented by the red line[41][42] – each subsequent mutation has a disproportionately large effect on the organism's fitness.

This hypothesis was proposed by Alexey Kondrashov, and is sometimes known as the *deterministic mutation hypothesis*.[37] It assumes that the majority of deleterious mutations are only slightly deleterious, and affect the individual such that the introduction of each additional mutation has an increasingly large effect on the fitness of the organism. This relationship between number of mutations and fitness is known as *synergistic epistasis*.

By way of analogy, think of a car with several minor faults. Each is not sufficient alone to prevent the car from running, but in combination, the faults combine to prevent the car from functioning.

Similarly, an organism may be able to cope with a few defects, but the presence of many mutations could overwhelm its backup mechanisms.

Kondrashov argues that the slightly deleterious nature of mutations means that the population will tend to be composed of individuals with a small number of mutations. Sex will act to recombine these genotypes, creating some individuals with fewer deleterious mutations, and some with more. Because there is a major selective disadvantage to individuals with more mutations, these individuals die out. In essence, sex compartmentalizes the deleterious mutations.

Sources

1. John Maynard Smith & Eörz Szathmáry, The Major Transitions in Evolution, W. H. Freeman and Company, 1995, p 149
2. Otto, Sarah P.; Lenormand, Thomas (1 April 2002). "Resolving the paradox of sex and recombination". *Nature Reviews Genetics*. 3 (4): 252–261. doi:10.1038/nrg761. PMID 11967550. S2CID 13502795.
3. John Maynard Smith *The Evolution of Sex* 1978.
4. Ridley M (2004) Evolution, 3rd edition. Blackwell Publishing, p. 314.
5. Hussin, Julie G; Hodgkinson, Alan; Idaghdour, Youssef; Grenier, Jean-Christophe; Goulet, Jean-Philippe; Gbeha, Elias; Hip-Ki, Elodie; Awadalla, Philip (2015). "Recombination affects accumulation of damaging and disease-associated mutations in human populations". *Nature Genetics*. 47 (4): 400–404. doi:10.1038/ng.3216. PMID 25685891. S2CID 24804649. Lay summary (4 March 2015).
6. N.J. Butterfield (2000). "Bangiomorpha pubescens n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes". *Paleobiology*. 26 (3): 386–404. doi:10.1666/0094-8373(2000)026<0386:BPNGNS>2.0.CO;2.
7. T.M. Gibson (2018). "Precise age of Bangiomorpha pubescens dates the origin of eukaryotic photosynthesis". *Geology*. 46 (2): 135–138. doi:10.1130/G39829.1.

Sources for Asexual Reproduction section

1. Engelstädter, Jan (June 2017). "Asexual but Not Clonal: Evolutionary Processes in Automictic Populations | Genetics". *Genetics*. 206 (2): 993–1009. doi:10.1534/genetics.116.196873. PMC 5499200. PMID 28381586. Retrieved 21 August 2018.
2. Dudgeon, Christine L.; Coulton, Laura; Bone, Ren; Ovenden, Jennifer R.; Thomas, Severine (16 January 2017). "Switch from sexual to parthenogenetic reproduction in a zebra shark". *Scientific Reports*. 7 (1): 40537. Bibcode:2017NatSR...740537D. doi:10.1038/srep40537. ISSN 2045-2322. PMC 5238396. PMID 28091617.
3. Narra, H. P.; Ochman, H. (2006). "Of what use is sex to bacteria?". *Current Biology*. 16 (17): R705–710. doi:10.1016/j.cub.2006.08.024. PMID 16950097.
4. "Cell reproduction". *Encyclopædia Britannica*.
5. Britannica Educational Publishing (2011). *Fungi, Algae, and Protists*. The Rosen Publishing Group. ISBN 978-1-61530-463-9.
6. P.Puranik; Asha Bhate (2007). *Animal Forms And Functions: Invertebrata*. Sarup & Sons. ISBN 978-81-7625-791-6.
7. Leeuwenhoek, Antoni Van (31 December 1703). "IV. Part of a letter from Mr Antony van Leeuwenhoek, F. R. S. concerning green weeds growing in water, and some animalcula found about them". *Philosophical Transactions of the Royal Society of London*. 23 (283): 1304–1311. doi:10.1098/rstl.1702.0042. ISSN 0261-0523. S2CID 186209549.
8. Smyth, James Desmond; Wakelin, Derek (1994). *Introduction to animal parasitology* (3 ed.). Cambridge University Press. pp. 101–102. ISBN 978-0-521-42811-8.
9. "Asexual Reproduction". Ucmp.berkeley.edu. Retrieved 13 August 2010.
10. "Celebrating Wildflowers - Fading Gold - How Aspens Grow". Fs.fed.us. 11 May 2010. Archived from the original on 23 September 2010.
11. Ruppert, E. E.; Fox, R. S.; Barnes, R. D. (2004). "Annelida". *Invertebrate Zoology* (7 ed.). Brooks / Cole. pp. 434–441. ISBN 978-0-03-025982-1.
12. Ruppert, E.E.; Fox, R.S. & Barnes, R.D. (2004). "Annelida". *Invertebrate Zoology* (7 ed.). Brooks / Cole. pp. 466–469. ISBN 978-0-03-025982-1.
13. Sköld, Helen Nilsson; Obst, Matthias; Sköld, Mattias; Åkesson, Bertil (2009). "Stem Cells in Asexual Reproduction of Marine Invertebrates". In Baruch Rinkevich; Valeria Matranga (eds.). *Stem Cells in Marine Organisms*. Springer. p. 125. ISBN 978-90-481-2766-5.

14. Neuhof, Moran; Levin, Michael; Rechavi, Oded (26 August 2016). "Vertically and horizontally-transmitted memories – the fading boundaries between regeneration and inheritance in planaria". *Biology Open*. 5 (9): 1177–1188. doi:10.1242/bio.020149. PMC 5051648. PMID 27565761.
15. Ramachandran, R.; McDaniel, C. D. (2018). "Parthenogenesis in birds: a review". *Reproduction (Cambridge, England)*. 155 (6): R245–R257. doi:10.1530/REP-17-0728. ISSN 1741-7899. PMID 29559496.
16. Ozias-Akins, Peggy; Conner, Joann A. (1 January 2012), Altman, Arie; Hasegawa, Paul Michael (eds.), "16 - Regulation of apomixis", *Plant Biotechnology and Agriculture*, San Diego: Academic Press, pp. 243–254, ISBN 978-0-12-381466-1, retrieved 12 December 2020

References

1. Letunic, I., & Bork, P. (2006). Interactive tree of life. Retrieved 23 July 2011.
2. Letunic, I., & Bork, P. (2007). Interactive tree of life (iTOL): An online tool for phylogenetic tree display and annotation. *Bioinformatics*, *23*(1), pp. 127–8. doi:10.1093/bioinformatics/btl529. PMID 17050570.
3. Letunic, I., & Bork, P. (2011). Interactive tree of life v2: Online annotation and display of phylogenetic trees made easy. *Nucleic Acids Research*, *39* (Web Server issue): W475–8. doi:10.1093/nar/gkr201. PMC 3125724. PMID 21470960.
4. Otto, S. (2014). Sexual reproduction and the evolution of sex. *Scitable*. Retrieved 28 February 2019.
5. Goodenough, U., & Heitman, J. (1 March 2014). Origins of eukaryotic sexual reproduction. *Cold Spring Harbor Perspectives in Biology*, *6*(3): a016154. doi:10.1101/cshperspect.a016154. ISSN 1943-0264. PMC 3949356. PMID 24591519.
6. Crow J.F. (1994). Advantages of sexual reproduction. *Dev. Gen.*, *15*, pp. 205-213.
7. Goldstein, R.N. (2010). *36 Arguments for the existence of God: A work of fiction*. Pantheon. ISBN 978-0-307-37818-7.
8. Heng, H.H.Q. (2007). Elimination of altered karyotypes by sexual reproduction preserves species identity. *Genome*, *50*(5), pp. 517–524. doi:10.1139/g07-039. PMID 17612621.
9. Gorelick, R., & Heng, H.H.Q. (2011). Sex reduces genetic variation: A multidisciplinary review. *Evolution*, *65*(4), pp. 1088–1098. doi:10.1111/j.1558-5646.2010.01173.x. PMID 21091466.
10. Birdsell, J.A., & Wills, C. (2003). The evolutionary origin and maintenance of sexual recombination: A review of contemporary models. *Evolutionary Biology*, *33*, pp. 27–137. doi:10.1007/978-1-4757-5190-1_2. ISBN 978-1-4419-3385-0.
11. Ridley, M. (1995). *The red queen: Sex and the evolution of human nature.* Penguin.
12. MacIntyre, R.J., & Clegg, M.T. (Eds.), Springer. Hardcover ISBN 978-0306472619, ISBN 0306472619 Softcover ISBN 978-1-4419-3385-0.
13. Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory*, *1*, pp. 1–30.
14. Hamilton, W.D., Axelrod, R., & Tanese, R. (1990). Sexual reproduction as an adaptation to resist parasites. *Proceedings of the National Academy of Sciences*, *87*(9), pp. 3566–3573. Bibcode:1990PNAS...87.3566H. doi:10.1073/pnas.87.9.3566. PMC 53943. PMID 2185476.
15. Kuma, K., Iwabe, N., & Miyata, T. (1995). Functional constraints against variations on molecules from the tissue-level - slowly evolving brain-specific genes demonstrated by protein-kinase and immunoglobulin supergene families. *Molecular Biology and Evolution*, *12*(1), pp. 123–130. doi:10.1093/oxfordjournals.molbev.a040181. PMID 7877487.
16. Wolfe, K.H., & Sharp, P.M. (1993). Mammalian gene evolution - nucleotide-sequence divergence between mouse and rat. *Journal of Molecular Evolution*, *37*(4), pp. 441–456. Bibcode:1993JMolE..37..441W. doi:10.1007/BF00178874. PMID 8308912. S2CID 10437152.
17. Jokela, J., Dybdahl, M., & Lively, C. (2009). The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of sexual and asexual snails. *The American Naturalist*, *174*(s1), pp. S43–53. doi:10.1086/599080. JSTOR 10.1086/599080. PMID 19441961. S2CID 6797643.
18. Parasites may have had a role in evolution of sex. *Science Daily*. 31 July 2009. Retrieved 19 September 2011.
19. Hanley, K.A., Fisher, R.N., & Case, T.J. (1995). Lower mite infestations in an asexual gecko compared with its sexual ancestors. *Evolution*, *49*(3), pp. 418–426. doi:10.2307/2410266. JSTOR 2410266. PMID 28565091.
20. Morran, L.T., Schmidt, O.G., Gelarden, I.A., Parrish, R., Raymond, C., & Lively, C.M. (2011). Running with the red queen: Host-parasite coevolution selects for biparental sex. *Science*, *333*(6039), pp. 216–218. Bibcode:2011Sci...333..216M. doi:10.1126/science.1206360. PMC 3402160. PMID 21737739.
21. Sex -- as we know it -- works thanks to ever-evolving host-parasite relationships, biologists find. *Science Daily*. 9 July 2011. Retrieved 19 September 2011.

22. Barrière, A., & Félix, M.A. (2005). High local genetic diversity and low outcrossing rate in *Caenorhabditis elegans* natural populations. *Curr. Biol.*, *15*(13), pp. 1176–84. arXiv:q-bio/0508003. Bibcode:2005q.bio.....8003B. doi:10.1016/j.cub.2005.06.022. PMID 16005289. S2CID 2229622.
23. Otto, S.P., & Nuismer, S.L. (2004). Species interactions and the evolution of sex. *Science, 304*(5673), pp. 1018–1020. Bibcode:2004Sci...304.1018O. doi:10.1126/science.1094072. PMID 15143283. S2CID 8599387.
24. Otto, S.P., & Gerstein, A.C. (2006). Why have sex? The population genetics of sex and recombination. *Biochemical Society Transactions, 34*(Pt 4), pp. 519–22. doi:10.1042/BST0340519. PMID 16856849.
25. Parker, M.A. (1994). Pathogens and sex in plants. *Evolutionary Ecology, 8*(5), pp. 560–584. doi:10.1007/BF01238258. S2CID 31756267.
26. Smith, J.M. (1978). *The Evolution of Sex*. Cambridge University Press. ISBN 9780521293020.
27. Stearns, S.C. (2005). *Evolution: An introduction*. Hoekstra, Rolf F. (2nd ed.). Oxford [England]: Oxford University Press. ISBN 978-0199255634. OCLC 56964580.
28. Hoekstra, R.F. (1987). The Evolution of Sexes. In Stearns, Stephen C. (ed.). *The Evolution of Sex and its Consequences*. Springer Basel AG. ISBN 9783034862738.
29. Ridley, M. (2003). *Evolution* (3rd ed.). Wiley. p. 314. ISBN 9781405103459.
30. Beukeboom, L., & Perrin, N. (2014). *The evolution of sex determination*. Oxford University Press, p. 5–6 [1]. Online resources, [2].
31. Bernstein, H., Byerly, H.C., Hopf, F.A., & Michod, R.E. (1984). Origin of sex. *J. Theor. Biol.*, *110*(3), pp. 323–51. Bibcode:1984JThBi.110..323B. doi:10.1016/S0022-5193(84)80178-2. PMID 6209512.
32. Bernstein, H., Byerly, H.C., Hopf, F.A., & Michod, R.E. (1985). Genetic damage, mutation, and the evolution of sex. *Science*, *229*(4719), pp. 1277–81. Bibcode:1985Sci...229.1277B. doi:10.1126/science.3898363. PMID 3898363.
33. Bernstein, H., Hopf, F.A., & Michod, R.E. (1987). The molecular basis of the evolution of sex. *Advances in Genetics, 24,* pp. 323–70. doi:10.1016/S0065-2660(08)60012-7. ISBN 9780120176243. PMID 3324702.
34. Cox, M.M. (2001). Historical overview: Searching for replication help in all of the rec places. *Proc. Natl. Acad. Sci. U.S.A.*, *98*(15), pp. 8173–80. Bibcode:2001PNAS...98.8173C. doi:10.1073/pnas.131004998. PMC 37418. PMID 11459950.
35. Darwin, C.R. (1876). The effects of cross and self fertilisation in the vegetable kingdom. *London: John Murray*. [3] see page 462
36. Griffiths, et al. (1999). Gene mutations, p197-234, *in* Modern Genetic Analysis, New York, W.H. Freeman and Company.
37. Kondrashov, A.S. (1988). Deleterious mutations and the evolution of sexual reproduction. *Nature*, *388*(6198), pp. 435–440. Bibcode:1988Natur.336..435K. doi:10.1038/336435a0. PMID 3057385. S2CID 4233528.
38. Muller, H.J. (1964). The relation of recombination to mutational advance. *Mutation Research, 1,* pp. 2–9. doi:10.1016/0027-5107(64)90047-8. PMID 14195748.
39. Niklas, K.J. (2014). The evolutionary-developmental origins of multicellularity. *American Journal of Botany*, *101*(1), pp. 6–25. doi:10.3732/ajb.1300314. ISSN 0002-9122. PMID 24363320.
40. Kuzdzal-Fick, L.J., Fox, S.A., Strassmann, J.E., & Queller, D.C. (2011). High relatedness is necessary and sufficient to maintain multicellularity in dictyostelium. *Science*, *334*(6062), pp. 1548–1551. Bibcode:2011Sci...334.1548K. doi:10.1126/science.1213272. ISSN 0036-8075. PMID 22174251. S2CID 206537272.
41. Ridley, M. (2004) *Evolution*, 3rd edition. Blackwell Publishing.
42. Charlesworth, B., Charlesworth, D. (2010) *Elements of Evolutionary Genetics*. Roberts and Company Publishers.
43. Whitlock, M.C., & Bourguet, D. (2000). Factors affecting the genetic load in Drosophila: synergistic epistasis and correlations among fitness components. *Evolution, 54*(5), pp. 1654–1660. doi:10.1554/0014-3820(2000)054[1654:fatgli]2.0.co;2. PMID 11108592.
44. Elena, S.F., & Lenski, R.E. (1997). Test of synergistic interactions among deleterious mutations in bacteria. *Nature*, *390*(6658), pp. 395–398. Bibcode:1997Natur.390..395E. doi:10.1038/37108. PMID 9389477. S2CID 205025450.
45. Drake, J.W., Charlesworth, B., Charlesworth, D., & Crow, J.F. (1998). Rates of spontaneous mutation. *Genetics*, *148*(4), pp. 1667–86. doi:10.1093/genetics/148.4.1667. PMC 1460098. PMID 9560386.
46. Sohail, M., Vakhrusheva, O.A., Sul, J.H., Pulit, S.L., Francioli, L.C., van den Berg, L.H., Veldink, J.H., de Bakker, P.I.W., Bazykin, G.A., Kondrashov, A.S., & Sunyaev, S.R. (2017). Negative selection in humans and fruit flies involves synergistic epistasis. *Science*, *356*(6337), pp. 539–542. Bibcode:2017Sci...356..539S. doi:10.1126/science.aah5238. PMC 6200135. PMID 28473589.

Contributors and Attributions

Modified by Dan Wetzel from Wikipedia: https://en.wikipedia.org/wiki/Sexual_reproduction, https://en.wikipedia.org/wiki/Asexual_reproduction, https://en.wikipedia.org/wiki/Evolution_of_sexual_reproduction

---

12.2: Sex determination and sex ratios

Sex determination

A **sex-determination system** is a biological system that determines the development of sexual characteristics in an organism. Most organisms that create their offspring using sexual reproduction have two sexes.

In some species there are hermaphrodites.[1] There are also some species that are only one sex due to parthenogenesis, the act of a female reproducing without fertilization.

In many species, sex determination is genetic: males and females have different alleles or even different genes that specify their sexual morphology. In animals this is often accompanied by chromosomal differences, generally through combinations of XY, ZW, XO, ZO chromosomes, or haplodiploidy. The sexual differentiation is generally triggered by a main gene (a "sex locus"), with a multitude of other genes following in a domino effect.

In other cases, sex of a fetus is determined by environmental variables (such as temperature). The details of some sex-determination systems are not yet fully understood.

Some species such as various plants and fish do not have a fixed sex, and instead go through life cycles and change sex based on genetic cues during corresponding life stages of their type. This could be due to environmental factors such as seasons, temperature, or even social context. In some gonochoric species, a few individuals may have sex characteristics of both sexes, a condition called intersex.[2]

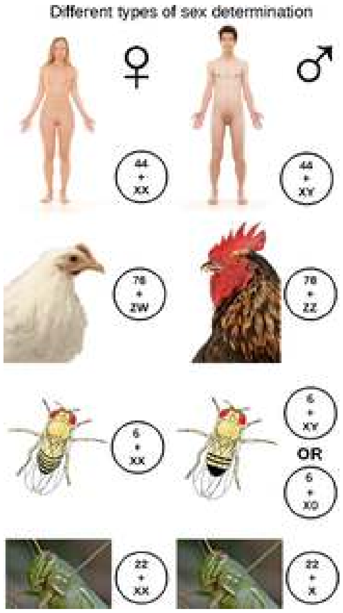


Figure 12.2.1 : Some chromosomal sex determination systems in animals.

Discovery

Sex determination was discovered in the mealworm by the American geneticist Nettie Stevens in 1903.[3][4][5]

Figure 12.2.2 : Nettie Stevens.

Chromosomal systems

XX/XY sex chromosomes

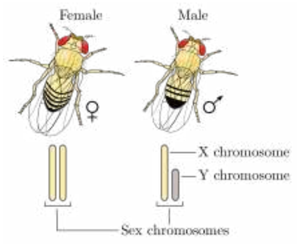


Figure 12.2.3: Drosophila sex-chromosomes.

The **XX/XY sex-determination system** is the most familiar, as it is found in humans. The XX/XY system is found in most other mammals, as well as some insects. In this system, most females have two of the same kind of sex chromosome (XX), while most males have two distinct sex chromosomes (XY). The X and Y sex chromosomes are different in shape and size from each other, unlike the rest of the chromosomes (autosomes), and are sometimes called allosomes. In some species, such as humans, organisms remain sex indifferent for a period of time after fertilization; in others, however, such as fruit flies, sexual differentiation occurs as soon as the egg is fertilized.[6]

X-centered sex determination

Some species, such as fruit flies, use the presence of two X chromosomes to determine femaleness.[12] Species that use the number of Xs to determine sex are nonviable with an extra X chromosome.

XX/X0 sex chromosomes

In this variant of the XY system, females have two copies of the sex chromosome (XX) but males have only one (X0). The *0* denotes the absence of a second sex chromosome. Generally in this method, the sex is determined by amount of genes expressed across the two chromosomes. This system is observed in a number of insects, including the grasshoppers and crickets of order Orthoptera and in cockroaches (order Blattodea). A small number of mammals also lack a Y chromosome. These include the Amami spiny rat (*Tokudaia osimensis*) and the Tokunoshima spiny rat (*Tokudaia tokunoshimensis*) and *Sorex araneus*, a shrew species. Transcaucasian mole voles (*Ellobius lutescens*) also have a form of XO determination, in which both sexes lack a second sex chromosome.[8] The mechanism of sex determination is not yet understood.[16]

The nematode *C. elegans* is male with one sex chromosome (X0); with a pair of chromosomes (XX) it is a hermaphrodite.[17] Its main sex gene is XOL, which encodes XOL-1 and also controls the expression of the genes TRA-2 and HER-1. These genes reduce male gene activation and increase it, respectively.[18]

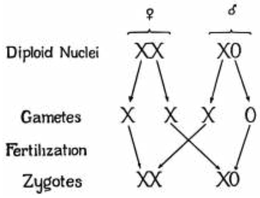


Figure 12.2.4: Heredity of sex chromosomes in XO sex determination.

ZW/ZZ sex chromosomes

The **ZW sex-determination system** is found in birds, some reptiles, and some insects and other organisms. The ZW sex-determination system is reversed compared to the XY system: females have two different kinds of chromosomes (ZW), and males have two of the same kind of chromosomes (ZZ). In the chicken, this was found to be dependent on the expression of DMRT1.[19] In birds, the genes FET1 and ASW are found on the W chromosome for females, similar to how the Y chromosome contains SRY.[6] However, not all species depend upon the W for their sex. For example, there are moths and butterflies that are ZW, but some have been found female with ZO, as well as female with ZZW.[17] Also, while mammals deactivate one of their extra X chromosomes when female, it appears that in the case of Lepidoptera, the males produce double the normal amount of enzymes, due to having two Z's.[17] Because the use of ZW sex determination is varied, it is still unknown how exactly most species determine their sex.[17] However, reportedly, the silkworm *Bombyx mori* uses a single female-specific piRNA as the primary determiner of sex.[20] Despite the similarities between the ZW and XY systems, these sex chromosomes evolved separately. In the case of the chicken, their Z chromosome is more similar to humans' autosome 9.[21] The chicken's Z chromosome also seems to be related to the X chromosome of the platypus.[22] When a ZW species, such as the Komodo dragon, reproduces parthenogenetically, usually only males are produced. This is due to the fact that the haploid eggs double their chromosomes, resulting in ZZ or WW. The ZZ become males, but the WW are not viable and are not brought to term.[23]

In both XY and ZW sex determination systems, the sex chromosome carrying the critical factors is often significantly smaller, carrying little more than the genes necessary for triggering the development of a given sex.[24]

Haplodiploidy

Haplodiploidy is found in insects belonging to Hymenoptera, such as ants and bees. Sex determination is controlled by the zygosity of a complementary sex determiner (*csd*) locus. Unfertilized eggs develop into haploid individuals which have a single, hemizygous copy of the *csd* locus and are therefore males. Fertilized eggs develop into diploid individuals which, due to high variability in the *csd* locus, are generally heterozygous females. In rare instances diploid individuals may be homozygous, these develop into sterile males. The gene acting as a *csd* locus has been identified in the honeybee and several candidate genes have been proposed as a *csd* locus for other Hymenopterans.[30][31][32] Most females in the Hymenoptera order can decide the sex of their offspring by holding received sperm in their spermatheca and either releasing it into their oviduct or not. This allows them to create more workers, depending on the status of the colony.[33]

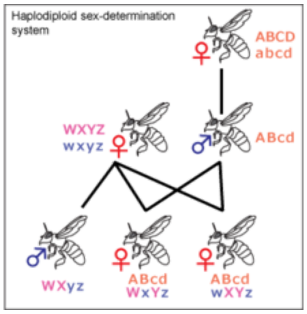


Figure 12.2.5: Haplodiploid sex chromosomes.

Environmental systems

Temperature-dependent

Many other sex-determination systems exist. In some species of reptiles, including alligators, some turtles, and the tuatara, sex is determined by the temperature at which the egg is incubated during a temperature-sensitive period. There are no examples of temperature-dependent sex determination (TSD) in birds. Megapodes had formerly been thought to exhibit this phenomenon, but were found to actually have different temperature-dependent embryo mortality rates for each sex.[34] For some species with TSD, sex determination is achieved by exposure to hotter temperatures resulting in the offspring being one sex and cooler temperatures resulting in the other. This type of TSD is called *Pattern I*. For others species using TSD, it is exposure to temperatures on both extremes that results in offspring of one sex, and exposure to moderate temperatures that results in offspring of the opposite sex, called *Pattern II* TSD. The specific temperatures required to produce each sex are known as the female-promoting temperature and the male-promoting temperature.[35] When the temperature stays near the threshold during the temperature sensitive period, the sex ratio is varied between the two sexes.[36] Some species' temperature standards are based on when a particular enzyme is created. These species that rely upon temperature for their sex determination do not have the SRY gene, but have other genes such as DAX1, DMRT1, and SOX9 that are expressed or not expressed depending on the temperature.[35] The sex of some species, such as the Nile tilapia, Australian skink lizard, and Australian dragon lizard, is initially determined by chromosomes, but can later be changed by the temperature of incubation.[13]

It is unknown how exactly temperature-dependent sex determination evolved.[37] It could have evolved through certain sexes being more suited to certain areas that fit the temperature requirements. For example, a warmer area could be more suitable for nesting, so more females are produced to increase the amount that nest next season.[37] Environmental sex determination preceded the genetically determined systems of birds and mammals; it is thought that a temperature-dependent amniote was the common ancestor of amniotes with sex chromosomes.[38]

Figure 12.2.6: All alligators determine the sex of their offspring by the temperature of the nest.

Other systems

There are other environmental sex determination systems including location-dependent determination systems as seen in the marine worm *Bonellia viridis* – larvae become males if they make physical contact with a female, and females if they end up on the bare sea floor. This is triggered by the presence of a chemical produced by the females, bonellin.[39] Some species, such as some snails, practice sex change: adults start out male, then become female. In tropical clown fish, the dominant individual in a group becomes female while the other ones are male, and bluehead wrasses (*Thalassoma bifasciatum*) are the reverse. Some species, however, have no sex-determination system. Hermaphrodite species include the common earthworm and certain species of snails. A few species of fish, reptiles, and insects reproduce by parthenogenesis and are female altogether. There are some reptiles, such as the boa constrictor and Komodo dragon that can reproduce both sexually and asexually, depending on whether a mate is available.[40]

Other unusual systems include those of the green swordtail (a polyfactorial system with the sex-determining genes on several chromosomes)[13]; the juvenile hermaphroditism of zebrafish, with an unknown trigger;[13] and the platyfish, which has W, X, and Y chromosomes. This allows WY, WX, or XX females and YY or XY males.[13]

Sex ratios

The **sex ratio** is the ratio of males to females in a population. In most sexually reproducing species, the ratio tends to be 1:1. This tendency is explained by Fisher's principle.[2] For various reasons, however, many species deviate from anything like an even sex ratio, either periodically or permanently. Examples include parthenogenic species, periodically mating organisms such as aphids, some eusocial wasps such as *Polistes fuscatus* and *Polistes exclamans*, bees, ants, and termites.[3] In most species, the sex ratio varies according to the age profile of the population.[7]

Fisher's principle

Fisher's principle explains why for most species, the sex ratio is approximately 1:1. Bill Hamilton expounded Fisher's argument in his 1967 paper on “Extraordinary sex ratios”[2] as follows, given the assumption of equal parental expenditure on offspring of both sexes.

1. Suppose male births are less common than female.
2. A newborn male then has better mating prospects than a newborn female, and therefore can expect to have more offspring.
3. Therefore parents genetically disposed to produce males tend to have more than average numbers of grandchildren born to them.
4. Therefore the genes for male-producing tendencies spread, and male births become more common.
5. As the 1:1 sex ratio is approached, the advantage associated with producing males dies away.
6. The same reasoning holds if females are substituted for males throughout. Therefore 1:1 is the equilibrium ratio.

In modern language, the 1:1 ratio is the evolutionarily stable strategy (ESS).[11] This ratio has been observed in many species, including the bee *Macrotera portalis*. A study performed by Danforth observed no significant difference in the number of males and females from the 1:1 sex ratio.[12]

References

1. Rosenfield, K.A. (2018). Hermaphrodite, in Vonk, Jennifer; Shackelford, Todd (eds.), *Encyclopedia of Animal Cognition and Behavior*, Cham: Springer International Publishing, pp. 1–2, doi:10.1007/978-3-319-47829-6_329-1, ISBN 978-3-319-47829-6, retrieved 4 May 2021
2. Minelli, A., & Fusco, G. (2019). *The Biology of Reproduction*. Cambridge University Press, pp. 116–117. ISBN 9781108499859. Archived from the original on 11 October 2020. Retrieved 11 October 2020.
3. "Nettie Stevens: A Discoverer of Sex Chromosomes | Learn Science at Scitable". *www.nature.com*. Retrieved 7 June 2018.
4. Ogilvie, M.B., & Choquette, C.J. (1981). Nettie Maria Stevens (1861–1912): Her life and contributions to cytogenetics. *Proceedings of the American Philosophical Society, 125*(4), pp. 292–311. JSTOR 986332. PMID 11620765.
5. "Nettie Maria Stevens (1861–1912) | The Embryo Project Encyclopedia". *embryo.asu.edu*. Retrieved 7 June 2018.
6. Hake, L. (2008). Genetic mechanisms of sex determination. *Nature Education, 1*(1). Retrieved 8 December 2011.
7. Goodfellow, P.N. & Camerino, G. (1999). DAX-1, an 'antitestis' gene. *Cellular and Molecular Life Sciences, 55*(6–7), pp. 857–863. doi:10.1007/PL00013201. PMID 10412368. S2CID 19764423.
8. Chandra, H.S. (1999). Another way of looking at the enigma of sex determination in *Ellobius lutescens*. *Current Science, 76*(8), pp. 1072.
9. Cox, J.J., Willatt, L., Homfray, T., & Woods, C.G. (2011). A SOX9 duplication and familial 46,XX developmental testicular disorder. *New England Journal of Medicine, 364*(1), pp. 91–93. doi:10.1056/NEJMc1010311. PMID 21208124.
10. Huang, B., Wang, S., Ning, Y., Lamb, A.N., & Bartley, J. (1999). Autosomal XX sex reversal caused by duplication of SOX9. *American Journal of Medical Genetics, 87*(4), pp. 349–353. doi:10.1002/(SICI)1096-8628(19991203)87:4<349::AID-AJMG13>3.0.CO;2-N. PMID 10588843.
11. Uhlenhaut, H.N., Jakob, S., Anlag, K., Eisenberger, T., Sekido, R., Kress, J., Treier, A.C., Klugmann, C., Klasen, C., Holter, N.I., Riethmacher, D., Schütz, G., Cooney, A.J., Lovell-Badge, R., & Treier, M. (2009). Somatic sex reprogramming of adult ovaries to testes by FOXL2 ablation". *Cell, 139*(6), pp. 1130–1142. doi:10.1016/j.cell.2009.11.021. PMID 20005806.
12. Penalva, L.O.F., & Sánchez. (2003). RNA binding protein sex-lethal (Sxl) and control of drosophila sex determination and dosage compensation. *Microbiology and Molecular Biology Reviews, 67*(3), pp. 343–359. doi:10.1128/MMBR.67.3.343-359.2003. PMC 193869. PMID 12966139.
13. Schartl, M. (2004). A comparative view on sex determination in medaka. *Mechanisms of Development, 121*(7–8), pp. 639–645. doi:10.1016/j.mod.2004.03.001. PMID 15210173. S2CID 17401686.
14. Warren, W.C., Hillier, L.W., Graves, J.A.M., Birney, E., Ponting, C.P., Grützner, F., Belov, K., Miller, W., et al. (2008). Genome analysis of the platypus reveals unique signatures of evolution. *Nature, 453*(7192), pp. 175–U1. Bibcode:2008Natur.453..175W. doi:10.1038/nature06936. PMC 2803040. PMID 18464734.
15. Gruetzner, F., Ashley, T., Rowell, D.M., & Graves, J.A.M. (2006). Analysis of the platypus reveals unique signatures of evolution. *Chromosoma, 115*(2), pp. 75–88. doi:10.1007/s00412-005-0034-4. PMID 16344965. S2CID 23603889.
16. Kuroiwa, A., Handa, S., Nishiyama, C., Chiba, E., Yamada, F., Abe, S., & Matsuda, Y. (2011). Additional copies of CBX2 in the genomes of males of mammals lacking SRY, the Amami spiny rat (*Tokudaia osimensis*) and the Tokunoshima spiny rat (*Tokudaia tokunoshimensis*). *Chromosome Res., 19*(5), pp. 635–44. doi:10.1007/s10577-011-9223-6. PMID 21656076. S2CID 23311263.
17. (Majerus 2003, p. 60)
18. Kuwabara, P.E., Okkema, P.G., & Kimble, J. (1992). tra-2 encodes a membrane protein and may mediate cell communication in the caenorhabditis elegans sex determination pathway. *Molecular Biology of the Cell, 3*(4), pp. 461–73. doi:10.1091/mbc.3.4.461. PMC 275596. PMID 1498366.
19. Smith, C.A., Roeszler, K.N., Ohnesorg, T., Cummins, D.M., Farlie, P.G., Doran, T.J., & Sinclair, A.H. (September 2009). The avian Z-linked gene DMRT1 is required for male sex determination in the chicken. *Nature, 461*(7261), pp. 267–271. Bibcode:2009Natur.461..267S. doi:10.1038/nature08298. PMID 19710650. S2CID 4413389.
20. Kiuchi, T., Koga, H., Kawamoto, M., Shoji, K., Sakai, H., Arai, Y., Ishihara, G., Kawaoka, S., Sugano, S., Shimada, T., Suzuki, Y., Suzuki, M., & Katsuma, S. (2014). A single female-specific piRNA is the primary determiner of sex in the silkworm. *Nature, 509*(7502), pp. 633–636. Bibcode:2014Natur.509..633K. doi:10.1038/nature13315. PMID 24828047. S2CID 205238635.
21. Stiglec, R, Ezaz, T., & Graves, J.A. (2007). A new look at the evolution of avian sex chromosomes. *Cytogenet. Genome Res., 117*(1–4), pp. 103–9. doi:10.1159/000103170. PMID 17675850. S2CID 12932564.
22. Grützner, F., Rens, W., Tsend-Ayush, E., El-Mogharbel, N., O'Brien, P.C.M., Jones, R.C., Ferguson-Smith, M.A., & Marshall, J.A. (2004). In the platypus a meiotic chain of ten sex chromosomes shares genes with the bird Z and mammal X

chromosomes. *Nature*, *432*(7019), pp. 913–917. Bibcode:2004Natur.432..913G. doi:10.1038/nature03021. PMID 15502814. S2CID 4379897.

23. "Virgin births for giant lizards". *BBC News*. 20 December 2006. Retrieved 13 March 2008.
24. "Evolution of the Y Chromosome". *Annenberg Media*. Annenberg Media. Archived from the original on 4 November 2004. Retrieved 1 April 2008.
25. Traut, W., Sahara, K., & Marec, F. (2007). Sex chromosomes and sex determination in *lepidoptera*. *Sexual Development, 1*(6), pp. 332–346. doi:10.1159/000111765. PMID 18391545. S2CID 6885122.
26. "Genetic Mechanisms of Sex Determination - Learn Science at Scitable". *www.nature.com*.
27. *Handbuch Der Zoologie / Handbook of Zoology*. Walter de Gruyter. 1925. ISBN 9783110162103 – via Google Books.
28. Bachtrog, D., Kirkpatrick, M., Mank, J.E., McDaniel, S.F., Pires, J.C., Rice, W., & Valenzuela, N. (2011). Are all sex chromosomes created equal? *Trends Genet, 27*(9), pp. 350–7. doi:10.1016/j.tig.2011.05.005. PMID 21962970.
29. Renner, S.S., Heinrichs, J., & Sousa, A. (2017). The sex chromosomes of bryophytes: Recent insights, open questions, and reinvestigations of *Frullania dilatata* and *Plagiochila asplenioides*. *Journal of Systematics and Evolution, 55*(4), pp. 333–339. doi:10.1111/jse.12266.
30. Beye, M., Hasselmann, M., Fondrk, M.K., Page, R.E., & Omholt, S.W. (2003). The gene csd is the primary signal for sexual development in the honeybee and encodes an SR-type protein. *Cell, 114*(4), pp. 419–429. doi:10.1016/S0092-8674(03)00606-8. PMID 12941271.
31. Privman, E., Wurm, Y., & Keller, L. (2013). Duplication and concerted evolution in a master sex determiner under balancing selection. *Proceedings of the Royal Society B: Biological Sciences, 280*(1758), pp. 20122968. doi:10.1098/rspb.2012.2968. PMC 3619454. PMID 23466984.
32. Miyakawa, M.O., Tsuchida, K., & Miyakawa, H. (2018). The doublesex gene integrates multi-locus complementary sex determination signals in the Japanese ant, *Vollenhovia emeryi*. *Insect Biochemistry and Molecular Biology, 94*, pp. 42–49. doi:10.1016/j.ibmb.2018.01.006. PMID 29408414.
33. Van Wilgenburg, E., Driessen, G., & Beukeboom, L. (2006). Single locus complementary sex determination in Hymenoptera: An "unintelligent" design? *Frontiers in Zoology, 3*(1), pp. 1. doi:10.1186/1742-9994-3-1. PMC 1360072. PMID 16393347.
34. Göth, A., & Booth, D.T. (2005). Temperature-dependent sex ratio in a bird. *Biology Letters, 1*(1), pp. 31–33. doi:10.1098/rsbl.2004.0247. PMC 1629050. PMID 17148121.
35. Torres Maldonado, L.C., Landa Piedra, A., Moreno Mendoza, N., Marmolejo Valencia, A., Meza Martínez, A., & Merchant Larios, H. (2002). Expression profiles of Dax1, Dmrt1, and Sox9 during temperature sex determination in gonads of the sea turtle Lepidochelys olivacea. *Gen. Comp. Endocrinol., 129*(1), pp. 20–6. doi:10.1016/s0016-6480(02)00511-7. PMID 12409092.
36. Bull, J.J. (1980). Sex determination in reptiles. *The Quarterly Review of Biology, 55*(1), pp. 3–21. doi:10.1086/411613. JSTOR 2826077. S2CID 85177125.
37. Valenzuela, N., & Janzen, F.J. (2001). Nest-site philopatry and the evolution of temperature-dependent sex determination. *Evolutionary Ecology Research, 3*, pp. 779–794. Retrieved 7 December 2011.
38. Janzen, F.J., & Phillips, P.C. (2006). Exploring the evolution of environmental sex determination, especially in reptiles. *Journal of Evolutionary Biology, 19*(6), pp. 1775–1784. doi:10.1111/j.1420-9101.2006.01138.x. PMID 17040374. S2CID 15485510.
39. Gilbert, S. (2006). *Developmental biology* (8th. ed.). Sunderland, Mass.: Sinauer Associates, Inc. Publishers. pp. 550–553. ISBN 9780878932504.
40. Watts, P.C., Buley, K.R., Sanderson, S., Boardman, W., Ciofi, C., & Gibson, R. (2006). Parthenogenesis in Komodo dragons. *Nature, 444*(7122), pp. 1021–1022. Bibcode:2006Natur.444.1021W. doi:10.1038/4441021a. PMID 17183308. S2CID 4311088.

References (Sex Ratios)

1. Data from the CIA World Factbook [1]. Map compiled in 2021, data from 2020.
2. Hamilton, W.D. (1967). Extraordinary sex ratios. *Science, 156*(3774), pp. 477–488. Bibcode:1967Sci...156..477H. doi:10.1126/science.156.3774.477. PMID 6021675.
3. Kobayashi, K., Hasegawa, E., Yamamoto, Y., Kawatsu, K., Vargo E.L., Yoshimura, J., & Matsuura, K. (2013). Sex ratio biases in termites provide evidence for kin selection. *Nat Commun., 4*, pp. 2048. Bibcode:2013NatCo...4.2048K. doi:10.1038/ncomms3048. PMID 23807025.
4. Trend analysis of the sex ratio at birth in the United States. U.S. Department of Health and Human Services, National Center for Health Statistics.

5. Davis, D.L., Gottlieb, M., & Stampnitzky, J. (1998). Reduced ratio of male to female births in several industrial countries. *Journal of the American Medical Association*, *279*(13), pp. 1018-1023.
6. "CIA Fact Book". The Central Intelligence Agency of the United States.
7. Coney, N.S., & Mackey, W.C. (1998). The woman as final arbiter: A case for the facultative character of the human sex ratio. *Journal of Sex Research*, *35*(2), pp. 169–175. doi:10.1080/00224499809551930.
8. Wilson, K., & Hardy, I.C.W. (2002). Statistical analysis of sex ratios: An introduction. In Hardy, I.C.W. (Eds.), *Sex Ratios: Concepts and Research Methods*, pp. 48–92. ISBN 0521665787
9. Székely T., Weissing F.J., & Komdeur, J. (2014). Adult sex ratio variation: Implications for breeding system evolution. *Journal of Evolutionary Biology*, *27*(8), pp. 1500–1512. doi:10.1111/jeb.12415. PMID 24848871. S2CID 8350737.
10. Charnov, E.L. (1982). *Sex allocation*. Princeton University Press, Princeton, New Jersey. ISBN 0-691-08312-6
11. Smith, J.M., & Price, G.R. (1973). The logic of animal conflict. *Nature*, *246*(5427), pp. 15–8. Bibcode:1973Natur.246...15S. doi:10.1038/246015a0. S2CID 4224989.
12. Danforth, B. (1991). Female foraging and intranest behavior of a communal bee, *Perdita portalis* (Hymenoptera: *Andrenidae*). *Annals of the Entomological Society of America*, *84*(5), pp. 537–548. doi:10.1093/aesa/84.5.537.

Contributors and Attributions

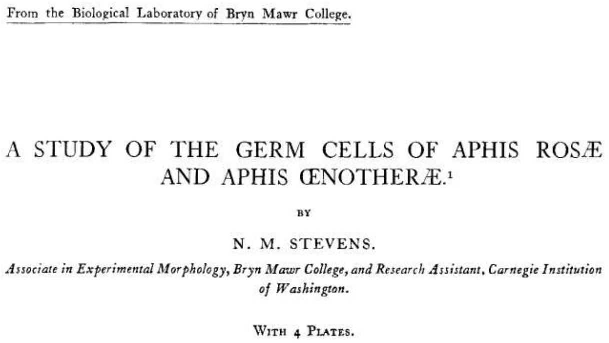
Modified by Dan Wetzel from Wikipedia: https://en.wikipedia.org/wiki/Sex-determination_system, https://en.wikipedia.org/wiki/Sex_ratio

12.3: Scientist Spotlight - Nettie Stevens

Famously, King Henry VIII had six wives in his efforts to have a male heir. He disposed of each for various acts of disrespect, but most especially, for not providing him a son. Throughout history, the birth of a female child, over the oft-preferred male child, has lain with the attitudes or defiance of women. Aptly, it would be a woman to discover the determining factor of sex at birth and free the future of women from such accusations. Within the scientific community, sex had been long-debated as either an inherited trait or one influenced by embryonic environmental influence, and it was ultimately Dr. Nettie Stevens who uncovered the truth.

Figure 12.3.1 : Photograph of Nettie Stevens, taken at Carnegie Institution of Washington and kept in the Bryn Mawr College Photo Archives. Image available in the public domain.

Stevens was a native of Vermont, born in 1861 and dying at the age of 51 in 1912. She studied biology at Westfield State College, where she was only one of three women to graduate between 1872 and 1883. After a few years of teaching, she went on to earn an MA at Stanford University and a PhD at Bryn Mawr College. In the early 1900s, she shifted her research from morphology to cytology and regeneration, leading her to the topic of embryo and chromosome variations. By 1905, she published her findings on yellow mealworms (*Tenebrio molitor*) and the X and Y chromosomes as the cause of an individual's sex at birth. Two X chromosomes (XX) results in a female, while one of each (XY) results in a male. It is now known that the first X is inherited from the egg, while the second (either X or Y) is inherited from the sperm. In her paper, Stevens concluded, "this seems to be a clear case of sex-determination…by a definite difference in the character of the elements of one pair of chromosomes…, the spermatozoa which contain the small chromosome determining the male sex, while those that contain 10 chromosomes of equal size determining the female sex" (1905, p. 13). Not only did Stevens' discovery resolve the debate surrounding sex origins, it was the first time that scientists could link a phenotype to a specific chromosome. Stevens' reputation and contributions to the field of genetics are often overlooked by subsequent findings on the topic during the same time period, with more credit given to her male contemporary Dr. Edmund Wilson, but the value of her discoveries have been incalculable.



From the Biological Laboratory of Bryn Mawr College.

A STUDY OF THE GERM CELLS OF APHIS ROSÆ
AND APHIS ŒNOTHERÆ.[1]

BY

N. M. STEVENS.

Associate in Experimental Morphology, Bryn Mawr College, and Research Assistant, Carnegie Institution of Washington.

WITH 4 PLATES.

Figure 12.3.2: Title page of Nettie Stevens academic paper, outlining her research and her findings on the genetics of assigned birth sex.

Figure 12.3.3: Carl Zeiss Jena 8261 Microscope used by Nettie Maria Stevens. This image was provided to Wikimedia Commons by Bryn Mawr College as part of a cooperation project (licensed under CC BY-SA 3.0).

As culture continues to evolve, modern scientists now know that there are more than the simple XX and XY, male and female binary, that Stevens had originally written about. Today, our concepts of sex pertain to the biological sense which Stevens focused on, though intersex has been added to the male or female classifications and we recognize in the present day that assigned birth at sex does not necessarily indicate gender identity. With science as an accumulated field, guided by the culture it exists within, our concepts of sex and gender will continue to adjust with time, using foundational knowledge like that afforded to us by Dr. Nettie Stevens as a stabilizer for the heights we will reach.

References

Brush, S.G. (1978). Nettie M. Stevens and the discovery of sex determination by chromosomes. *The University of Chicago Press*, *69*(2), pp.162-172. https://www.jstor.org/stable/230427.

The Editors of Encyclopaedia Britannica. (n.d.). Henry VIII. Britannica. https://www.britannica.com/biography/Henry-VIII-king-of-England. Accessed 1/26/2024.

The Editors of Encyclopaedia Britannica. (n.d.). *Nettie Stevens*. Britannica. https://www.britannica.com/biography/Nettie-Stevens. Accessed 1/26/2024.

Stevens, N.M. (1905). Studies in spermatogenesis. Carnegie Institution of Washington, 36, pp. 33-74.

12.4: Mating systems in sexual animals

The content for this subtopic is found in an external page. Please click the link below to access this information.

Mating systems in sexual animals

12.5: Mating Systems in Plants

Asexual Reproduction

Many plants are facultatively sexual rather than obligately sexual. Asexual reproduction is a type of reproduction where the offspring comes from one parent only, thus, inheriting the characteristics of the parent. Asexual reproduction in plants occurs in two fundamental forms vegetative reproduction and agamospermy.[1] Vegetative reproduction involves a vegetative piece of the original plant producing new individuals by budding, tillering, etc. and is distinguished from apomixis, which is a replacement of sexual reproduction, and in some cases involves seeds. Apomixis occurs in many plant species such as dandelions (*Taraxacum* species) and also in some non-plant organisms. For apomixis and similar processes in non-plant organisms, see parthenogenesis.

Natural vegetative reproduction is a process mostly found in perennial plants, and typically involves structural modifications of the stem or roots and in a few species leaves. Most plant species that employ vegetative reproduction do so as a means to perennialize the plants, allowing them to survive from one season to the next and often facilitating their expansion in size. A plant that persists in a location through vegetative reproduction of individuals constitutes a clonal colony. A single ramet, or apparent individual, of a clonal colony is genetically identical to all others in the same colony. The distance that a plant can move during vegetative reproduction is limited, though some plants can produce ramets from branching rhizomes or stolons that cover a wide area, often in only a few growing seasons. In a sense, this process is not one of reproduction but one of survival and expansion of biomass of the individual. When an individual organism increases in size via cell multiplication and remains intact, the process is called vegetative growth. However, in vegetative reproduction, the new plants that result are new individuals in almost every respect except genetic. A major disadvantage of vegetative reproduction, is the transmission of pathogens from parent to offspring. It is uncommon for pathogens to be transmitted from the plant to its seeds (in sexual reproduction or in apomixis), though there are occasions when it occurs.[2]

Seeds generated by apomixis are a means of asexual reproduction, involving the formation and dispersal of seeds that do not originate from the fertilization of the embryos. Hawkweeds (*Hieracium*), dandelions (*Taraxacum*), some species of *Citrus* and Kentucky blue grass (*Poa pratensis*) all use this form of asexual reproduction. Pseudogamy occurs in some plants that have apomictic seeds, where pollination is often needed to initiate embryo growth, though the pollen contributes no genetic material to the developing offspring.[3] Other forms of apomixis occur in plants also, including the generation of a plantlet in replacement of a seed or the generation of bulbils instead of flowers, where new cloned individuals are produced.

Sexual Reproduction

Sexual reproduction involves two fundamental processes: meiosis, which rearranges the genes and reduces the number of chromosomes, and fertilisation, which restores the chromosome to a complete diploid number. In between these two processes, different types of plants and algae vary, but many of them, including all land plants, undergo alternation of generations, with two different multicellular structures (phases), a gametophyte and a sporophyte.

In mosses and liverworts, the gametophyte is relatively large, and the sporophyte is a much smaller structure that is never separated from the gametophyte. In ferns, gymnosperms, and flowering plants (angiosperms), the gametophytes are relatively small and the sporophyte is much larger. In gymnosperms and flowering plants the megagametophyte is contained within the ovule (that may develop into a seed) and the microgametophyte is contained within a pollen grain.

In the evolution of early plants, abiotic means, including water and much later, wind, transported sperm for reproduction. The first plants were aquatic, and released sperm freely into the water to be carried with the currents. Ancestral land plants like liverworts and mosses have motile sperm that swam in a thin film of water or were splashed in water droplets. As taller and more complex plants evolved, modifications in the alternation of generations evolved. In the Paleozoic era progymnosperms reproduced by using spores dispersed on the wind and many gymnosperms and some angiosperms still rely on wind for gamete dispersal. The seed plants including seed ferns, conifers and cordaites have pollen grains that contain the male gametes for protection of the sperm during the process of transfer from the male to female parts. Angiosperms, or flowering plants, are the most derived and most abundant plant species and they rely on flowers producing pollen and ovules for reproduction.

Self-Fertilization and Self-Incompatibility

Many species of plants, particularly those which produce both staminate and pistillate flowers or produce ‘perfect’ bisexual flowers, also have the ability to reproduce sexually with themselves. This is advantageous particularly if pollination services are unreliable or unpredictable, as it ensures the plant still has some fitness. **Self-pollination** is a form of pollination in which pollen from the same plant arrives at the stigma of a flower (in flowering plants) or at the ovule (in gymnosperms). The term **selfing** that is often used as a synonym, is not limited to self-pollination, but also applies to other types of self-fertilization. Plants may either be obligately self-fertilizing, or facultatively so. In facultatively selfing plants, there may be mechanisms which delay selfing, such as stamens that are initially reflexed but move to come into contact with the stigma. About 42% of flowering plants exhibit a mixed mating system in nature.[4] In the most common kind of system, individual plants produce a single flower type and fruits may contain self-pollinated, out-crossed or a mixture of progeny types. Another mixed mating system is referred to as dimorphic cleistogamy. In this system a single plant produces both open, potentially out-crossed and closed, obligately self-pollinated cleistogamous flowers.[5]

Still other species are self-incompatible, and will reject their own pollen grains if they land on their own stigmatic surface. These plants are obligately outcrossing, and must successfully sexually reproduce with another member of their species. In plants with SI, when a pollen grain produced in a plant reaches a stigma of the same plant or another plant with a matching allele or genotype, the process of pollen germination, pollen-tube growth, ovule fertilization, or embryo development is inhibited, and consequently no seeds are produced. SI is one of the most important means of preventing inbreeding and promoting the generation of new genotypes in plants and it is considered one of the causes of the spread and success of angiosperms on the earth.

Outcrossing Fertilization

Plants that use insects or other animals to move pollen from one flower to the next have developed greatly modified flower parts to attract pollinators and to facilitate the movement of pollen from one flower to the insect and from the insect back to the next flower. Flowers of wind-pollinated plants tend to lack petals and or sepals; typically large amounts of pollen are produced and pollination often occurs early in the growing season before leaves can interfere with the dispersal of the pollen. Many trees and all grasses and sedges are wind-pollinated.

Plants have a number of different means to attract pollinators including color, scent, heat, nectar glands, edible pollen and flower shape. Along with modifications involving the above structures two other conditions play a very important role in the sexual reproduction of flowering plants, the first is the timing of flowering and the other is the size or number of flowers produced. Often plant species have a few large, very showy flowers while others produce many small flowers, often flowers are collected together into large inflorescences to maximize their visual effect, becoming more noticeable to passing pollinators. Flowers are attraction strategies and sexual expressions are functional strategies used to produce the next generation of plants, with pollinators and plants having co-evolved, often to some extraordinary degrees, very often rendering mutual benefit. Specialization can be advantageous because it results in more consistent pollination services. As a result, the specialized pollinator and plant can exert strong selective pressure on each other, leading to coevolution. Examples of this include the coevolution between figs and fig wasps, or yucca and yucca moths, wherein the yucca moths are both the obligate pollinators and the antagonistic herbivores of yucca. Another visually striking example is the co-evolution of long floral corollas and long beaks or proboscii in pollinators $12.5.1 A+B$.

Figure 12.5.1: (A) Sword-billed Hummingbird in Ecuador ("Sword-Billed Hummingbird" by Andrew Morffew is licensed under CC BY 2.0); (B) Rufous Hummingbird pollinating Scarlet Gilia in the Rocky Mountains ("Rufous Hummingbird" by Smallman12q is licensed under CC BY 2.0).

Plants which share pollination methods or pollinators often accumulate suites of related traits called pollination syndromes. These have evolved in response to natural selection imposed by different pollen vectors, which can be abiotic (wind and water) or biotic, such as birds, bees, flies, etc. through a process called pollinator-mediated selection.[6,7] These traits include flower shape, size, colour, odor, reward type and amount, nectar composition, and timing of flowering. For example, tubular red flowers with copious nectar often attract birds; foul smelling flowers attract carrion flies or beetles, etc. Different species which use the same pollinators may either flower synchronously, to attract pollinators more successfully, or asynchronously, to avoid heterospecific pollen transfer (or stigma gunking). The latter is an example of niche partitioning.

The largest family of flowering plants is the orchids (Orchidaceae), estimated by some specialists to include up to 35,000 species,[8] which often have highly specialized flowers that attract particular insects for pollination. The stamens are modified to produce pollen in clusters called pollinia, which become attached to insects that crawl into the flower. The flower shapes may force insects to pass by the pollen, which is "glued" to the insect. Some orchids are even more highly specialized, with flower shapes that mimic the shape of insects to attract them to attempt to 'mate' with the flowers, a few even have scents that mimic insect pheromones ($12.5.2$).

Figure $12.5.2$: A bee-mimic orchid evolved to resemble a sexually receptive female bee and attract naïve male bees to pollinate it ("Bee Orchid (*Ophrys apifera*)" by Ian Capper is licensed under CC BY 2.0).

Examples of Pollination Syndromes

- Wind: Flowers may be small and inconspicuous, as well as green and not showy. They produce enormous numbers of relatively small pollen grains (hence wind-pollinated plants may be allergens, but seldom are animal-pollinated plants allergenic). Their stigmas may be large and feathery to catch the pollen grains.
- Water: Water-pollinated plants are aquatic and pollen is released into the water. Water currents therefore act as a pollen vector in a similar way to wind currents. Their flowers tend to be small and inconspicuous with many pollen grains and large, feathery stigmas to catch the pollen. However, this is relatively uncommon (only 2% of pollination is hydrophily) and most aquatic plants are insect-pollinated, with flowers that emerge into the air. *Vallisneria* is an example.
- Bee: Some bee flowers tend to be yellow or blue, often with ultraviolet nectar guides and scent. Nectar, pollen, or both are offered as rewards in varying amounts. The sugar in the nectar tends to be sucrose-dominated. A few bees collect oil from special glands on the flower.[10]
- Butterfly: Butterfly-pollinated flowers tend to be large and showy, pink or lavender in colour, frequently have a landing area, and are usually scented. Since butterflies do not digest pollen (with one exception), more nectar is offered than pollen. The flowers have simple nectar guides with the nectaries usually hidden in narrow tubes or spurs, reached by the long tongue of the butterflies.
- Moth: Among the more important moth pollinators are the hawk moths (Sphingidae). Their behaviour is similar to hummingbirds: they hover in front of flowers with rapid wingbeats. Most are nocturnal or crepuscular. Moth-pollinated flowers tend to be white, night-opening, large and showy with tubular corollas and a strong, sweet scent produced in the evening, night or early morning. Much nectar is produced to fuel the high metabolic rates needed to power their flight.

- Bat: There are major differences between bat pollination in the Americas as opposed to the Afro-Eurasia. Afro-Eurasian pollinating bats are large fruit bats of the family Pteropodidae which do not have the ability to hover and must perch in the plant to lap the nectar; these bats furthermore do not have the ability to echolocate.[11] Bat-pollinated flowers in this part of the world tend to be large and showy, white or light coloured, open at night and have strong musty odours. They are often large balls of stamens. In the Americas pollinating bats are tiny creatures called glossophagines which have both the ability to hover as well as echolocate, and have extremely long tongues. Plants in this part of the world are often pollinated by both bats and hummingbirds, and have long tubular flowers.[11] In one essay, von Helversen *et al*. speculate that maybe some bell-shaped flowers have evolved to attract bats in the Americas, as the bell-shape might reflect the sonar pulses emitted by the bats in a recognisable pattern.[12]
- Fly: Myophilous plants tend not to emit a strong scent, are typically purple, violet, blue, and white, and have open dishes or tubes.[13]
- Sapromyophilous plants try to attract flies which normally visit dead animals or dung. Flowers mimic the odor of such objects. The plant provides them with no reward and they leave quickly unless it has traps to slow them down. Such plants are far less common than myophilous ones.[14]
- Beetle: Beetle-pollinated flowers are usually large, greenish or off-white in color and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Most beetle-pollinated flowers are flattened or dish shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plant's ovaries are usually well protected from the biting mouthparts of their pollinators.[15] A number of cantharophilous plants are thermogenic, with flowers that can increase their temperature. This heat is thought to help further spread the scent, but the infrared light produced by this heat may also be visible to insects during the dark night, and act as a shining beacon to attract them.[16]
- Bird: Flowers pollinated by specialist nectarivores tend to be large, red or orange tubes with a lot of dilute nectar, secreted during the day. Since birds do not have a strong response to scent, they tend to be odorless. Flowers pollinated by generalist birds are often shorter and wider. Hummingbirds are often associated with pendulous flowers, whereas passerines (perching birds) need a landing platform so flowers and surrounding structures are often more robust. Also, many plants have anthers placed in the flower so that pollen rubs against the birds head/back as the bird reaches in for nectar.

…and many more!

References

1. Barrett, S.C.H. (2008). Major evolutionary transitions in flowering plant reproduction. *University of Chicago Press*. p. 157. ISBN 978-0-226-03816-2.

2. ^ Fritz, R.E. & Simms, E.L. (1992). Plant resistance to herbivores and pathogens: Ecology, evolution, and genetics. *Chicago: University of Chicago Press*. p. 359. ISBN 978-0-226-26554-4.

3. ^ "Archived copy". Archived from the original on 2009-10-26. Retrieved 2009-10-25.

4. Goodwillie, C., Kalisz, S., & Eckert, C.G. (2005). The evolutionary enigma of mixed mating systems in plants: Occurrence, theoretical explanations, and empirical evidence. *Annu. Rev. Ecol. Evol. Syst., 36*, pp. 47–79. doi:10.1146/annurev.ecolsys.36.091704.175539.

5. ^ Munguía-Rosas, M.A., Campos-Navarrete, M.J., & Parra-Tabla, V. (2013). The effect of pollen source vs. flower type on progeny performance and seed predation under contrasting light environments in a cleistogamous herb. *PLOS ONE*, *8*(11): e80934. Bibcode:2013PLoSO...880934M. doi:10.1371/journal.pone.0080934. PMC 3829907. PMID 24260515.

6. Faegri & Pijl 1980.

7. ^ Proctor, M., Yeo, P., & Lack, A. (1996). The natural history of pollination. *HarperCollins, London*. ISBN 978-0-88192-352-0.

8. Orchidaceae in Flora of North America @ efloras.org

9. ^ Asteraceae in Flora of North America @ efloras.org

10. Martins, A.C., Melo, G.A.R., & Renner, S.S. (2014). The corbiculate bees arose from New World oil-collecting bees: Implications for the origin of pollen baskets. *Molecular Phylogenetics and Evolution, 80*, pp. 88–94. doi:10.1016/j.ympev.2014.07.003. PMID 25034728.

11. Fleming, T.H., Geiselman, C., & Kress, W.J. (2009). The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany, 104*(6), pp. 1017–1043. doi:10.1093/aob/mcp197. PMC 2766192. PMID 19789175.

12. ^ Von Helversen, D., Holderied, M.W., & von Helversen, O. (2003). Echoes of bat-pollinated bell-shaped flowers: conspicuous for nectar-feeding bats?. *Journal of Experimental Biology, 206*(6), pp. 1025–1034. doi:10.1242/jeb.00203. PMID 12582145.

13. Kastinger, C., & Weber, A. (2001). Bee-flies (Bombylius spp., Bombyliidae, Diptera) and the pollination of flowers. *Flora, 196*(1), pp. 3–25. doi:10.1016/S0367-2530(17)30015-4.

14. ^ Jones, G.D., & Jones, S.D. (2001). The uses of pollen and its implication for Entomology. *Neotropical Entomology, 30*(3), pp. 314–349. doi:10.1590/S1519-566X2001000300001.

15. ^ Gullan, P.J., & Cranston, P.S. (2005). The insects: An outline of Entomology. *Blackwell Publishing Ltd*. p. 282. ISBN 978-1-4051-1113-3.

16. ^ Korotkova, N., & Barthlott, W. (2009). On the thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Signalling and Behaviour, 4*(11), pp. 1096–1098. doi:10.4161/psb.4.11.9872. PMC 2819525. PMID 19838070.

Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) from the following sources:

- https://en.wikipedia.org/wiki/Plant_reproduction
- https://en.wikipedia.org/wiki/Self-incompatibility
- https://en.wikipedia.org/wiki/Self-pollination
- https://en.wikipedia.org/wiki/Pollination_syndrome
- Original text by Castilleja Olmsted

12.6: Scientist Spotlight - Ernest Everett Just

For those who enjoy them sunny side up, scrambled, or hard boiled, the word “egg” may bring chickens to mind. However, eggs don’t always take the form of smooth, oval-shaped objects that constitute your breakfast, nor do they only come from birds. Scientifically speaking, an “egg” is a gamete, or a sex cell, central to the process of sexual reproduction. This means that eggs are common to all sexually reproducing organisms, even the ones that don’t lay the eggs we’re familiar with.

One type of reproduction, called sexual reproduction, occurs *when a sperm cell fertilizes an egg cell*. The fertilized egg cell is called a “zygote”. When two organisms are involved, the zygote contains genetic material from two different parents. However, sexual reproduction can also occur when one hermaphroditic organism (possessing male and female gametes) self-fertilizes. No matter the number of contributors, the defining mechanism of sexual reproduction is *when a sperm cell fertilizes an egg cell*. This process occurs on a microscopic level, so how do we know what fertilization looks like? One answer to this broad question was unearthed by embryologist Ernest Everett Just. Just was born in Charleston, South Carolina in 1883, and his father died 4 years later (Selassie 2007). He went on to graduate from Dartmouth College, teach English and biology at Howard University, and earn a PhD in zoology at the University of Chicago (Byrnes and Newman 2014). Prior to his time in Chicago, Just conducted research at the Woods Hole Biological Marine Laboratory, where his work with marine invertebrates revealed that the ectoplasm (egg surface) significantly influences the fertilization and development of eggs (Just 1919, 1922; Wellner 2010).

Throughout his career, Just authored more than seventy papers and two books. Despite his major contributions to our understanding of fertilization and evolutionary developmental biology, his work was “...largely forgotten and invisible to the world of biology” (Byrnes and Newman 2014). As an African American man in the early 20th century, Just belonged to a historically marginalized group of people, and he is only now receiving recognition for his pioneering work.

Figure 12.6.1: "Ernest Everett Just" is available in the public domain.

References

Scientist Spotlight Inspiration from the Scientist Spotlights Initiative

Byrnes, M.W., & Newman, S.A. (2014). Ernest Everett Just: Egg and embryo as excitable systems. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4277254/>. Accessed October 5, 2021.

Just, Ernest Everett. 1919. The Fertilization Reaction in Echinarachnius Parma. *Biological Bulletin*, *36*(1), pp. 1-10.

Just, Ernest Everett. 1922. Initiation of development in the egg of Arbacia. II. Fertilization of eggs in various stages of artificially induced mitosis. *Biological Bulletin*, *43*(6), pp. 401-410.

Selassie I, & Gabriel, W. (2007). Ernest Everett Just (1883-1941). <https://www.blackpast.org/african-am...ett-1883-1941/>. Accessed October 5, 2021.

Wellner, K. (2010). Ernest Everett Just (1883-1941). *Embryo Project Encyclopedia*. <http://embryo.asu.edu/handle/10776/2039>. Accessed October 5, 2021.

12.7: Sexual selection

The content for this subtopic is found in an external page. Please click the link below to access this information.

Sexual selection

Chapter summary

The paradox of sexual reproduction is that although it is ubiquitous in multicellular organisms, there are many disadvantages to reproducing sexually when we compare it to asexual reproduction. This chapter explores some of the multitude of hypotheses for why sexual reproduction exists, the variety of ways in which sexes are determined in plants and animals, and some of the variation in mating systems of sexual organisms. This chapter also focuses on sexual selection, a form of natural selection that occurs when traits that improve mating success are favored by selection, even if they cause a decrease in survival.

CHAPTER OVERVIEW

13: The Ecology of Intraspecific Variation

Learning Objectives

- Understand the difference between interspecific variation, intraspecific variation, and phenotypic plasticity
- Describe animal personality and how it is quantified
- Learn some of the current tools that ecologists use to study intraspecific variation in foraging behavior and diet

What is Intraspecific Variation?

Dog breeds vary considerably in their physical and behavioral traits, so it can be easy to forget that they are all members of the same species, *Canus lupus familiaris* (Figure **13.1**). Given their very different phenotypes, dogs like chihuahuas and great danes would play very different roles in their ecosystems if they lived in the wild. This type of variation is known as **intraspecific variation** ("within species" variation), or variation among individuals of the same species. In contrast, **interspecific variation** ("across species" variation) is variation that occurs when comparing individuals of differing species. Interspecific variation, for example, would instead refer to differences in the physical and behavioral traits of cats and dogs.

Figure 13.1: Examples of different breeds of the species *Canus familiaris.* Image is available in the public domain.

Intraspecific variation can be attributed to pre-defined classifications (breed, age, sex) or to random differences among individuals. Anyone with two pets of the same breed, age, and sex is likely to be able to list off a variety of ways in which their pets differ whether these differences be size, temperament, or dietary preferences. These differences can be driven by genetics ("nature") and environmental factors ("nurture").

In the case of *Canus familiaris* and other domesticated species, intraspecific variation is created and maintained by artificial selection by humans. Artificial selection is not necessary for the development and maintenance of intraspecific variation, however. In natural populations, considerable variation exists between individuals of the same species for both intrinsic and extrinsic reasons, causing differences in the way that conspecifics look, behave, and respond to natural selection pressures, such as predation risk, food availability, and novel environments (Bolnick et al. 2003). This variation plays an important role in the dynamics of populations, communities, and ecosystems.

What is Phenotypic Plasticity?

In addition to individuals varying in their average traits, ecologists are increasingly interested in how individuals vary in the flexibility of these traits. That is, how much and in what way do individuals change their behavior, morphology, physiology, or phenology in response to changing internal (e.g., physiological state) or external (e.g., temperature) stimuli? This flexibility in behavior is known as **phenotypic plasticity** (Figure 13.2). The term was originally used to describe developmental effects on morphological characters, but is now more broadly used to describe all phenotypic responses to environmental change, such as acclimation or learning. Developmental plasticity is often associated with irreversible phenotypic plasticity, or changes in phenotype that are permanent and cannot be reversed once they occur.

Reversible plasticity occurs when an organism can switch between different phenotypes in response to changing environmental conditions. This type of plasticity is often most effective when environmental cues are reliable, or can consistently predict changes in the environment. For example, temperature changes with seasons are a reliable cue, and many animals and plants use them to trigger seasonal adaptations. When environmental cues become less reliable (e.g., in the case of unprecedented extremes caused by rapid climate change), plasticity may not be an effective mechanism for adaptation.

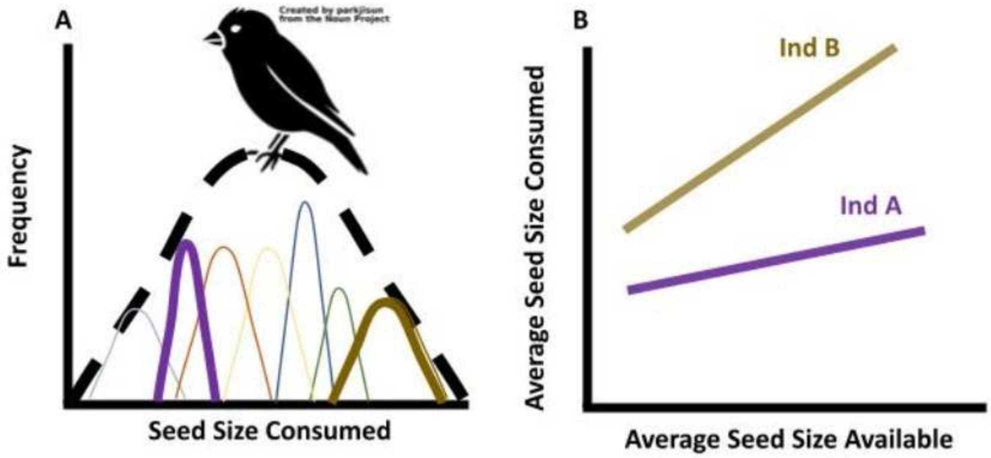


Figure 13.2: An example of intraspecific variation in a species of finch consuming seeds, where a) depicts the overall one-dimensional niche of this species (black dashed line) in terms of the seed sizes that they consume. Within this niche, different individuals (lined of varying colors) specialize on different size seeds, showing intraspecific variation. b) shows how two of these individuals (Individual A and Individual B) vary their resource use with changes in resource availability. Here, Ind B shows greater phenotypic plasticity because this individual alters their resource use to a greater extent when resources change (i.e., the slope of the line for Ind B is greater).

Generally, phenotypic plasticity is more important for immobile organisms (e.g. plants) than mobile organisms (e.g. most animals), as mobile organisms can often move away from unfavorable environments (Schlichting 1968). Nevertheless, mobile organisms also have at least some degree of plasticity in at least some aspects of the phenotype. One mobile organism with substantial phenotypic plasticity is *Acyrthosiphon pisum* of the aphid family, which exhibits the ability to interchange between asexual and sexual reproduction, as well as growing wings between generations when plants become too populated (Figure 13.3) (Eisen et al. 2010). For more information on Sex Strategies and on plasticity in mating systems, see Chapter 12.

Figure 13.3: "*Acyrthosiphon pisum*" by Whitney Cranshaw is Licensed under CC SA 3.0.

The Importance of Understanding Intraspecific Variation in a Changing World

Given that there is substantial variation among individuals, it is inevitable that when presented with anthropogenic stressors, individuals from the same species will respond in different ways (Bolnick et al. 2011). These varied responses may define the difference between success and failure; the likelihood of mortality or the ability to emigrate, to adapt through genetic changes, or to respond via phenotypic plasticity (Engås et al. 1996; Höglund et al. 2008; Cripps et al. 2014).

Intraspecific variation in responses can also have far-reaching impacts on the population dynamics, community structure and ecosystem function of entire groups of animals (Post et al. 2008; Rudman et al. 2015; Charette and Derry 2016; Des Roches et al. 2017). Indeed, in some cases intraspecific variation can have a greater influence than interspecific differences on overall community responses to environmental change (Crutsinger et al. 2006; Siefert and Ritchie 2016; Raffard et al. 2019).

Furthermore, varied responses set the stage for future evolution, as the cohort of individuals capable of reproducing following an anthropogenic stress event defines the evolutionary potential of the population that remains after the disturbance event (Medina et al. 2007; Bijlsma and Loeschcke 2012). To consider only "mean" responses to anthropogenic stressors is therefore to underappreciate the likely consequences of the disturbance; a lack of population-level impacts may be masking more subtle but important within-population changes. Conversely, consideration of intraspecific variation facilitates a more comprehensive understanding of the impacts of anthropogenic stressors on animals, the likely consequences for wider ecosystems, and the best management strategies to address these changes.

Unprecedented rates of climate change are predicted to occur over the next 100 years as a result of human activity. Phenotypic plasticity is a key mechanism with which organisms can cope with a changing climate, as it allows individuals to respond to change within their lifetime. This is thought to be particularly important for species with long generation times, as evolutionary responses via natural selection may not produce change fast enough to mitigate the effects of a warmer climate.

The North American red squirrel (*Tamiasciurus hudsonicus*) has experienced an increase in average temperature over this last decade of almost 2°C. This increase in temperature has caused an increase in abundance of white spruce cones, the main food source for winter and spring reproduction. In response, the mean lifetime parturition date of this species has advanced by 18 days. Food abundance showed a significant effect on the breeding date with individual females, indicating a high amount of phenotypic plasticity in this trait (Réale et al. 2003).

While phenotypic plasticity can play a role in the persistence of individuals under changing environmental conditions (Nicotra et al., 2010), the extent of phenotypic plasticity can be limited by ecological and evolutionary constraints (Valladares et al., 2007). The distribution of traits within a community is expected to reflect variation around a mean optimal phenotype for fitness and/or growth rate (Norberg et al., 2001; Enquist et al., 2015). This idea follows from a central paradigm in ecology (Whittaker, 1972) and evolutionary biology (Levins, 1968) where observed shifts in phenotypes, species' abundances, and composition across environmental gradients reflect the arrangement of phenotypes or species that maximizes fitness in different environments. Abiotic filters such as temperature or moisture that limit successful survival strategies promote convergence of traits around this optimal local phenotype (Keddy, 1992; Weiher and Keddy, 1999; Violle et al., 2012).

The Study of Intraspecific Variation

Two of the most studied aspects of intraspecific variation are variation in the behavior of individuals within a species, often called “**animal personality,**” and variation in the diet of individuals within a species, often called “**individual specialization.**”

Animal Personality

Personality in animals has been investigated across a variety of different scientific fields including agricultural science, animal behavior, anthropology, psychology, veterinary medicine, and zoology (Gosling 2001). Thus, the definition for animal personality may vary according to the context and scope of study. However, there is recent consensus in the literature for a broad definition that describes animal personality as individual differences in behavior that are consistent across time and ecological context (Wolf et al. 2012). Here, consistency refers to the repeatability of behavioral differences between individuals and not a trait that presents itself the same way in varying environments (Réale et al. 2007; Stamps and Groothuis 2010). In a meta-analysis of published, peer-reviewed repeatability estimates, reviewers found that, in general, approximately 35% of behavioral variation among individuals could be attributed to individual differences (Bell et al. 2009).

Animal personality traits are measurable and are described in over 100 species (Carere and Locurto 2011). Personality in animals has also been referred to as animal disposition, coping style, and temperament (Gosling 2001). The diversity of animal personality can be compared in cross-species studies, demonstrating its pervasiveness in the evolutionary process of animals (Gosling 2001). Research on animal personality variation has been burgeoning since the mid 1990s (Kralj-Fišer and Schuett 2014). Recent studies have focused on its proximate causation and the ecological and evolutionary significance of personality in animals (Stamps and Groothuis 2010).

Example: The spider *Anelosimus studiosus* forms groups in which some females show an aggressive personality type and engage more in colony defense and prey capture, while others are docile and engage more in brood care. Groups containing both these two different personalities have better fitness than groups of only one personality type. This is because aggressive females are more efficient at foraging, web construction and defense, while docile females are better at raising the young. When groups contain a mix of both personalities, overall group performance is improved benefiting all group members (Grinsted and Bacon 2014). In the social spider *Stegodyphus dumicola* individuals differ in their boldness, with bolder individuals having a greater risk appetite. Boldness changes were found to relate to social interactions with nest mates, indicating that individual personality is more plastic in groups (Hunt et al. 2018).

Animal personality vs. human personality

The extent of personality phenomenon considered when examining animal personality is significantly reduced compared to those studied in humans. Concepts such as personal objects, identity, attitudes and life stories are not considered relevant in animals. Similarly, any approach that requires the subject to explain motives, beliefs or feelings is not applicable to the study of animal behavior (Gosling 2001).

The study of animal personality is largely based on the observation and investigation of behavioral traits. In an ecological context, traits or ‘characters’ are attributes of an organism that are shared by members of a species. Traits can be shared by all or only a portion of individuals in a population. For example, studies in animal personality often examine traits such as aggressiveness (antagonistic interactions with other individuals of the same species), boldness (reaction to risky situations), exploration (reaction to new situations), activity (movement in a familiar environment), and sociality (positive interactions with other individuals of the same species).

Evolutionary potential

The degree of variation in a population has been determined to influence the direction and outcome of natural selection. Most scientific research has focused on genetic and phenotypic variation or differences in resource use; however, variation in consistent behaviors (i.e. personality) also has important evolutionary consequences. For example, personality in animals can affect the way individuals interact with their environment and with each other which can affect the relative fitness of individuals (Biro and Stamps 2008). Therefore, personality can influence selection.

Natural or artificial selection cannot act on personality unless there is a mechanism for its inheritance. Heritability is a statistic used in the fields of breeding and genetics that estimates the degree of *variation* in a phenotypic trait in a population that is due to genetic variation between individuals in that population. Heritability ranges from 0 to 1, with a value of 0 indicating that individual variation is driven by environmental differences and a value of 1 indicating that it is driven by individual differences. The concept of heritability can be expressed in the form of the following question: "What is the proportion of the variation in a given trait within a population that is *not* explained by the environment or random chance?"

In rhesus macaques (*Maccaca mulatta*), the personality traits of Meek, Bold, Aggressive, Passive, Loner and Nervous have heritability values of 0.14 to 0.35, thus indicating that there is some genetic basis to the expression of personality traits in animals. In apes, including humans, heritability estimates of personality dimensions range from 0.07 to 0.63 (Brent et al. 2014). In horses, heritability estimates range mostly between 0.15 and 0.40 for traits assessed in personality tests. Values at this level are considered as "promising" for artificial selection (Brent et al. 2014).

✓ Personality in Practice 13.1

Reaction norms help us study personality and plasticity

A potentially useful way to understand how individual variation interacts with the factors known to influence phenotypic traits is to view a phenotypically plastic trait using a reaction norm. A reaction norm is the set of phenotypes a genotype/individual could express across a set of environments (Via et al. 1995). The reaction norm has a long history for studying phenotypic variation (Stearns 1989; Pigliucci 2001). Using a reaction norm model (see below) we can study individual variation in a phenotypic trait in terms of individual deviation from the population mean, as well as individual variation from the mean population response to the environmental (individual phenotypic plasticity). A reaction norm approach can also allow insight into how and why individuals vary in different dimensions, both in their mean expression of a trait (reaction norm height) and the plasticity of the trait (reaction norm slope). The basic reaction norm to study how a trait (y) varies with some environmental factor (E) can be written as:

$$y_{ij} = \mu + \beta E_j + p_i + p_{Ei} E_j + \varepsilon_{ij}$$

where y_{ij} is the phenotype of individual i on occasion j. This equation contains two main effects, the fixed effects and the random effects, and the residual error effects. The fixed effects represent the population average response of the trait (y) to the change in the environment (E). The fixed effects include the variables μ, which is the population mean phenotype in the average environment, and β, which is the population mean slope of y on E. The random effects represent individual phenotypic differences from the population average height and slope. The random effects include the variables p_i, which is the permanent deviation of individual i from the mean population phenotype independent of E (**personality**: individual reaction norm height), and p_{Ei}, which is the deviation of individual i from the population average slope (**individual plasticity**). The best way to interpret this equation may be to visualize what each component means in graphical form (Figure 13.4). The reaction norm approach allows us to estimate the variance in a trait that is due to the effect of individual variation. We can also test for significant differences in the variance in height of the individual reaction norms (Vp) to see if individuals differ in their average phenotype, as well as test for differences in the variance of individual slopes of the reaction norms (VpE; Figure 13.5).

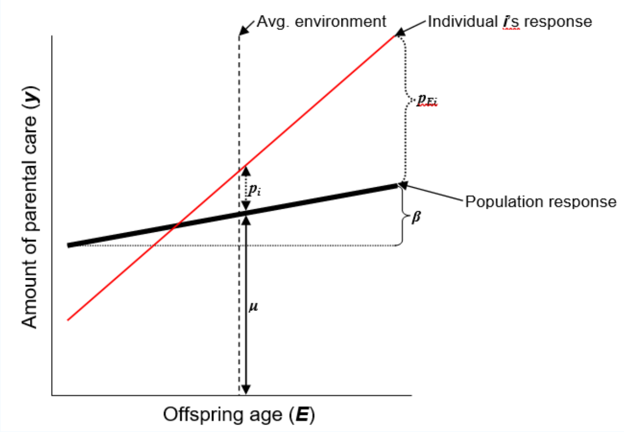


Figure 13.4: This diagram represents the basic reaction norm model, where the phenotype y is the amount of parental care and the environment E is the age of offspring. The variable μ represents the population mean phenotype in the average environment, and β is the population mean slope. The random effects are represented by pi, which is the permanent deviation of individual i from the mean population phenotype (**personality**: individual reaction norm height), and pEi, which is the deviation of individual i from the population average slope (individual **plasticity**).

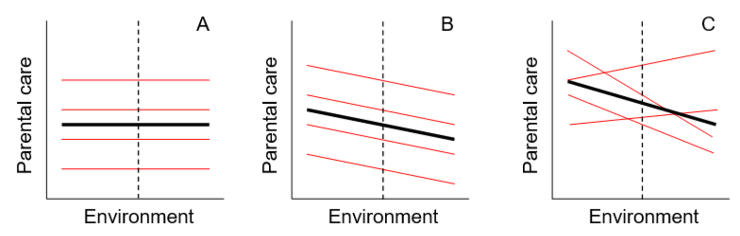


Figure 13.5: These diagrams represent examples of reaction norms with different degrees of variation. The thick black line is the mean population response to the environment, and each thin red line represents an individual's phenotype across the environment. The diagrams show that: **(A)** there is individual variation in the phenotype (personality: heights of the red lines), but that there is no phenotypic plasticity, **(B)** there is individual variation in the phenotype (personality: heights of the red lines), there is population-level phenotypic plasticity (slopes of the red lines are non-zero), but individuals do not differ in their response to the environment (slopes of the red lines are equal), and **(C)** there is individual variation in the phenotype (personality: heights of the red lines), there is population-level phenotypic plasticity (slopes of the red lines are non-zero), and individuals differ in their response to the environment (individual plasticity: slopes of the red lines vary).

Individual Specialization in Foraging and Diet

Individuals can vary in the quantity of resources they consume, the type of resources they consume, and how they obtain these resources (i.e., in their foraging behavior). This variation in diet and foraging behavior can be linked to animal personality. For example, more aggressive individuals are likely to benefit from social dominance that allows them access to higher quality resources than subordinate individuals (Toscano et al. 2016).

Individual specialization is specifically used to describe variation in diet among individuals that is not driven by *a priori* factors like morphology, sex, or age. In the formula below, diet is driven by variation due to sex, age, morphology, and random differences among individuals; these random differences represent intraspecific variation in diet (Bolnick et al. 2003).

diet = sex + age + morphology + random differences

Measuring Intraspecific Variation

Intraspecific variation in diet and foraging is studied using traditional tools (e.g., observation, gut content analysis) as well as more modern tools such as stable isotope analysis and animal tagging. These tools have considerable advantages in studying animal foraging behavior (tagging) and diet (stable isotope analysis).

Tagging data is particularly useful because it provides high-frequency, continuous data that allows researchers to determine multiple ways in which animals vary in their foraging (e.g., foraging distance, foraging location, diving depth) and how they alter this behavior when conditions change. In Figure 13.6, for example, individual great black-backed gulls (*Larus marinus*) vary in where they forage and in how they shift their foraging locations when food availability declines.

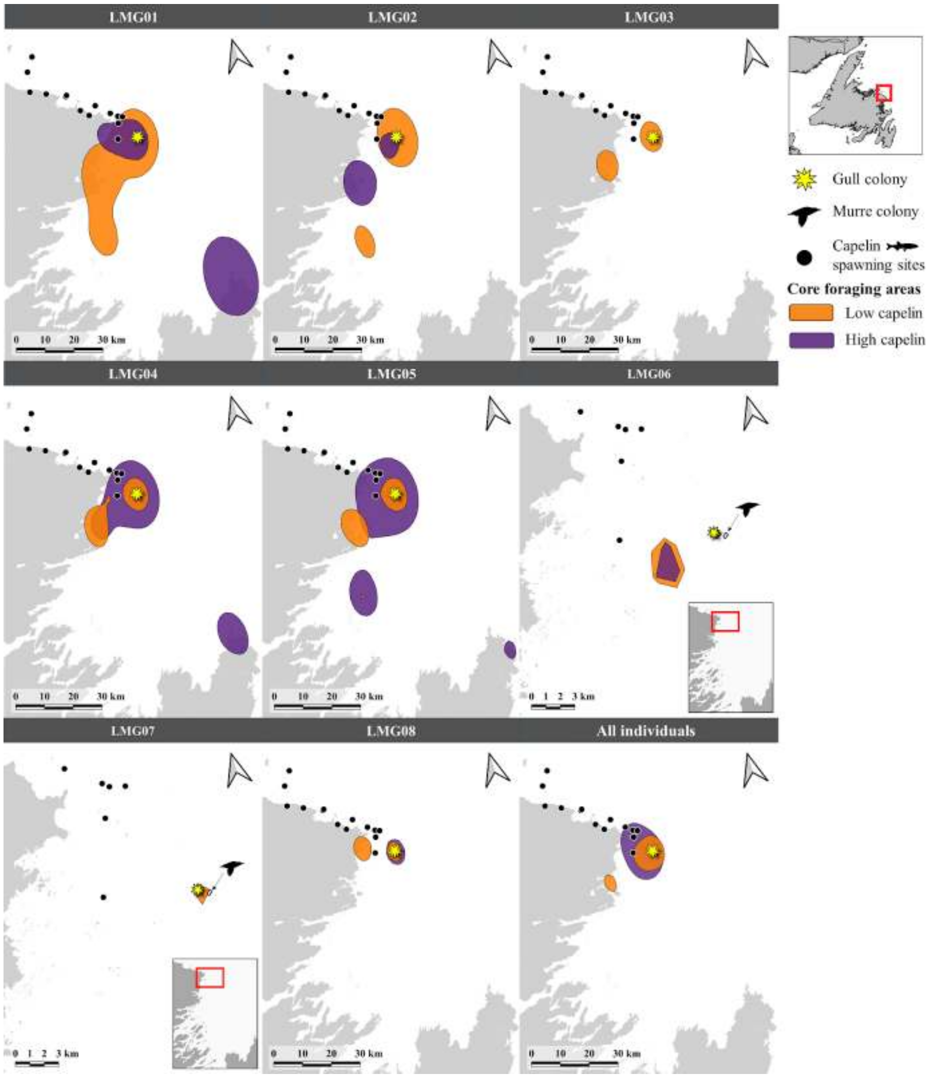


Figure 13.6: Differences in space use of individual great black-backed gulls (*Larus marinus*) foraging on capelin (*Mallotus villosus)*, a small schooling fish species, in Newfoundland, Canada. Individuals vary not only in the average size and location of their foraging areas, but also in how much they shift these areas from high food availability (High capelin; purple) to low food

availability (Low capeline; orange). Murre (*Uria aalge*) are another species of seabird that breed in this region and consume capelin.

The concept of intraspecific variation in diet is closely related to the concept of **generalist** versus **specialist** populations. In a **specialist population**, all individuals use similar resources and a narrow range of resources. **Generalist populations** use a wide range of resources, but this can be due to 1) individuals in the population all using a wide range of resources (true generalists) or 2) individuals in the population specializing on different resources, so that the overall population niche is wide but individual niches are not (generalist-specialists). In Figure 13.2, for example, the generalist population is made up of specialists. More information on these concepts can be found in the Behavioral Ecology chapter, and specifically in the sections on Foraging Ecology and Movement Ecology.

Individual variation in diet is often studied using stable isotope analysis. Stable isotope analysis of diet is based on the idea that "you are what you eat". In other words, your elemental composition is determined by that of what you consume. All biologically active elements exist in a number of different isotopic forms, of which two or more are stable. For example, most carbon is present as ^{12}C, with approximately 1% being ^{13}C. The ratio of the two isotopes may be altered by biological and geophysical processes, and these differences can be used in a number of ways by ecologists. The main elements used in diet studies are carbon and nitrogen (Michener and Lajtha 2007).

Carbon-13

Carbon isotopes aid us in determining the primary production source responsible for the energy flow in an ecosystem. The transfer of ^{13}C through trophic levels remains relatively the same, except for a small increase (an enrichment < 1 ‰). Large differences of δ^{13}C between animals indicate that they have different food sources or that their food webs are based on different primary producers (i.e. different species of phytoplankton, marsh grasses.) Because δ^{13}C indicates the original source of primary producers, the isotopes can also help us determine shifts in diets, both short term, long term or permanent. These shifts may even correlate to seasonal changes, reflecting phytoplankton abundance (Michener and Kaufman 2007). Scientists have found that there can be wide ranges of δ^{13}C values in phytoplankton populations over a geographic region. While it is not quite certain as to why this may be, there are several hypotheses for this occurrence. These include isotopes within dissolved inorganic carbon pools (DIC) may vary with temperature and location and that growth rates of phytoplankton may affect their uptake of the isotopes.

Nitrogen-15

Nitrogen isotopes indicate the trophic level position of organisms (reflective of the time the tissue samples were taken). There is a larger enrichment component with δ^{15}N because its retention is higher than that of ^{14}N. This can be seen by analyzing the waste of organisms (Michener and Kaufman 2007). Cattle urine has shown that there is a depletion of ^{15}N relative to the diet (Kelly et al. 2002). As organisms eat each other, the ^{15}N isotopes are transferred to the predators. Thus, organisms higher in the trophic pyramid have accumulated higher levels of ^{15}N (and higher δ^{15}N values) relative to their prey and others before them in the food web. Numerous studies on marine ecosystems have shown that on average there is a 3.2‰ enrichment of ^{15}N vs. diet between different trophic level species in ecosystems (Michener and Kaufman 2007). In the Baltic sea, Hansson et al. (1997) found that when analyzing a variety of creatures (such as particulate organic matter (phytoplankton), zooplankton, mysids, sprat, smelt and herring,) there was an apparent fractionation of 2.4‰ between consumers and their apparent prey (Doucett et al. 2007).

In addition to comparing signatures across individuals, stable isotopes can be used to examine phenotypic plasticity because different tissue types (fur, blood, muscle) have different turnover rates and therefore reflect the diet of individuals across different timescales (Figure 13.7). Therefore, if multiple tissue types are collected from an individual, the diet of that individual can be examined over multiple temporal scales to determine how much variation there is within the individual's diet (i.e., how flexible their diet is).

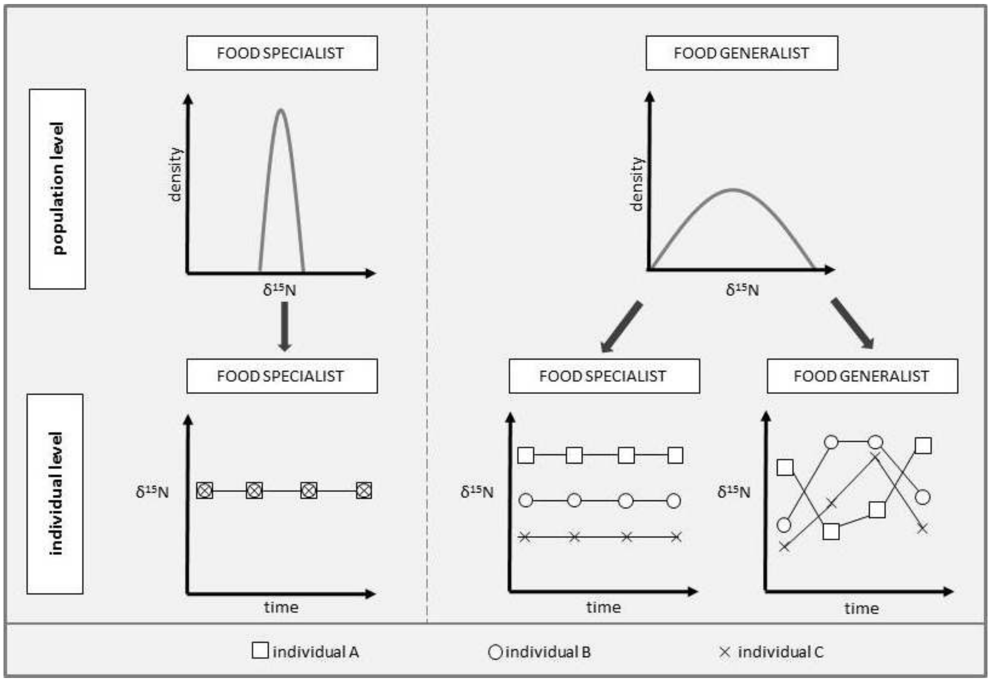


Figure 13.7: Conceptual diagram of how individuals can contribute to the population's dietary niche. Specialized populations consist of specialized individuals which all consume certain resources (left). Therefore, their total dietary niche represents a small dietary variation within and between individuals. In contrast, generalistic populations can consist either of specialized or generalistic individuals (right). In this case, specialized individuals show small dietary variation within individuals, but a large dietary variation between individuals leads to a broad overall resource spectrum and dietary variation at the population level. If individuals of a generalistic population forage generalistic then those are characterized by a large within-individual dietary variation (credit: Scholz et al. 2020).

Quantifying Intraspecific Variation

Whether using isotope data or another continuous indicator of resources use (e.g., seed size; Figure 13.2 and Figure 13.8), intraspecific variation can be quantified by comparing the average width of the individual niche (WIC - within individual component of niche variation) to the total niche width (TNW). The total niche width is equal to the WIC plus the BIC, or the between-individual component of niche variation (Bolnick et al. 2003). When BIC/TNW is relatively high, there is high intraspecific variation (i.e., individuals have consistent dietary preferences but these preferences vary across individuals) and the population is a specialist-generalist population (Figure 13.8A). When WIC/TNW is relatively high, all individuals show considerable variation in diet but have highly overlapping niches and the population is a true population of generalists (Figure 13.8B).

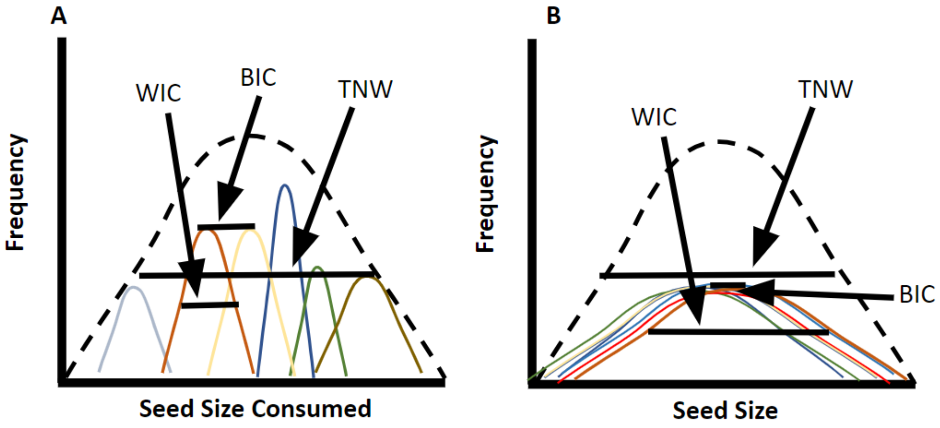


Figure 13.8: An example of intraspecific variation in a species of finch consuming seeds. Figure 13.8A shows a generalist population of specialists. While the range of seed sizes consumed by the population is large, individuals within the population each only consume a small range of seed sizes. Therefore, the within-individual component of variation (WIC) is a small proportion of the total niche width (TNW) and intraspecific variation is high. Figure 13.8B shows a generalist population of generalists. Since all individuals within this population consume a wide range of seed sizes, the WIC is high and intraspecific variation is low.

✓ Case Study 13.1

Intraspecific Variation in the Diet of Red Foxes

Some carnivores are known to survive well in urban habitats, yet the underlying behavioral tactics are poorly understood. One likely explanation for the success in urban habitats might be that carnivores are generalist consumers. However, urban populations of carnivores could as well consist of specialist feeders.

Scholz et al. (2020) compared the isotopic specialization of red foxes in urban and rural environments, using both a population and an individual level perspective. They measured stable isotope ratios in increments of red fox whiskers and potential food sources. Their results reveal that red foxes have a broad isotopic dietary niche and a large variation in resource use (Figure 13.9).

Despite this large variation, they found significant differences between the variance of the urban and rural population for $\delta^{13}C$ as well as $\delta^{15}N$ values, suggesting a habitat-specific foraging behavior. Although urban regions have more heterogeneous land cover than rural regions, the dietary range of urban foxes was smaller compared with that of rural conspecifics. Moreover, the higher $\delta^{13}C$ values and lower $\delta^{15}N$ values of urban foxes suggest a relatively high input of anthropogenic food sources.

The diet of most individuals remained largely constant over a longer period. The low intraindividual variability of urban and rural red foxes suggests a relatively constant proportion of food items consumed by individuals. Urban and rural foxes utilized a small proportion of the potentially available isotopic dietary niche as indicated by the low within-individual variation compared to the between-individual variation. Scholz et al. (2020) conclude that generalist fox populations consist of individual food specialists in urban and rural populations.

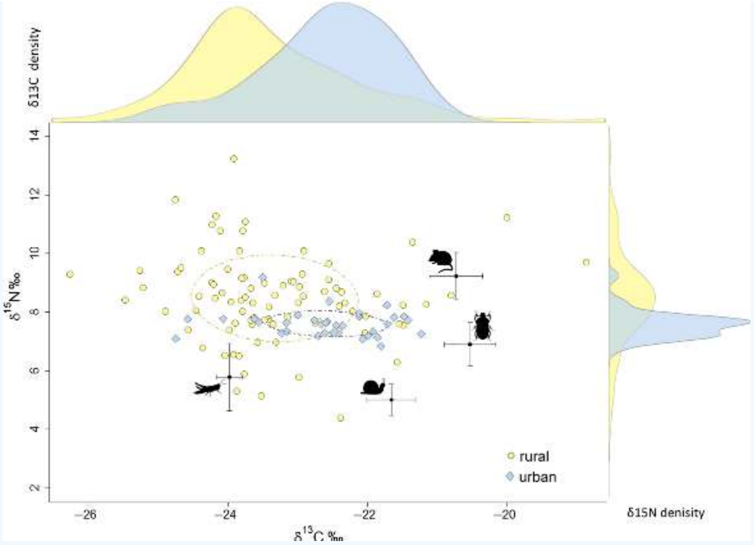


Figure 13.9: Isospace and density plot for raw $\delta^{13}C$ and $\delta^{15}N$ values of urban (blue diamonds) and rural (yellow circles) red foxes whisker samples ($n = 119$) from Berlin and Brandenburg, Germany. Dashed ellipses represent SEAc of the urban (blue) and rural (yellow) fox population. Black dots show trophic corrected mean (±SE bars) $\delta^{13}C$ and $\delta^{15}N$ values for the four prey taxa including (1) grasshopper, (2) land slug, land snail, earthworm (pooled together), (3) dor beetle, and (4) house mouse. Taken from Scholz et al. 2020.

Summary

While ecological studies sometimes focus on variation among species (interspecific variation) there is often substantial variation in the traits and behaviors of individuals within a species (intraspecific variation). Individuals might vary in their mean phenotype and in how much their phenotype responds to changes in their environment (phenotypic plasticity). Two key fields of research into intraspecific variation include animal personality, variation in the behavior of individuals within a species, and individual specialization, variation in the diet of individuals within a species.

References

Bell, A.M., Hankison, S.J., & Laskowski, K.L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour, 77*(4), pp. 771–783. doi:10.1016/j.anbehav.2008.12.022. PMC 3972767. PMID 24707058.

Bijlsma R., & Loeschcke, V. (2012). Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications, 5*, pp. 117–129.

Biro, P.A., & Stamps, J.A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution, 23*(7), pp. 361–368. doi:10.1016/j.tree.2008.04.003. PMID 18501468.

Biro, P.A., & Stamps, J.A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Animal Behaviour, 105*, pp. 223–230. doi:10.1016/j.anbehav.2015.04.008. S2CID 53203738.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., & Vasseur, D. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution, 26*, pp. 183–192.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., & Forister, M.L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist, 161*(1), pp. 1-28.

Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology, 57*(4), pp. 491–498. doi:10.1093/czoolo/57.4.491.

Charette, C., & Derry, A.M. (2016). Climate alters intraspecific variation in copepod effect traits through pond food webs. *Ecology, 97*, pp. 1239–1250.

Cripps, G., Lindeque, P., & Flynn, K.J. (2014). Have we been underestimating the effects of ocean acidification in zooplankton? *Global Change Biology, 20*, pp. 3377–3385.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., & Sanders, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science, 313*, pp. 966–968.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., Schweitzer, J.A., & Palkovacs, E.P. (2017). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*, pp. 57–64.

Doucett, R.R., Marks, J.C., Blinn, D.W., Caron, M., & Hungate, B.A. (2007). Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. *Ecology, 88*(6), pp. 1587–1592. doi:10.1890/06-1184. PMID 17601150.

Engås, A., Løkkeborg, S., Ona, E., & Soldal, A.V. (1996). Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Canadian Journal of Fisheries and Aquatic Sciences, 53*, pp. 2238–2249.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., et al. (2015). Scaling from traits to ecosystems: Developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research, 52*, pp. 249–318. doi:10.1016/bs.aecr.2015.02.001.

Gosling, S.D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin, 127*(1), pp. 45–86. doi:10.1037/0033-2909.127.1.45. PMID 11271756.

Gosling, S. (2008). Personality in non-human animals. *Social and Personality Psychology Compass, 2*(2), pp. 985–1001. doi:10.1111/J.1751-9004.2008.00087.X. S2CID 43114990.

Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science, 17*, pp. 255–260. doi:10.1111/j.1654-1103.2006.tb02444.x1.

Grinsted, L., & Bacon, J.P. (2014). Animal behaviour: Task differentiation by personality in spider groups. *Current Biology, 24*(16), R749–R751. doi:10.1016/j.cub.2014.07.008. PMID 25137587.

Höglund, E., Gjøen, H., Pottinger, T.G., & Øverli, Ø. (2008). Parental stress-coping styles affect the behaviour of rainbow trout Oncorhynchus mykiss at early developmental stages. *Journal of Fish Biology, 73*, pp. 1764–1769.

Hunt, E.R., et al. (2018). Social interactions shape individual and collective personality in social spiders. *Proceedings of the Royal Society B, 285*(1886), 20181366. doi:10.1098/rspb.2018.1366. PMC 6158534. PMID 30185649.

International Aphid Genomics Consortium (2010). In Eisen, J.A. (Eds.), Genome sequence of the pea aphid *Acyrthosiphon pisum*. *PLOS Biology, 8*(2), e1000313. doi:10.1371/journal.pbio.1000313. PMC 2826372. PMID 20186266.

Keddy, P.A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science, 3*, pp. 157–164. doi:10.2307/3235676.

Kelly, J.F., Atudorei, V., Sharp, Z.D., & Finch, D.M. (2002). Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia, 130*(2), pp. 216–221. doi:10.1007/s004420100789. PMID 28547144. S2CID 23355570.

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: Why bother? *Animal Behaviour, 91*, pp. 41–52. doi:10.1016/j.anbehav.2014.02.016. S2CID 53171945.

Lajoie, G., & Vellend, M. (2018). Characterizing the contribution of plasticity and genetic differentiation to community-level trait responses to environmental change. *Ecology and Evolution, 8*, pp. 3895–3907. doi:10.1002/ece3.3947.

Leclerc, M., Wal, E.V., Zedrosser, A., Swenson, J.E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia, 180*(3), pp. 697–705. doi:10.1007/s00442-015-3500-6. PMID 26597548.

Levins, R. (1968). Evolution in changing environments: Some theoretical explorations. *Princeton, NJ: Princeton University Press.*

Medina, M.H., Correa, J.A., & Barata, C. (2007). Micro-evolution due to pollution: Possible consequences for ecosystem responses to toxic stress. *Chemosphere, 67*, pp. 2105–2114.

Michener, R.H., & Kaufman, L. (2007). Stable isotope ratios as tracers in marine food webs: An Update. In: *Stable isotopes in ecology and environmental science*, pp. 238–82. doi:10.1002/9780470691854.ch9. ISBN 978-0-470-69185-4.

Michener, R., & Lajtha, K., eds. (2007-10-08). Stable isotopes in ecology and environmental science (2nd ed.). Blackwell Pub. pp. 4–5. ISBN 978-1-4051-2680-9.

Mitchell, R.M., Wright, J.P., & Ames, G.M. (2018). Species' traits do not converge on optimum values in preferred habitats. *Oecologia, 186*, pp. 719–729. doi:10.1007/s00442-017-4041-y.

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B, 283*, 20152434. doi:10.1098/rspb.2015.2434.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., et al. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science, 15*, pp. 684–692. doi:10.1016/j.tplants.2010.09.008.

Norberg, J.J., Swaney, D.P., Dushoff, J.J., Lin, J.J., Casagrandi, R.R., & Levin, S.A. (2001). Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 11376–11381. doi:10.1073/pnas.171315998.

Pacala, S., & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist, 143*, pp. 222–257. doi:10.1086/285602.

Pigliucci, M. (2001). Phenotypic plasticity: Beyond nature and nurture. *JHU Press*.

Post, D.M., Palkovacs, E.P., Schielke, E.G., & Dodson, S.I. (2008). Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology, 89*, pp. 2019–2032.

Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: A meta-analysis. *Biological Reviews, 94*, pp. 648–661.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*(2), pp. 291–318. doi:10.1111/j.1469-185x.2007.00010.x.

Rudman, S.M., Rodriguez-Cabal, M.A., Stier, A., Sato, T., Heavyside, J., El-Sabaawi, R.W., & Crutsinger, G.M. (2015). Adaptive genetic variation mediates bottom-up and top-down control in an aquatic ecosystem. *Proceedings of the Royal Society B, 282*, 20151234.

Schlichting, C.D. (1986). The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics, 17*, pp. 667–93. doi:10.1146/annurev.es.17.110186.003315.

Siefert, A., & Ritchie, M.E. (2016). Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia, 181*, pp. 245–255.

Stamps, J., & Groothuis, T.G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews, 85*(2), pp. 301–325. doi:10.1111/j.1469-185x.2009.00103.x.

Stearns, S.C. (1989). The evolutionary significance of phenotypic plasticity. *Bioscience, 39*(7), pp. 436-445.

Toscano, B.J., Gownaris, N.J., Heerhartz, S.M., & Monaco, C.J. (2016). Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. *Oecologia, 182*(1), pp. 55-69.

Valladares, F., Gianoli, E., & Gómez, J.M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist, 176*, pp. 749–763.

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D., & Van Tienderen, P.H. (1995). Adaptive phenotypic plasticity: Consensus and controversy. *Trends in Ecology & Evolution, 10*(5), pp. 212-217.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., et al. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution, 27*, pp. 244–252.

Weiher, E., & Keddy, P. (1999). Assembly rules as general constraints on community composition. In *Ecological assembly rules: Perspectives, advances, retreats*, pp. 251–271. doi:10.1017/CBO9780511542237.010.

Whittaker, R. (1972). Evolution and measurement of species diversity. *Taxon*, *21*, pp. 213–251.

Wolf, M., & Weissing, F.J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), pp. 452–461. doi:10.1016/j.tree.2012.05.001. PMID 22727728.

Contributors and Attributions

This chapter was written by N. Gownaris (Gettysburg College) and D. Wetzel (University of Pittsburgh) with text taken from the following CC-BY resources:

- **Isotope analysis by Wikipedia, the free encyclopedia**
- **Phenotypic plasticity by Wikipedia, the free encyclopedia**
- **Personality in Animal by Wikipedia, the free encyclopedia**
- Harding, H. R., Gordon, T. A., Eastcott, E., Simpson, S. D., & Radford, A. N. (2019). Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. *Behavioral Ecology*, *30*(6), 1501-1511. **https://doi.org/10.1093/beheco/arz114**
- Henn, J. J., Buzzard, V., Enquist, B. J., Halbritter, A. H., Klanderud, K., Maitner, B. S., ... & Vandvik, V. (2018). Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, *9*, 1548. **https://doi.org/10.3389/fpls.2018.01548**
- Scholz, C., Firozpoor, J., Kramer-Schadt, S., Gras, P., Schulze, C., Kimmig, S. E., ... & Ortmann, S. (2020). Individual dietary specialization in a generalist predator: A stable isotope analysis of urban and rural red foxes. *Ecology and Evolution*, *10*(16), 8855-8870. **https://doi.org/10.1002/ece3.6584**

CHAPTER OVERVIEW

14: Introduction to Species Interactions

Learning Objectives

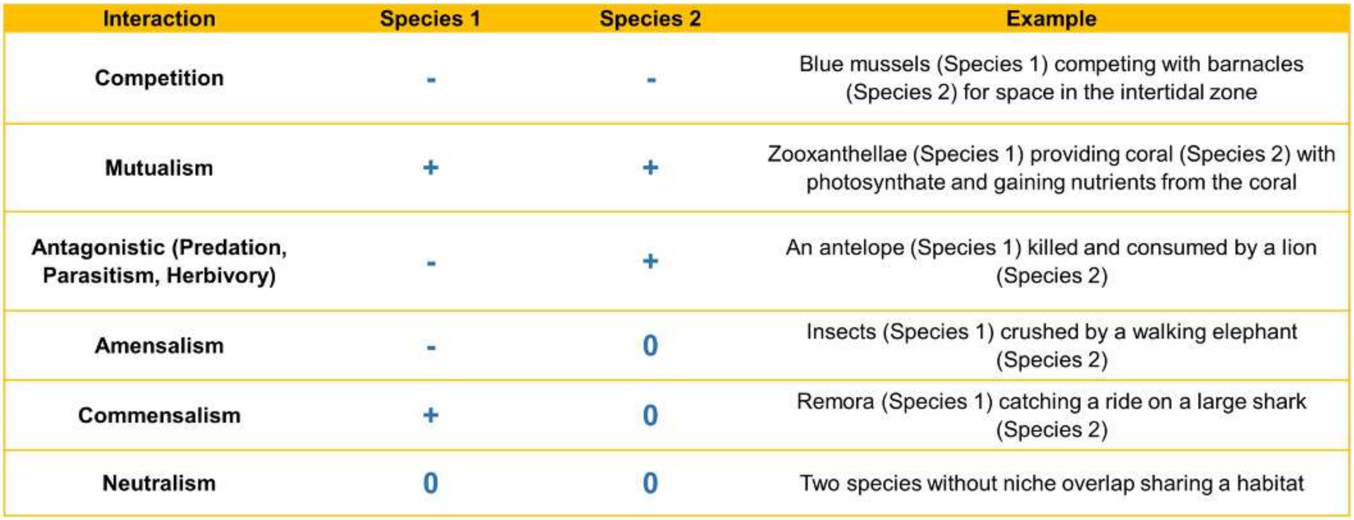
- Develop an appreciation of the interconnected nature of ecological communities
- Organize species interactions based on their impacts on the species involved
- Understand some of the factors that structure ecological communities

Introduction to Species Interactions

Populations rarely, if ever, live in isolation from populations of other species. All populations occupying the same habitat form a **community** (populations of multiple species inhabiting a specific area at the same time). The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

The interactions among populations of different species play a major role in regulating population growth and abundance. A **species interaction** is the effect that a pair of organisms living together in a community have on each other. Interactions range from mutualism, which benefits both species involved, to competition, which harms both species involved (Wootton and Emmerson 2005). Interactions can be indirect, through intermediaries such as shared resources or common enemies. All of these interactions can be organized by the effects the species have on each other (Figure 14.1).

Species interactions may be short-term, like pollination and predation, or long-term; both often strongly influence the evolution of the species involved. Short-term interactions are short-lived in terms of the duration of a single interaction: a predator kills and eats a prey; a pollinator transfers pollen from one flower to another; but they are extremely durable in terms of their influence on the evolution of both partners. As a result, the partners coevolve (Bengtson 2002, Lunau 2004).



Interaction	Species 1	Species 2	Example
Competition	-	-	Blue mussels (Species 1) competing with barnacles (Species 2) for space in the intertidal zone
Mutualism	+	+	Zooxanthellae (Species 1) providing coral (Species 2) with photosynthate and gaining nutrients from the coral
Antagonistic (Predation, Parasitism, Herbivory)	-	+	An antelope (Species 1) killed and consumed by a lion (Species 2)
Amensalism	-	0	Insects (Species 1) crushed by a walking elephant (Species 2)
Commensalism	+	0	Remora (Species 1) catching a ride on a large shark (Species 2)
Neutralism	0	0	Two species without niche overlap sharing a habitat

Figure 14.1: Summary of species interactions, showing how each species is impacted by the interaction. Produced by N. Gownaris.

Figure 14.2: The black walnut secretes a chemical from its roots that harms neighboring plants, an example of competitive antagonism.

Figure 14.3: Predation is a short-term interaction, in which the predator, here an osprey, kills and eats its prey.

Competition

Competition can be defined as an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Competition is often for a resource such as food, water, or territory in limited supply, or for access to females for reproduction (Begon et al. 1996). Competition among members of the same species is known as **intraspecific competition**, while competition between individuals of different species is known as **interspecific competition**.

According to the **competitive exclusion principle**, no two species with the same ecological niche can coexist, and the species less suited to compete for resources should either adapt or die out (Hardin 1960; Pocheville 2015). Competition within and between species for resources plays a critical role in natural selection (Sahney et al. 2010). Ecologists model competition using the Lotka-Volterra competition model, and use this model to predict the conditions under which two species will coexist or one species outcompetes the other. These models will be covered in more detail in the chapter on Competition.

Figure 14.4: Direct intraspecific competition for mates between two male red deer.

Mutualism

A mutualism is an interaction between two or more species, where both species derive a mutual benefit. One or both species involved in the interaction may be obligate, meaning they cannot survive in the short or long term without the other species (**obligate mutualism**). In other cases, though both species benefit, they may not need the mutualistic interaction to survive (**facultative mutualism**). Though mutualism has historically received less attention than other interactions such as predation (Begon et al. 1996), it is an ecologically important interaction.

Figure 14.5: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Examples of Mutualism: Pollination and Seed Dispersal

Figure 14.6: Hummingbird hawkmoth drinking from *Dianthus*.

In pollination, pollinators including insects (**entomophily**), some birds (**ornithophily**), and some bats, transfer pollen from a male flower part to a female flower part, enabling fertilization, in return for a reward of pollen or nectar (CropsReview.Com 2015). Plants and pollinators are often coevolved (Ehrlich and Raven 1964; Pollan 2001; Lunau 2004). Insect-pollinated flowers have bright colors, patterns, scent, nectar, and sticky pollen to attract insects, guide them to pick up and deposit pollen, and reward pollinators. Conversely, pollinator insects like bees are adapted to detect flowers by color, pattern, and scent, to collect pollen (such as with bristles shaped to form pollen baskets on their hind legs), and nectar.

Seed dispersal is the movement, spread or transport of seeds. Plants have limited mobility and rely upon a variety of dispersal vectors to transport their propagules, including both abiotic vectors such as the wind and living (biotic) vectors like birds (Lim ad Burns 2021) patterns of seed dispersal are determined in large part by the dispersal mechanism and this has important implications for the demographic and genetic structure of plant populations, as well as migration patterns and species interactions. There are five main modes of seed dispersal: gravity, wind, ballistic, water, and animals.

Antagonistic Interactions

Predation

In predation, one organism, the predator, kills and eats another organism, its prey. Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency. Predation has a powerful selective effect on prey, causing them to develop antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage and defensive spines and chemicals (Royal Saskatchewan Museum 2012, Bar-Yam 2018, Vermeij 1993). Predation has been a major driver of evolution since at least the Cambrian period (Bengston 2002). Predators control the population dynamics of their prey and vice versa and ecologists model these dynamics using coupled equations known as the Lotka-Volterra predator-prey model. These models will be covered in more detail in the chapter on Antagonistic Interactions.

Figure 14.7: The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen).

Herbivory

Herbivory is a form of consumption in which an organism principally eats autotrophs such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs in general are known as **primary consumers**. Herbivory is usually limited to animals that eat plants. Insect herbivory can cause a variety of physical and metabolic alterations in the way the host plant interacts with itself and other surrounding biotic factors (Cannicci et al. 2008; Peschiutta et al. 2018).

Parasitism

Parasitism is a relationship between species, where one organism, the parasite, lives on or in another organism, the host, causing it some harm, and is adapted structurally to this way of life (Poulin 2007). The parasite either feeds on the host, or, in the case of intestinal parasites, consumes some of its food (Martin and Schwab 2013). Not all parasites kill their hosts, but some do. **Parasitoids** are parasites that lay their eggs within a host. The larvae of parasitoids eventually hatch out of the host's body, killing the host.

Other Types of Interactions

Amensalism

Amensalism (a term introduced by Haskell; Toepfer) is an interaction where an organism inflicts harm to another organism without any costs or benefits received by itself (Willey et al. 2013). Amensalism describes the adverse effect that one organism has on another organism. A classic example of amensalism is where sheep or cattle trample grass. Whilst the presence of the grass causes negligible detrimental effects to the animal's hoof, the grass suffers from being crushed.

Amensalism is often used to describe strongly asymmetrical competitive interactions, such as has been observed between the Spanish ibex and weevils of the genus *Timarcha* which feed upon the same type of shrub. Whilst the presence of the weevil has almost no influence on food availability, the presence of ibex has an enormous detrimental effect on weevil numbers, as they consume significant quantities of plant matter and incidentally ingest the weevils upon it (Gómez and González-Megías 2002).

Commensalism

Commensalism benefits one organism while the other organism neither benefits nor is harmed. A good example is a remora living with a manatee. Remoras feed on the manatee's feces, and therefore benefits from this interaction. The manatee is not affected by this interaction, as the remora does not deplete the manatee's resources (Williams and Williams 2003).

Figure 14.8: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed (credit: “Hanay”/Wikimedia Commons).

Overview of Community Structure and Dynamics

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef. Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

Figure 14.9: Coral is the foundation species of coral reef ecosystems (credit: Jim E. Maragos, USFWS).

✓ Case Study: Non-Trophic Interactions and Foundation Species 14.5

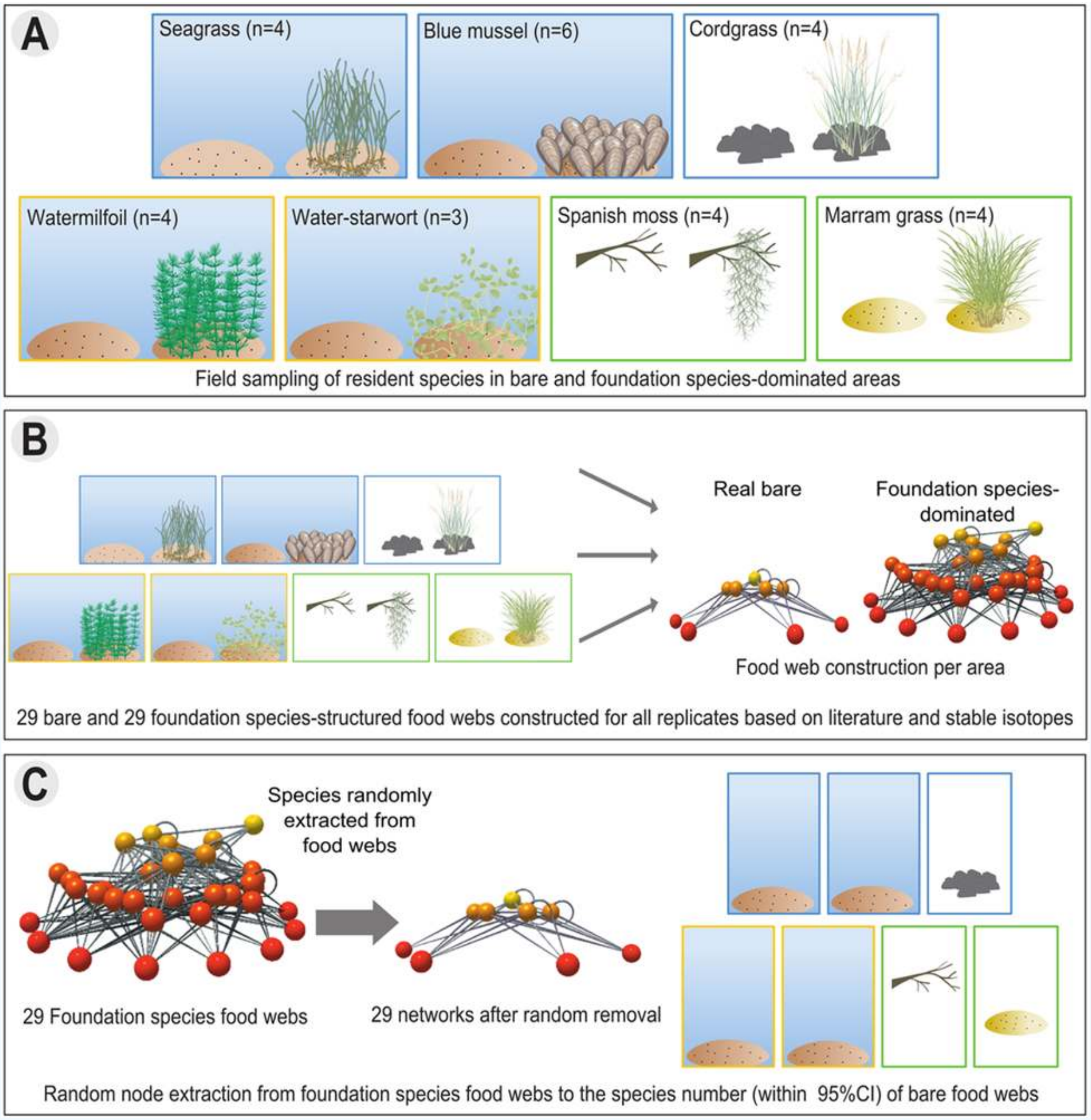


Figure 14.10: Foundational species increase food web complexity by facilitating species higher in the food chain. (A) Seven ecosystems with foundation species were sampled: coastal (seagrass, blue mussel, cordgrass), freshwater (watermilfoil, water-starwort) and terrestrial (Spanish moss, marram grass). (B) Food webs were constructed for both bare and foundation species-dominated replicate areas. (C) From each foundation species structured-food web, nodes (species) were randomly removed until the species number matched the species number of the bare food webs.

Although we often focus on trophic (food-related) interactions among species, there is growing evidence that non-trophic interactions can indirectly affect food web topology and trophic dynamics by affecting the species in the network and the strength of trophic links (Sanders et al. 2014; Kefi et al. 2015; van der Zee et al. 2016). Some examples of non-trophic interactions are habitat modification and competition for space.

Foundation species are spatially dominant habitat-structuring organisms (Dayton 1972; Governar 2010; Angelini et al. 2011). Although foundation species are part of the food web like any other species (e.g. as prey or predator), numerous studies have shown that they strongly facilitate the associated community by creating new habitat and alleviating physical stress (Bertness et al. 1999; Jones et al. 2010; Reid and Lortie 2012; Angelini and Silliman 2014; Kefi et al. 2015; van der Zee EM et al. 2015; van der Zee et al. 2016; Filazzola et al. 2017). This form of non-trophic facilitation by foundation species has been found to occur across a wide range of ecosystems and environmental conditions (Bertness and Callaway 1994; Bruno et al. 2003). In harsh coastal zones, corals, kelps, mussels, oysters, seagrasses, mangroves, and salt marsh plants facilitate organisms by attenuating currents and waves, providing aboveground structure for shelter and attachment, concentrating nutrients, and/or reducing desiccation stress during low tide exposure (Bertness and Callaway 1992; Angelini et al. 2011). In more benign systems, foundation species such as the trees in a forest, shrubs and grasses in savannahs, and macrophytes in freshwater systems, have also been found to play a major habitat-structuring role (Jeppesen et al. 1992; Bertness and Callaway 1994; Bruno et al. 2003; Ellison et al. 2005). Ultimately, all foundation species increase habitat complexity and availability, thereby partitioning and enhancing the niche space available to other species (Bruno et al. 2003; Bulleri et al. 2016; Borst et al. 2018).

Borst et al. (2018) tested the general hypothesis that foundation species modify food webs by enhancing their size as indicated by species number, and their complexity as indicated by link density, via facilitation of species, regardless of ecosystem type (Figure 14.6). Additionally, Borst et al. 2018 examined whether any change in food web properties caused by foundation species occurs via random facilitation of species throughout the entire food web or via targeted facilitation of specific species that belong to certain trophic levels or functional groups. They found that species at the base of the food web are less strongly facilitated, and carnivores are more strongly facilitated, in foundation species' food webs than predicted based on random facilitation, resulting in a higher mean trophic level and a longer average chain length. This indicates foundation species strongly enhance food web complexity through non-trophic facilitation of species across the entire trophic network (Borst et al. 2018).

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species. Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.

Figure 14.11: The *Pisaster ochraceus* sea star is a keystone species (credit: Jerry Kirkhart).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Figure 14.12: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species (credit: Forest and Kim Starr).

✓ Everyday Connection: Invasive Species 14.5

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 14.13 below. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

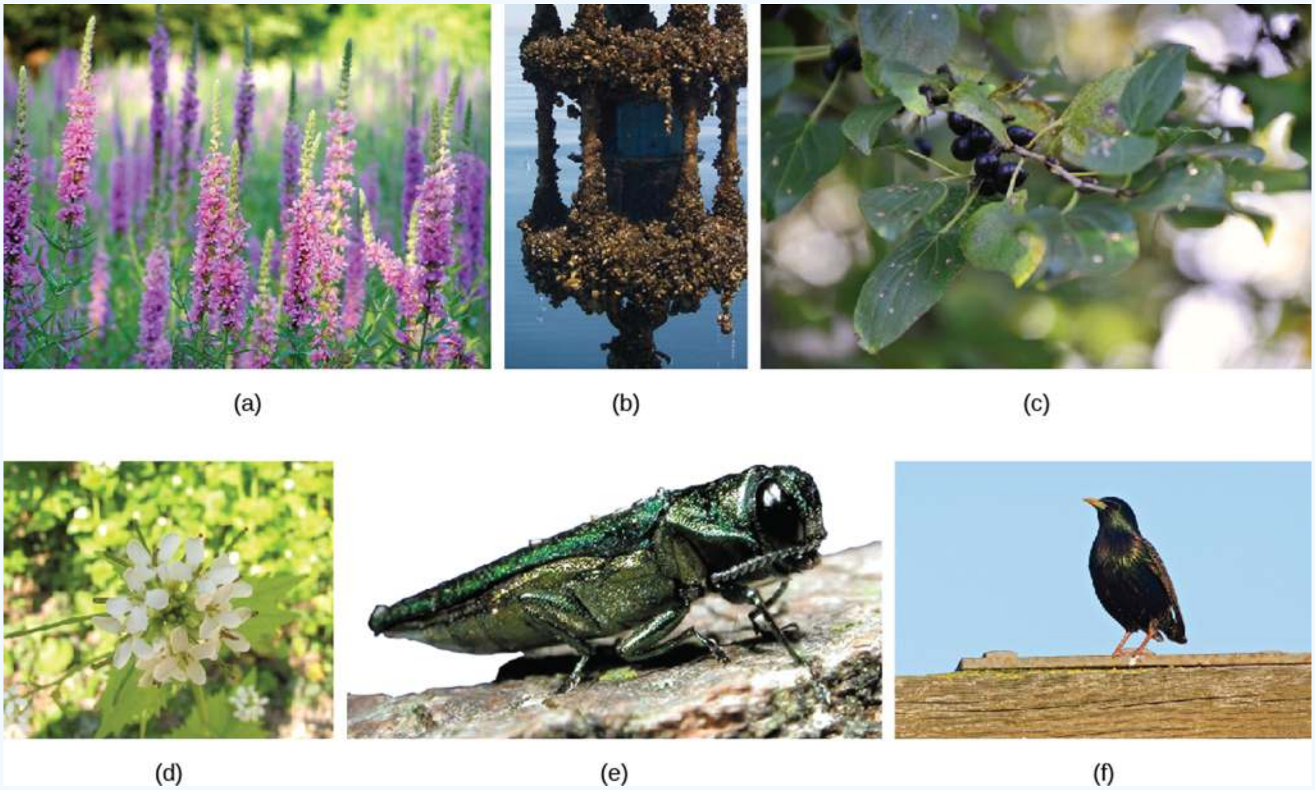


Figure 14.13: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Summary

Populations of species do not exist in isolation – they exist in the context of coevolved ecological communities. Species interactions can harm both species involved (competition), benefit both involved (mutualism), or benefit one and harm the other (predation, parasitism, herbivory). These interactions play a key role in evolution (e.g., prey evolve to avoid detection by predators) and in structuring ecological communities (e.g., loss of top predators can lead to drastic reductions in biodiversity). While some of these interactions involved trophic relationships, others, such as habitat-formation by foundation species, do not.

References

Predator & prey: Adaptations. (2012). Royal Saskatchewan Museum. Archived from the original (PDF) on 3 April 2018. Retrieved 19 April 2018.

"Types of Pollination, Pollinators and Terminology". CropsReview.Com. Retrieved 2015-10-20.

Angelini, C., Altieri, A.H., Silliman, B.R., & Bertness, M.D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience, 61*(10), pp. 782–9.

Angelini, C., & Silliman, B.R. (2014). Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree epiphyte system. *Ecology, 95*(1), pp. 185–96. pmid:24649658

Bar-Yam. Predator-prey relationships. *New England Complex Systems Institute*. Retrieved 7 September 2018.

Begon, M., Harper, J.L., & Townsend, C.R. (1996). Ecology: Individuals, populations, and communities, Third Edition. *Blackwell Science Ltd., Cambridge, Massachusetts, USA.*

Bengtson, S. (2002). Origins and early evolution of predation. In Kowalewski, M., & Kelley, P.H. (eds.). The fossil record of predation. The Paleontological Society Papers 8. The Paleontological Society. pp. 289–317.

Bertness, M.D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution, 9*(5), pp. 191–3.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., & Ingraham, A.O. (1999). Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology, 80*(8), pp. 2711–26.

Borst, A.C., Verberk, W.C., Angelini, C., Schotanus, J., Wolters, J.W., Christianen, M.J., van der Zee, E.M., Derksen-Hooijberg, M., & van der Heide, T. (2018). Foundation species enhance food web complexity through non-trophic facilitation. *PLOS ONE, 13*(8): e0199152. doi:10.1371/journal.pone.0199152. Material was copied from this source, which is available under a Creative Commons Attribution 4.0 International License.

Bruno, J.F., Stachowicz, J.J., & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution, 18*(3), pp. 119–25.

Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology, 30*(1), pp. 70–8.

Cannicci, S., Burrows, D., Fratini, S., Smith, T.J., Offenberg, J., & Dahdouh-Guebas, D. (2008). Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review. Mangrove Ecology – Applications in Forestry and Costal Zone Management. *Aquatic Botany, 89*(2), pp. 186–200.

Dayton, P.K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In Parker, B. (Eds.), *Proceedings of the colloquium on conservation problems in Antarctica*. Lawrence, Kansas: Allen Press.

Ehrlich, P.R., & Raven, P.H. (1964). Butterflies and plants: A study in coevolution. *Evolution 18*(4), pp. 586–608. doi:10.2307/2406212. JSTOR 2406212.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., et al. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment, 3*(9), pp. 479–86.

Filazzola, A., Westphal, M., Powers, M., Liczner, A.R., Woollett, D.A., Johnson, B., et al. (2017). Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species. *Basic and Applied Ecology, 20*, pp. 51–61.

Gómez, J.M., & González-Megías, A. (2002). Asymmetrical interactions between ungulates and phytophagous insects: Being different matters. *Ecology, 83*(1), pp. 203–11. doi:10.1890/0012-9658(2002)083[0203:AIBUAP]2.0.CO;2.

Govenar, B. (2010). Shaping vent and seep communities: Habitat provision and modification by foundation species. In Kiel, S., (Eds.), *The vent and seep biota*. Topics in Geobiology. 33: Springer Netherlands, pp. 403–32.

Hardin, G. (1960). The competitive exclusion principle. *Science, 131*(3409), pp. 1292–1297. Bibcode:1960Sci...131.1292H. doi:10.1126/science.131.3409.1292. PMID 14399717.

Jeppesen, E., Sondergaard, M., Sondergaard, M., & Christofferson, K. (1992). The structuring role of submerged macrophytes in lakes. *New York: Springer.*

Jones, C.G., Gutierrez, J.L., Byers, J.E,. Crooks, J.A., Lambrinos, J.G., & Talley, T.S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*(12), pp. 1862–9.

Kefi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., et al. Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, *96*(1), pp. 291–303. pmid:26236914.

Lim, G., & Burns, K.C. (2021). Do fruit reflectance properties affect avian frugivory in New Zealand? *New Zealand Journal of Botany*, pp. 1–11. doi:10.1080/0028825X.2021.2001664. ISSN 0028-825X. S2CID 244683146.

Lunau, K. (2004). Adaptive radiation and coevolution — pollination biology case studies. *Organisms Diversity & Evolution*, *4*(3), pp. 207–224. doi:10.1016/j.ode.2004.02.002.

Martin, B.D., & Schwab, E. (2013). Current usage of symbiosis and associated terminology. *International Journal of Biology*, *5*(1), pp. 32–45. doi:10.5539/ijb.v5n1p32.

Peschiutta, M.L., Scholz, F.G., Goldstein, G., & Bucci, S.J. (2018). Herbivory alters plant carbon assimilation, patterns of biomass allocation and nitrogen use efficiency. *Acta Oecologica*, *86*, pp. 9–16. doi:10.1016/j.actao.2017.11.007.

Pocheville, A. (2015). The ecological niche: History and recent controversies. In Heams, T., Huneman, P., Lecointre, G., et al. (Eds.). *Handbook of evolutionary thinking in the sciences*. Dordrecht: Springer. pp. 547–586. ISBN 978-94-017-9014-7.

Pollan, M. (2001). The botany of desire: A plant's-eye view of the world. *Bloomsbury*. ISBN 978-0-7475-6300-6.

Poulin, R. (2007). Evolutionary ecology of parasites. *Princeton University Press*, pp. 4–5. ISBN 978-0-691-12085-0.

Reid, A.M., & Lortie, C.J. (2012). Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere*, *3*(11).

Sahney, S., Benton, M.J., & Ferry, P.A. (2010). Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biology Letters*, *6*(4), pp. 544–547. doi:10.1098/rsbl.2009.1024. PMC 2936204. PMID 20106856.

Sanders, D., Jones, C.G., Thébault, E., Bouma, T.J., Heide Tvd, Belzen Jv, et al. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*(5), pp. 513–24.

Toepfer, G. "Amensalism". In: BioConcepts. link.

Van der Zee, E.M., Angelini, C., Govers, L.L., Christianen, M.J.A., Altieri, A.H., van der Reijden, K.J., et al. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proceedings of the Royal Society B-Biological Sciences*, *283*(1826). pmid:26962135.

Van der Zee, E.M., Tielens, E., Holthuijsen, S., Donadi, S., Eriksson, B.K., van der Veer, H.W., et al. (2015). Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem. *Journal of Experimental Marine Biology and Ecology*, *465*, pp. 41–8.

Vermeij, G.J. (1993). Evolution and escalation: An ecological history of life. *Princeton University Press*. pp. 11 and passim. ISBN 978-0-691-00080-0.

Willey, J.M., Sherwood, L.M., & Woolverton, C.J. (2013). Prescott's Microbiology (9th ed.). pp. 713–38. ISBN 978-0-07-751066-4.

Williams, E., Mignucci, W.L., & Bonde. (2003). Echeneid-sirenian associations, with information on sharksucker diet. *Journal of Fish Biology*, *5*(63), pp. 1176–1183. doi:10.1046/j.1095-8649.2003.00236.x. Retrieved 17 June 2020.

Wootton, J.T., & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, *36*, pp. 419–44. doi:10.1146/annurev.ecolsys.36.091704.175535. JSTOR 30033811.

Contributors and Attributions

This chapter was written by N. Gownaris, A. Howard, C. Olmstead, and T. Zallek, with text taken from the following CC-BY resources:

- **45.6: Community Ecology** by OpenStax, is licensed CC BY
- Biological Interaction by Wikipedia, the free encyclopedia
- Herbivore by Wikipedia, the free encyclopedia

14.1: Scientist Spotlight - Anurag Agrawal

During summer 2021, social media users may have noticed a brief spotlight shone on the invasive spotted lanternfly. This beautiful bug feeds on a wide array of lumber/silviculturally valuable trees, and officials have encouraged people to squash them on site. There may be ecological and evolutionary history explaining the spread of the spotted lanternfly in the United States. The story of the viburnum leaf beetle, revealed by ecologist Anurag Agrawal, may shed some light on this phenomenon.

The invasive viburnum leaf beetle has wreaked havoc on species of *Viburnum* shrub in the Northeastern United States by eating their leaves and laying eggs on their twigs. However, this antagonistic relationship did not always mean decimation for species of *Viburnum* shrub. Some *Viburnum* species share evolutionary history with the beetle, and this translates into an astonishing mechanism of plant defense. Anurag Agrawal is an ecologist at Cornell University studying the ecology and evolution of plant-insect interactions. His lab discovered the aforementioned evolutionary defense mechanism- old-world *Viburnum* shrubs crushing beetle eggs. Insect herbivory incites something called an "evolutionary arms race", where the plant evolves defense mechanisms to avoid predation, the insect evolves in response to evolutionary pressure imposed by that defense mechanism, and the race goes back and forth as each party tries to 'out-evolve' the other. This is also called the "red queen hypothesis." In contrast, North American *Viburnum* species did not coevolve with the beetle. While they mount the same defense response as their old-world cousins, it is distinctly weaker. This "convergent continental difference" in defense response is one of many plant-insect interactions Agrawal has studied in relation to evolution.

Dr. Agrawal shared that "In general Asian-Americans are well-represented in STEM, but less so in ecology and evolution." He rarely thinks of himself as under-represented, but "Recognizing this has occasionally brought out an important insight."

"Viburnum leaf beetle" by Eltore Balocchi is licensed under CC BY 2.0. "Anurag Agrawal with Asclepias welshii" by Anuragagrawal99 is licensed under CC BY-SA 4.0.

References

Spotlight inspiration from Project Biodiversify

Project Biodiversify. Anurag Agrawal: Seed-eating moths had dramatic impacts on plant ecology and evolution. <https://projectbiodiversify.org/2019/07/10/anurag-agrawal-2/>. Accessed September 21, 2021.

CHAPTER OVERVIEW

15: Competition

Learning Objectives

- Characterize the various types of competition between individuals, both within (intraspecific) and between (interspecific) species
- Develop an appreciation for the role competition plays in driving evolution
- Determine competitive outcomes using linked population models of two competitors (Lotka-Volterra Model)

Summary

Competition is any interaction in which two individuals need the same limited supply, resulting on a negative impact on both individuals involved. Competition can occur among two individuals of the same species (intraspecific competition) or among two individuals of different species (interspecific competition) and can involve direct interactions (interference or contest competition) or indirect interactions (exploitation or scramble competition). The logistic growth model is a model of intraspecific competition, as the carrying capacity is a result of competition among individuals for limited resources (food, mates, etc.). To model interspecific competition, ecologists modify the logistic growth model to consider the impact of other species on shared resources. The resulting Lotka-Volterra Model can be used to predict competitive outcomes between two species, which include coexistence or competitive exclusion.

15.1: Introduction and Types of Competition

Competition

Competition is an interaction between organisms or species in which both require a resource that is in limited supply (such as food, water, or territory) (Begon et al. 1996). Competition lowers the fitness of both organisms involved, since the presence of one of the organisms always reduces the amount of the resource available to the other (Lang & Benbow 2013).

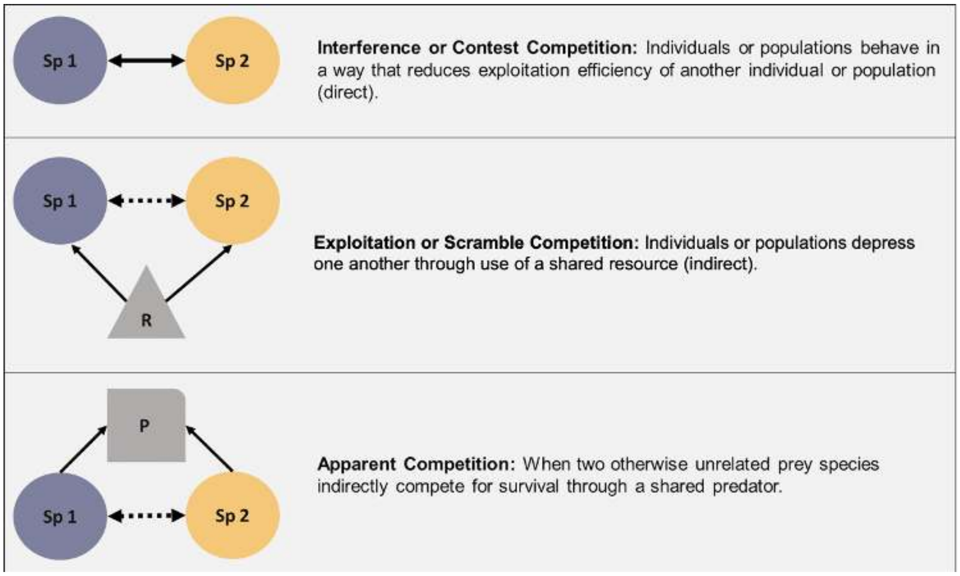
Figure 15.1.1 Sea anemones compete for the territory in tide pools.

In the study of community ecology, competition within and between members of a species is an important biological interaction. Competition is one of many interacting biotic and abiotic factors that affect community structure, species diversity, and population dynamics (shifts in a population over time) (Lang & Benbow 2013). Competition within and between species for resources is important in natural selection.

There are three major mechanisms of competition: interference, exploitation, and apparent competition (in order from most direct to least direct). Interference and exploitation competition can be classed as "real" forms of competition, while apparent competition is not, as organisms do not share a resource, but instead share a predator (Lang & Benbow 2013). Competition among members of the same species is known as **intraspecific competition**, while competition between individuals of different species is known as **interspecific competition**. Diffuse competition refers to the summed effects of all competitors.

Studies show that intraspecific competition can regulate population dynamics (changes in population size over time). This occurs because individuals become crowded as a population grows. Since individuals within a population require the same resources, crowding causes resources to become more limited. Some individuals (typically small juveniles) eventually do not acquire enough resources and die or do not reproduce. This reduces population size and slows population growth. The logistic growth model, which includes a term for the species’ carrying capacity, is a model of intraspecific competition.

Species also interact with other species that require the same resources. Consequently, interspecific competition can alter the sizes of many species' populations at the same time. Experiments demonstrate that when species compete for a limited resource, one species eventually drives the populations of other species extinct. According to the competitive exclusion principle, species less suited to compete for resources must either adapt or die out, although competitive exclusion is rarely found in natural ecosystems (Lang & Benbow 2013). Ecologists use a modified version of coupled logistic growth models for competing species, known as the Lotka-Volterra Competition model, to model interspecific competition.



Interference or Contest Competition: Individuals or populations behave in a way that reduces exploitation efficiency of another individual or population (direct).

Exploitation or Scramble Competition: Individuals or populations depress one another through use of a shared resource (indirect).

Apparent Competition: When two otherwise unrelated prey species indirectly compete for survival through a shared predator.

Figure 15.1.2: The three different mechanisms of competition. Solid arrows indicate direct relationships, dashed lines represent indirect relationships. Developed by N. Gownaris.

15.1 Types of Competition

15.1.1 Interference Competition

Figure 15.1.3: Male-male competition in red deer during rut is an example of interference competition within a species.

During **interference competition**, also called contest competition, organisms of the same species or of two or more different species interact directly by competing for scarce resources. For example, large aphids defend feeding sites on cottonwood leaves by ejecting smaller aphids from better sites. Male-male competition in red deer during rut is an example of interference competition that occurs within a species (intraspecific competition).

Interference competition occurs directly between individuals via aggression when the individuals interfere with foraging, survival, reproduction of others, or by directly preventing their physical establishment in a portion of the habitat. An example of this can be seen between the ant *Novomessor cockerelli* and red harvester ants, where the former interferes with the ability of the latter to forage by plugging the entrances to their colonies with small rocks (Barton et al. 2002). Male bowerbirds, who create elaborate structures called *bowers* to attract potential mates, may reduce the fitness of their neighbors directly by stealing decorations from their structures (Le Bourlot et al. 2014).

In animals, interference competition is a strategy mainly adopted by larger and stronger organisms within a habitat. As such, populations with high interference competition have adult-driven generation cycles. At first, the growth of juveniles is stunted by larger adult competitors. However, once the juveniles reach adulthood, they experience a secondary growth cycle (Le Bourlot et al. 2014). Plants, on the other hand, primarily engage in interference competition with their neighbors through allelopathy, or the production of biochemicals (Schenk 2006).

Interference competition can be seen as a strategy that has a clear cost (injury or death) and benefit (obtaining resources that would have gone to other organisms) (Case & Gilpin 1975). In order to cope with strong interference competition, other organisms often either do the same or engage in exploitation competition. For example, depending on the season, larger ungulate red deer males are competitively dominant due to interference competition. However, does and fawns have dealt with this through temporal resource partitioning — foraging for food only when adult males are not present (Stone et al. 2018).

15.1.2 Exploitation Competition

Exploitation competition, or scramble competition, occurs indirectly when organisms both use a common limiting resource or shared food item. Instead of fighting or exhibiting aggressive behavior in order to win resources, exploitative competition occurs when resource use by one organism depletes the total amount available for the other organism. These organisms might never interact directly, but compete by responding to changes in resource levels. Very obvious examples of this phenomenon include a diurnal species and a nocturnal species that nevertheless share the same resources, or a plant that competes with neighboring plants for light, nutrients, and space for root growth (Jensen 1987).

This form of competition typically rewards those organisms who claim the resource first. As such, exploitation competition is often size-dependent and smaller organisms are favored since smaller organisms typically have higher foraging rates (Le Bourlot et al. 2014). Since smaller organisms have an advantage when exploitative competition is important in an ecosystem, this mechanism of competition might lead to a juvenile-driven generation cycle: individual juveniles succeed and grow fast, but once they mature they are outcompeted by smaller organisms (Le Bourlot et al. 2014).

In plants, exploitative competition can occur both above- and below-ground. Aboveground, plants reduce the fitness of their neighbors by vying for sunlight. Plants consume nitrogen by absorbing it into their roots, making nitrogen unavailable to nearby plants. Plants that produce many roots typically reduce soil nitrogen to very low levels, eventually killing neighboring plants.

Exploitative competition has also been shown to occur both within species (intraspecific) and between different species (interspecific). Furthermore, many competitive interactions between organisms are some combination of exploitative and interference competition, meaning the two mechanisms are far from mutually exclusive. For example, a recent 2019 study found that the native thrips species *Frankliniella intonsa* was competitively dominant over an invasive thrips species *Frankliniella occidentalis* because it not only exhibited greater time feeding (exploitative competition) but also greater time guarding its resources (interference competition) (Bhuyain & Lim 2019). Plants may also exhibit both forms of competition, not only scrambling for space for root growth but also directly inhibiting other plants' development through allelopathy.

15.1.3 Apparent Competition

Apparent competition occurs when two otherwise unrelated prey species indirectly compete for survival through a shared predator (Holt 1977). This form of competition typically manifests in new equilibrium abundances of each prey species. For example, suppose there are two species (species A and species B), which are preyed upon by food-limited predator species C. Scientists observe an increase in the abundance of species A and a decline in the abundance of species B. In an apparent competition model, this relationship is found to be mediated through predator C; a population explosion of species A increases the abundance of the predator species C due to a greater total food source. Since there are now more predators, species A and B would be hunted at higher rates than before. Thus, the success of species A was to the detriment of species B — not because they competed for resources, but because their increased numbers had indirect effects on the predator population.

References

Barton, K.E., Sanders, N.J., & Gordon, D.M. (2002). The effects of proximity and colony age on interspecific interference competition between the desert ants, *Pogonomyrmex barbatus* and *Aphaenogaster cockerelli*. *The American Midland Naturalist, 148*(2), pp. 376–382. doi:10.1674/0003-0031

Begon, M., Harper, J.L., & Townsend, C.R. (1996). Ecology: Individuals, populations and communities. *Blackwell Science*.

Bhuyain, M.M.H., & Lim, U.T. (2019). Interference and exploitation competition between *Frankliniella occidentalis* and *F. intonsa* (Thysanoptera: Thripidae) in laboratory assays. *Florida Entomologist, 102*(2), pp. 322–328. doi:10.1653/024.102.0206

Case, T.J., & Gilpin, M.E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America, 71*(8), pp. 3073–3077. doi:10.1073/pnas.71.8.3073

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology, 12*(2), pp. 197–229.

Jensen, A.L. (1987). Simple models for exploitative and interference competition. *Ecological Modelling, 35*(1), pp. 113–121. doi:10.1016/0304-3800(87)90093-7

Lang, J.M., & Benbow, M.E. (2013). Species interactions and competition. *Nature Education Knowledge, 4*(4), pp. 8.

Le Bourlot, V., Tully, T., & Claessen, D. (2014). Interference versus exploitative competition in the regulation of size-structured populations. *The American Naturalist, 184*(5), pp. 609–623. doi:10.1086/678083

Schenk, H.J. (2006). Root competition: Beyond resource depletion. *Journal of Ecology, 94*(4), pp. 725–739. doi:10.1111/j.1365-2745.2006.01124.x

Stone, D.B., Martin, J.A., Cohen, B.S., Prebyl, T.J., Killmaster, C., & Miller, K.V. (2018). Intraspecific temporal resource partitioning at white-tailed deer feeding sites. *Current Zoology, 65*(2), pp. 139–146. doi:10.1093/cz/zoy05

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Competition biology by Wikipedia, the free encyclopedia

15.2: Intraspecific (Single Species) Competition

Figure 15.2.1: Male hartebeest locking horns and fiercely defending their territories. An example of direct competition.

Intraspecific competition is an interaction in population ecology, whereby members of the same species compete for limited resources. This leads to a reduction in fitness for both individuals, but the more fit individual survives and is able to reproduce (Townsend, 2008). By contrast, interspecific competition occurs when members of different species compete for a shared resource. Members of the same species have rather similar requirements for resources, whereas different species have a smaller contested resource overlap, resulting in intraspecific competition generally being a stronger force than interspecific competition (Connell, 1983).

Intraspecific competition does not just involve direct interactions between members of the same species (such as male deer locking horns when competing for mates) but can also include indirect interactions where an individual depletes a shared resource (such as a grizzly bear catching a salmon that can then no longer be eaten by bears at different points along a river).

When resources are infinite, intraspecific competition does not occur and populations can grow exponentially. Exponential population growth is exceedingly rare, but has been documented, most notably in humans since 1900. Elephant (*Loxodonta africana*) populations in Kruger National Park (South Africa) also grew exponentially in the mid-1900s after strict poaching controls were put in place (Young & Ferreira, 2009). However, prolonged exponential growth is rare in nature because resources are finite and so not every individual in a population can survive, leading to intraspecific competition for the scarce resources. Individuals can compete for food, water, space, light, mates, or any other resource which is required for survival or reproduction. The resource must be limited for competition to occur; if every member of the species can obtain a sufficient amount of every resource then individuals do not compete and the population grows exponentially (Townsend, 2008).

When resources are limited, an increase in population size reduces the quantity of resources available for each individual, reducing the per capita fitness in the population. As a result, the growth rate of a population slows as intraspecific competition becomes more intense, making it a negatively density dependent process.

The falling population growth rate as population increases can be modeled effectively with the logistic growth model. The rate of change of population density eventually falls to zero, the point ecologists have termed the **carrying capacity (*K*)**. However, a population can only grow to a very limited number within an environment. The carrying capacity, defined by the variable K, of an environment is the maximum number of individuals or species an environment can sustain and support over a longer period of time.

The **logistic growth equation** is an effective tool for modeling intraspecific competition despite its simplicity, and has been used to model many real biological systems. Here N is the size of the population at a given time, r is inherent per-capita growth rate, and K is the carrying capacity. At low population densities, N_t is much smaller than K and so the main determinant for population growth is just the per capita growth rate. However, as N_t approaches the carrying capacity the second term in the logistic equation becomes smaller, reducing the rate of change of population density (Hanson, 1981). Eventually, the population size equals the carrying capacity, and the population growth rate equals zero.

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

dN/dt = rate of change of population density

N = population size at time *t*

r = per capita growth rate

K = carrying capacity

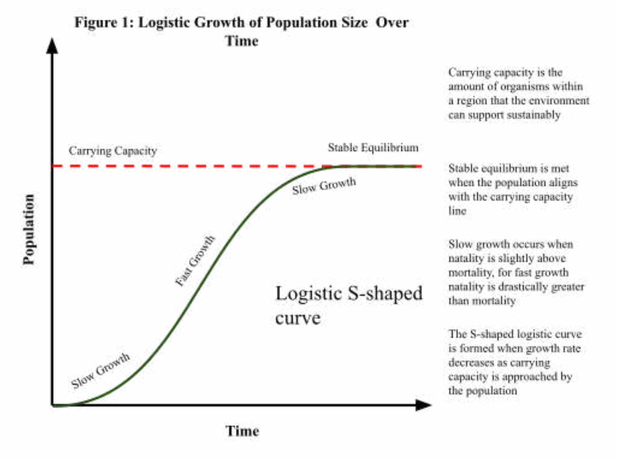


Figure 15.2.2: The growth of a population following a logistic curve, resulting in the S-shaped graph. This model reaches a stable equilibrium, sustaining the population at the carrying capacity as time continues. Developed by Nchisick under CC-BY-SA.

The logistic growth curve is initially very similar to the exponential growth curve. When population density is low, individuals are free from competition and can grow rapidly. However, as the population reaches its maximum (the carrying capacity), intraspecific competition becomes fiercer and the per capita growth rate slows until the population reaches a stable size. At the carrying capacity, the rate of change of population density is zero because the population is as large as possible based on the resources available. Experiments on *Daphnia* growth rates showed a striking adherence to the logistic growth curve (Schoener, 1973). The inflexion point in the *Daphnia* population density graph occurred at half the carrying capacity, as predicted by the logistic growth model.

In summary, the resources within an environment are limited. Therefore, the environment can only support a certain number of individuals before its resources completely diminish. Numbers larger than this will suffer a negative population growth until eventually reaching the carrying capacity, whereas populations smaller than the carrying capacity will grow until they reach it.

References

Connell, J. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Naturalist, 122*(5), pp. 661–696. doi:10.1086/284165

Hanson, F. (1981). Logistic growth with random density independent disasters. *Theoretical Population Biology, 19*(1), pp. 1–18. doi:10.1016/0040-5809(81)90032-0

Schoener, T. (1973). Population growth regulated by intraspecific competition for energy or time: Some simple representations. *Theoretical Population Biology, 4*(1), pp. 56–84. doi:10.1016/0040-5809(73)90006-3

Townsend. (2008). Essentials of Ecology. pp. 103–105. ISBN 978-1-4051-5658-5

Young, K., Ferreira, S., & van Aarde, R. (2009). The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology, 34*(3), pp. 329–342. doi:10.1111/j.1442-9993.2009.01934.x

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Intraspecific competition by Wikipedia, the free encyclopedia

---

15.3: Interspecific (Two Species) Competition

Figure 15.3.1 : Subadult male lion and spotted hyena in the Masai Mara. The two species share the same ecological niche, and are thus in competition with each other.

Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities, and the evolution of interacting species. An example among animals could be the case of cheetahs and lions; since both species feed on similar prey, they are negatively impacted by the presence of the other because they will have less food, however, they still persist together, despite the prediction that under competition one will displace the other. In fact, lions sometimes steal prey items killed by cheetahs. Potential competitors can also kill each other, in so-called 'intraguild predation'. For example, in southern California coyotes often kill and eat gray foxes and bobcats, all three carnivores sharing the same stable prey (small mammals) (Fedriani et al., 2000).

15.3.1 Interspecific Competition: The Lotka-Volterra Model

Given two populations, *N*1 and *N*2, with logistic dynamics, the Lotka–Volterra formulation adds an additional term to account for the species' interactions. Thus the competitive **Lotka–Volterra equations** are:

Population 1:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{d_t} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

Here, $\alpha 12$ represents the effect species 2 has on the population of species 1 and $\alpha 21$ represents the effect species 1 has on the population of species 2. These values do not have to be equal. Because this is the competitive version of the model, all interactions must be harmful (competition) and therefore all α-values are positive. Note that each species can have its own growth rate and carrying capacity. The Lotka-Volterra model for competition and how it is used to predict competitive outcomes is described in more detail in the Quantifying Competition section of this chapter.

15.3.2 Resource-Ratio Hypothesis (R* rule)

The **R* rule** (also called the **resource-ratio hypothesis**) is a hypothesis that attempts to predict which species will become dominant as the result of competition for resources (Tilman, 1982). It predicts that if multiple species are competing for a single limiting resource, then whichever species can survive at the lowest **equilibrium resource level** (i.e., the **R***) can outcompete all other species (Tilman, 1982). If two species are competing for two resources, then coexistence is only possible if each species has a lower R* on one of the resources (Tilman, 1982). For example, two phytoplankton species may be able to coexist if one is more limited by nitrogen, and the other is more limited by phosphorus.

Consider a community with multiple species. We will assume that each species competes for a single resource, and ignore the effects of interference or apparent competition. Each population increases by consuming resources, and declines when resources are too scarce. For example, we could model their population dynamics as

$$\frac{dN_j}{dt} = N_j\left(a_jR - d\right)$$

$$\frac{dR}{dt} = r - R\sum_j a_jN_j$$

where N_j is the density of species j, R is the density of the resource, a is the rate at which species j eats the resource, d is species j's death rate, and r is the rate at which resources grow when not consumed. It is easy to show that when species j is at equilibrium by itself (i.e., $dN_j/dt = 0$), that the equilibrium resource density, $R*_j$, is

$$R^*_j = d/a_j$$

When $R > R*_j$, species j's population will increase; when R is less than $R*_j$, species j's population will decline. Because of this, the species with the lowest $R*$ will eventually dominate. Consider the two species case, where $R*_1 < R*_2$. When species 2 is at equilibrium, $R = R*_2$, and species 1's population will be increasing. When species 1 is at equilibrium, $R = R*_1$, and species 2's population will be decreasing (Tilman, 1982).

References

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., & York, E.C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, *125*, pp. 258-270. doi:10.1016/0040-5809(77)90042-9

Tilman, D. (1982). Resource competition and community structure. *Princeton: Princeton University Press*. ISBN 9780691083025.

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Interspecific competition by Wikipedia, the free encyclopedia
- R* rule (ecology) by Wikipedia, the free encyclopedia

15.4: Ecological and Evolutionary Consequences of Competition

15.4.1 Competitive Exclusion

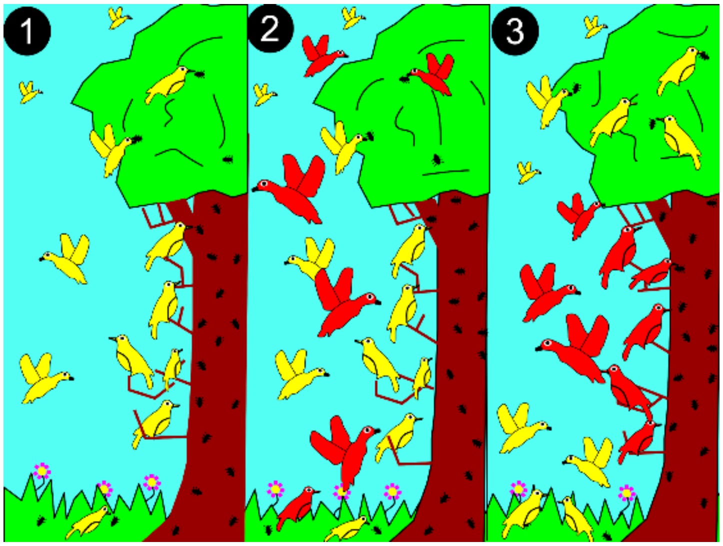


Figure 15.4.1 : 1) A smaller (yellow) species of bird forages across the whole tree. 2) A larger (red) species competes for resources. 3) Red dominates in the middle for the more abundant resources. Yellow shifts to a new niche, avoiding competition.

The **competitive exclusion principle** postulates that two species which compete for the same limited resource cannot coexist at constant population values. When one species has even the slightest advantage over another, the one with the advantage will dominate in the long term. This leads either to the extinction of the weaker competitor or to an evolutionary or behavioral shift toward a different ecological niche. The principle has been paraphrased in the maxim "complete competitors cannot coexist" (Hardin, 1960).

Georgy Gause formulated the law of competitive exclusion based on laboratory competition experiments using two species of *Paramecium*, *P. aurelia* and *P. caudatum*. The conditions were to add fresh water every day and input a constant flow of food. Although *P. caudatum* initially dominated, *P. aurelia* recovered and subsequently drove *P. caudatum* extinct via exploitative resource competition. However, Gause was able to let the *P. caudatum* survive by differing the environmental parameters (food, water). Thus, Gause's law is valid only if the ecological factors are constant.

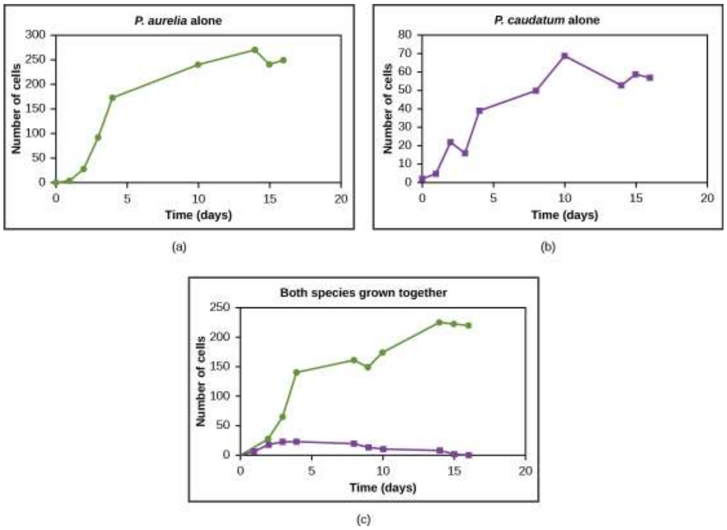


Figure 15.4.2: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, *P. aurelia* outcompetes *P. caudatum.*

Competitive exclusion is predicted by mathematical and theoretical models such as the Lotka–Volterra models of competition. However, competitive exclusion is rarely observed in natural ecosystems and many biological communities appear to violate Gause's law. The best-known example is the so-called "paradox of the plankton" (Hutchinson, 1960). All plankton species live on a very limited number of resources, primarily solar energy and minerals dissolved in the water. According to the competitive exclusion principle, only a small number of plankton species should be able to coexist on these resources. Nevertheless, large numbers of plankton species coexist within small regions of open sea.

15.4.2 Niche Differentiation

Niche differentiation (also known as **niche separation** and **niche partitioning**) refers to the process by which competing species use the environment differently in a way that helps them to coexist. When two species differentiate their niches, they tend to compete less strongly, and are thus more likely to coexist. Species can differentiate their niches in many ways, such as by consuming different foods, or using different areas of the environment.

As an example of niche partitioning, several anole lizards in the Caribbean islands share common diets—mainly insects. They avoid competition by occupying different physical locations. Although these lizards might occupy different locations, some species can be found inhabiting the same range, with up to 15 in certain areas. For example, some live on the ground while others are arboreal. Species who live in different areas compete less for food and other resources, which minimizes competition between species. However, species who live in similar areas typically compete with each other (Pacala, 1985).

Figure $15.4.3$: Niche differentiation by size: greater duckweed, lesser duckweed and rootless dwarf duckweed.

Competing species can partition their niche in different ways. This list is not exhaustive, but illustrates several classic examples.

- **Resource Partitioning** is the phenomenon where two or more species divide out resources like food, space, resting sites etc. to coexist. For example, some lizard species appear to coexist because they consume insects of differing sizes (Caldwell & Vitt, 1999). Alternatively, species can coexist on the same resources if each species is limited by different resources, or differently able to capture resources. Different types of phytoplankton can coexist when different species are differently limited by nitrogen, phosphorus, silicon, and light (Grover, 1997). In the Galapagos Islands, finches with small beaks are more able to consume small seeds, and finches with large beaks are more able to consume large seeds. If a species' density declines, then the food it most depends on will become more abundant (since there are so few individuals to consume it). As a result, the remaining individuals will experience less competition for food. Although "resource" generally refers to food, species can partition other non-consumable objects, such as parts of the habitat. For example, warblers are thought to coexist because they nest in different parts of trees (MacArthur, 1958). Species can also partition habitat in a way that gives them access to different types of resources. As previously stated, anole lizards appear to coexist because each uses different parts of the forests as perch locations (Grover, 1997). This likely gives them access to different species of insects.
- **Predator Partitioning** occurs when species are attacked differently by different predators (or natural enemies more generally). For example, trees could differentiate their niche if they are consumed by different species of specialist herbivores, such as herbivorous insects. If a species density declines, so too will the density of its natural enemies, giving it an advantage. Thus, if each species is constrained by different natural enemies, they will be able to coexist (Grover, 1994). Early work focused on

specialist predators; however, more recent studies have shown that predators do not need to be pure specialists, they simply need to affect each prey species differently (Chesson & Kuang, 2008; Sedio et al., 2013).

- **Conditional Differentiation** (sometimes called **temporal niche partitioning**) occurs when species differ in their competitive abilities based on varying environmental conditions. For example, in the Sonoran Desert, some annual plants are more successful during wet years, while others are more successful during dry years (Angert et al., 2013). As a result, each species will have an advantage in some years, but not others. When environmental conditions are most favorable, individuals will tend to compete most strongly with members of the same species. For example, in a dry year, dry-adapted plants will tend to be most limited by other dry-adapted plants.
- **Competition-Predation Trade-Off:** Species can differentiate their niche via a competition-predation trade-off if one species is a better competitor when predators are absent, and the other is better when predators are present. Defenses against predators, such as toxic compounds or hard shells, are often metabolically costly. As a result, species that produce such defenses are often poor competitors when predators are absent. Species can coexist through a competition-predation trade-off if predators are more abundant when the less defended species is common, and less abundant if the well-defended species is common (Holt et al. 1994). This effect has been criticized as being weak, because theoretical models suggest that only two species within a community can coexist because of this mechanism (Chase et al. 2002).

15.4.3 Coexistence

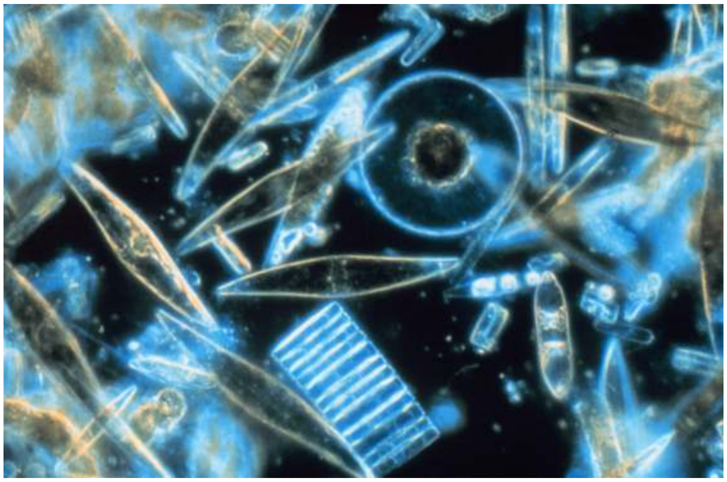


Figure 15.4.4: Coexistence theory attempts to explain the paradox of the plankton - how can ecologically similar species coexist without competitively excluding each other?

Coexistence theory is a framework to understand how competitor traits can maintain species diversity and stave-off competitive exclusion even among similar species living in ecologically similar environments.

Coexistence theory explains the stable coexistence of species as an interaction between two opposing forces: fitness differences between species, which should drive the best-adapted species to exclude others within a particular ecological niche, and stabilizing mechanisms, which maintains diversity via niche differentiation. For many species to be stabilized in a community, population growth must be negative density-dependent, i.e. all participating species have a tendency to increase in density as their populations decline. In such communities, any species that becomes rare will experience positive growth, pushing its population to recover and making local extinction unlikely. As the population of one species declines, individuals of that species tend to compete predominantly with individuals of other species. Thus, the tendency of a population to recover as it declines in density reflects reduced intraspecific competition (within-species) relative to interspecific competition (between-species), the signature of niche differentiation.

Figure 15.4.5: Groundhog and a raccoon eating together.

Two qualitatively different processes can help species to coexist: a reduction in average fitness differences between species or an increase in niche differentiation between species. These two factors have been termed equalizing and stabilizing mechanisms, respectively (Chesson, 2000). For species to coexist, any fitness differences that are not reduced by equalizing mechanisms must be overcome by stabilizing mechanisms.

- **Equalizing mechanisms** reduce fitness differences between species. As its name implies, these processes act in a way that merge the competitive abilities of multiple species closer together. Equalizing mechanisms affect interspecific competition (the competition between individuals of different species). For example, when multiple species compete for the same resource, competitive ability is determined by the minimum level of resources a species needs to maintain itself (known as an R*, or equilibrium resource density) (Tilman, 1980). Thus, the species with the lowest R* is the best competitor and excludes all other species in the absence of any niche differentiation. Any factor that reduces the differences in R* level between species (like increased harvest of the dominant competitor) is classified as an equalizing mechanism. Environmental variation (which is the focus of the Intermediate Disturbance Hypothesis) can be considered an equalizing mechanism. Since the fitness of a given species is intrinsically tied to a specific environment, when that environment is disturbed (e.g. through storms, fires, volcanic eruptions, etc.) some species may lose components of their competitive advantage which were useful in the previous version of the environment.
- **Stabilizing mechanisms** promote coexistence by concentrating intraspecific competition relative to interspecific competition. In other words, these mechanisms "encourage" an individual to compete more with other individuals of its own species, rather than with individuals of other species. Stabilizing mechanisms increase the low-density growth rate of all species. Resource partitioning (a type of niche differentiation) is a stabilizing mechanism because interspecific competition is reduced when different species primarily compete for different resources. Similarly, if species are differently affected by environmental variation (e.g., soil type, rainfall timing, etc.), this can create a stabilizing mechanism called the storage effect. The theory proposes one way for multiple species to coexist: in a changing environment, no species can be the best under all conditions (Chesson & Warner, 1981). Instead, each species must have a unique response to varying environmental conditions, and a way of buffering against the effects of bad years. The storage effect gets its name because each population "stores" the gains in good years or microhabitats (patches) to help it survive population losses in bad years or patches.

15.4.4 Character Displacement

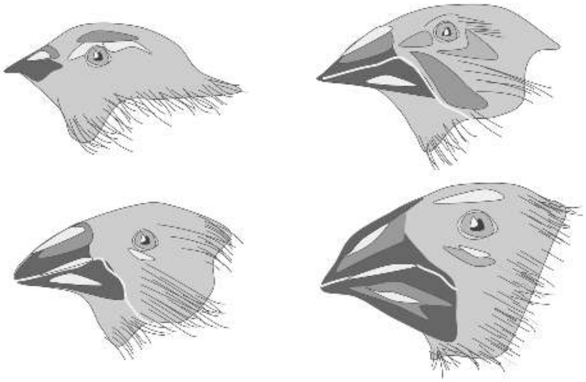


Figure 15.4.6: Several species of Galapagos finches display character displacement. Each closely related species differs in beak size and beak depth, allowing them to coexist in the same region since each species eats a different type of seed: the seed best fit for its unique beak. The finches with the deeper, stronger beaks consume large, tough seeds, while the finches with smaller beaks consume the smaller, softer seeds.

Character displacement is the phenomenon where differences among similar species whose distributions overlap geographically are accentuated in regions where the species co-occur, but are minimized or lost where the species' distributions do not overlap. This pattern results from evolutionary change driven by biological competition among species for a limited resource (e.g. food). The rationale for character displacement stems from the competitive exclusion principle, which contends that to coexist in a stable environment two competing species must differ in their respective ecological niche; without differentiation, one species will eliminate or exclude the other through competition.

For example, Darwin's finches can be found alone or together on the Galapagos Islands. Both species' populations actually have more individuals with intermediate-sized beaks when they live on islands without the other species present. However, when both species are present on the same island, competition is intense between individuals that have intermediate-sized beaks of both species because they all require intermediate sized seeds. Consequently, individuals with small and large beaks have greater survival and reproduction on these islands than individuals with intermediate-sized beaks. Different finch species can coexist if they have traits—for instance, beak size—that allow them to specialize on particular resources. When *Geospiza fortis* and *Geospiza fuliginosa* are present on the same island, *G. fuliginosa* tends to evolve a small beak and *G. fortis* a large beak. The observation that competing species' traits are more different when they live in the same area than when competing species live in different areas is called character displacement. For the two finch species, beak size was displaced: beaks became smaller in one species and larger in the other species.

References

Angert, A.L., Huxman, T.E., Chesson, P., & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences, 106*(28), pp. 11641–11645. doi:10.1073/pnas.0904512106

Caldwell, J.P., & Vitt, L.J. (1999). Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. *Oikos, 84*(3), pp. 383–397. doi:10.2307/3546419

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M., & Case, T.J. (2002). The interaction between predation and competition: A review and synthesis. *Ecology Letters, 5*(2), pp. 302–315. doi:10.1046/j.1461-0248.2002.00315.x

Chesson, P., & Warner, R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist, 117*(6), pp. 923–943. doi:10.1086/283778

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics, 31*, pp. 343–366. doi:10.1146/annurev.ecolsys.31.1.343

Chesson, P., & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, *456*(7219), pp. 235–238. doi:10.1038/nature07248

Grover, J.P. (1997). Resource competition (1st ed.). *London: Chapman & Hall*. ISBN 978-0412749308

Hardin, G. (1960). The competitive exclusion principle. *Science*, *131*(3409), pp. 1292–1297. doi:10.1126/science.131.3409.1292

Holt, R.D., Grover, J., & Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *The American Naturalist*, *144*(5), pp. 741–771. doi:10.1086/285705

Hutchinson, G.E. (1961). The paradox of the plankton. *The American Naturalist*, *95*(882), pp. 137–145. doi:10.1086/282171

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, *39*(4), pp. 599-619.

Pacala, S.W., & Roughgarden, J. (1985). Population experiments with the Anolis lizards of St. Maarten and St. Eustatius. *Ecology*, *66*(1), pp. 129–141. doi:10.2307/1941313

Sedio, B.E., Ostling, A.M. (2013). How specialised must natural enemies be to facilitate coexistence among plants? *Ecology Letters*, *16*(8), pp. 995–1003. doi:10.1111/ele.12130

Tilman, D. (1980). Resources: A graphical-mechanistic approach to competition and predation. *The American Naturalist*, *116*(3), pp. 362–393. doi:10.1086/283633

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Competitive exclusion principle by Wikipedia, the free encyclopedia
- Ecological niche by Wikipedia, the free encyclopedia
- Coexistence theory by Wikipedia, the free encyclopedia
- Character displacement by Wikipedia, the free encyclopedia

15.5: Quantifying Competition Using the Lotka-Volterra Model

Real populations do not exist in isolation, but share habitats with populations of other species. In many cases, coexisting species will interact by interspecific competition, predation, parasitism, mutualism, or other ecological interactions. More realistic models must take such interactions into account. In the 1920s, Vito Volterra and Alfred Lotka (1932) independently developed models of **interspecific competition** (competition between two species), and investigated the conditions that would permit competing species to coexist indefinitely.

An important ecological generalization, the **competitive exclusion principle**, has grown out of the Lotka-Volterra model and from other sources. This principle states that *two species cannot coexist unless their niches are sufficiently different that each limits its own population growth more than it limits that of the other*. In other words, if there is too much niche overlap, one species will competitively exclude the other. In reality, whether two species coexist depends not only on their competitive interactions with each other, but also on their interactions with the abiotic environment and with other species not included in this simple model. Nevertheless, the competitive exclusion principle has proven fruitful in stimulating research and understanding ecological interactions in the natural world.

In broad terms, the questions Lotka and Volterra asked were:

- What will happen to the population dynamics of these two populations, given various values of the model parameters?
- Are there parameter values that will produce a winner and a loser—one population that persists while the other goes extinct? This would be competitive exclusion.
- Will other values result in coexistence, in which both competing populations persist indefinitely?

Model Development – Starting with One Species

The logistic model of population growth focuses on **intraspecific competition** (competition between individuals of the same species). To keep things (relatively) simple, we will develop our model of interspecific competition beginning with this form of the logistic model:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

where K is the carrying capacity, or largest sustainable population. The value of K is set by available resources and by each individual’s resource demand. This version of the logistic model has intraspecific competition built into it in the term $(K - N_t)/K$. This term reduces the population growth rate in response to the addition of each new member of the population, representing the reduction in per capita birth rate, and increase in per capita death rate, caused by competition for limited resources.

The Lotka-Volterra model of interspecific competition builds on the logistic model of a single population. It begins with a separate logistic model of the population of each of the two, competing species.

Population 1:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right)$$

Note the use of subscripts 1 and 2 to denote which species' population is being modeled. Each population has its own rate of increase *r* and carrying capacity *K*, and these may differ between the two species.

Model Development – Coupling Two Competitors

Next, we build interspecific competition into each of these equations. We assume that each new member of Population 1 reduces resources available to each member of Population 2, and thus reduces population growth rate. Additionally, new members of Population 2 will also reduce resources available to members of Population 1—this is, after all, the meaning of interspecific competition.

The simplest way to model this would be to modify the $(K - N_t)/K$ term into $(K_1 - N_{1,t} - N_{2,t})/K$. However, this assumes that each additional member of Population 2 will affect Population 1 exactly as much as an additional member of Population 1. That is not necessarily the case, so we multiply $N_{2,t}$ in this term by a **competition coefficient**, α_{12} to express how much effect each additional member of Population 2 has on Population 1, relative to the effect of a new member of Population 1. We modify the model for Population 2 in a parallel way. The resulting Lotka-Volterra model of two-species competition is:

Population 1:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

Note the subscripts on the competition coefficients: α_{12} expresses the effect of one member of Population 2 on the growth rate of Population 1; α_{21} expresses the effect of one member of Population 1 on the growth rate of Population 2.

The value of the competition coefficient tells us something about the relative importance of interspecific and intraspecific competition on the population dynamics of a species.

- When the competition coefficient is less than 1, intraspecific competition has a stronger per capita impact on resource availability for that species.
- When the competition coefficient is greater than 1, interspecific competition has a stronger per capita impact on resource availability for that species.
- When the competition coefficient is equal to 1, inter and intraspecific competition have a similar per capita impact on resource availability for that species.

Equilibrium Solutions for Coupled Competitors

To understand the outcome of competition between these two species, we must first find the equilibrium solutions to the coupled equations above. The equilibrium is the population size at which the population stops growing. We can solve for this equilibrium by setting dN/dt for each species to zero and solving for N.

For Population 1, for example:

$$\mathrm{N}_1 = K_1 - a_{12}N_2$$

The resulting equation is the equation of a line, $y = a + bx$. We call this line a **zero net growth isocline**, or **ZNGI**, because anywhere along it, Population 1 has zero net growth. In other words, this is an equilibrium solution for Population 1.

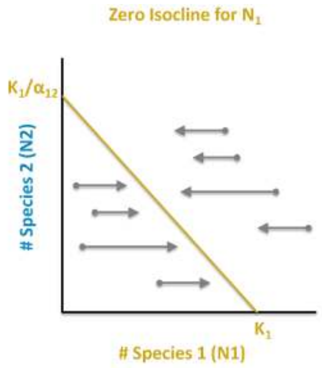
Just as x and y in the general linear equation $y = a + bx$ can be used as coordinates for graphing, so we can use $N1$ and $N2$ as coordinates to graph each species ZNGI. We can graph this isocline by finding any two points along it and connecting them with a straight line.

Two convenient points are where $N_{2,t} = 0$ and where $N_{1,t} = 0$**. If we solve for these intercepts, we wind up with the following two coordinates for Population 1: [0, K_1/a_{12}] (setting x, or the size of Population 1, to 0) and [K_1, 0] (setting y, or the population size of Population 2, to 0).** In words, if there are no members of Population 2 in the habitat, Population 1 will stabilize at its own carrying capacity, $K1$. This seems a reasonable solution. If there are no members of Population 1, Population 2 will stabilize at the carrying capacity of Population 1 accounting for the relative per capita resource requirements of Population 2 relative to Population 1. These points can be plotted and connected to visualize the ZNGI.

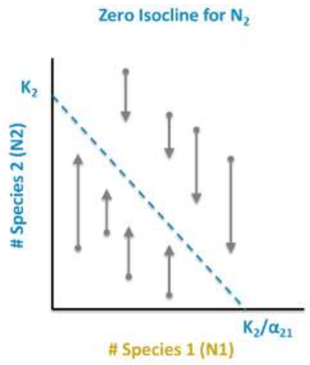
The same is done for Population 2:

$$\mathrm{N}_2 = K_2 - a_{21}N_1$$

This results in the following ZNGI coordinates: [0, K_2] and [K_2/a_{21},0].



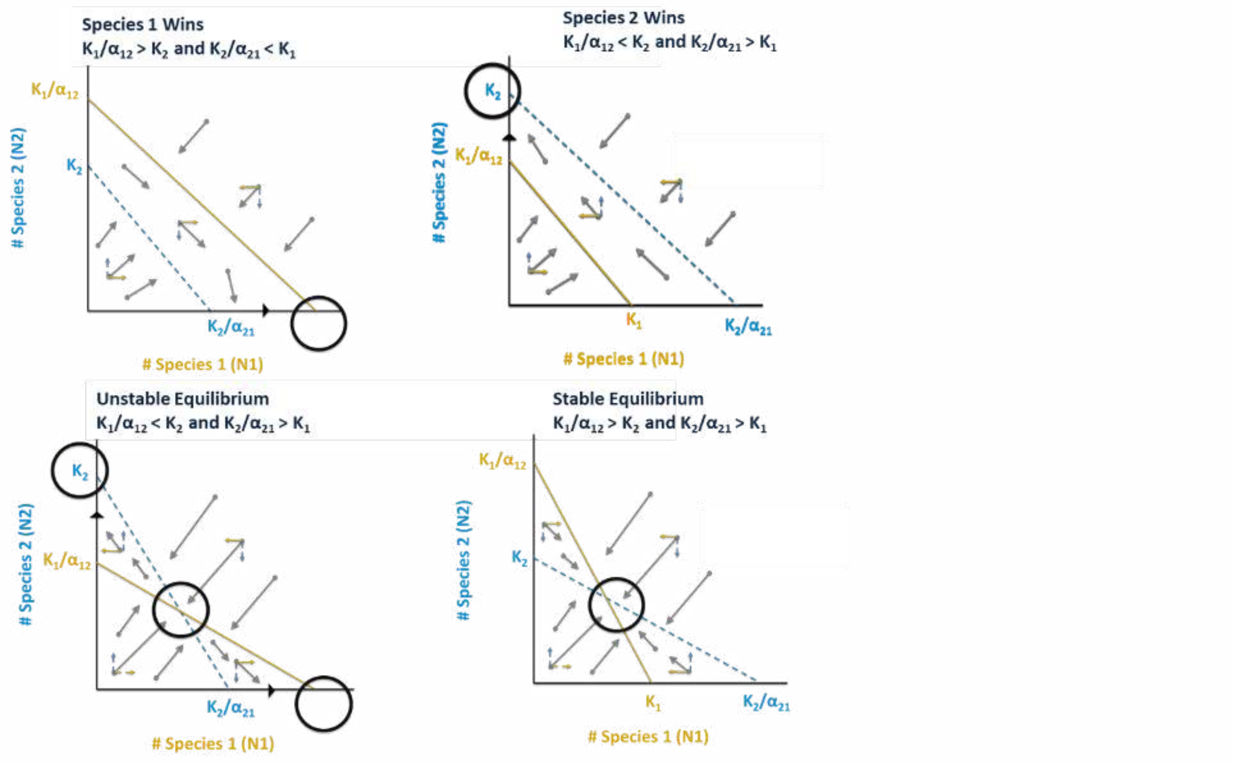
$$N_1 = K_1 - a_{12}N_2$$



$$N_2 = K_2 - a_{21}N_1$$

To determine the outcome of competition, we must be able to find the ZNGI lines and the initial sizes of each population and graph them. We can graph the populations of the two species at any time by a point on a graph. Population 1 should always be plotted on the x-axis and Population 2 is on the y-axis. If the point falls below (Population 1) and/or to the left (Population 2) of a species' isocline, that population will continue to increase. If the point falls above (Population 1) and/or to the right (Population 2) of a species' isocline, that population will decrease. This will continue to occur as the coupled populations change sizes, and the point describing the two populations will trace some trajectory across the graph, eventually reaching an equilibrium of coexistence or competition exclusion.

Notice that time does not appear on either axis of this graph. The plots above are called **phase diagrams**, and the space bounded by its axes is called **phase space**. You can plot the trajectory of two changing populations through the phase space and from that determine whether one species excludes the other, or if they coexist.



A Quick Summary of Coupled Interspecific Competition Models

Based on the Logistic Model:

- Alone, Species 1 and 2 increase to their K
- Species 1 and 2 reduce each others' K

Outcomes Depend On:

- Competition coefficient
- Species 1 and Species 2 carrying capacity
- Species 1 and Species 2 starting population size

Steps to Determining Outcomes:

- Find and plot Species 1 isocline (K_1 on x; K_1/α_{12} on y)
- Find and plot Species 2 isocline (K_2/α_{21} on x; K_2 on y)
- Plot initial population size
- Determine vectors and outcome

Models Review - Exponential, Logistic, Competition

Exponential (Review) – No Carrying Capacity

$$\frac{dN_1}{dt} = r_1 N_1$$

r_1 = intrinsic growth rate of species 1

N_1 = population size of species 1

Logistic (Review) – Single Species, Carry Capacity

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

K_1 = carrying capacity of species 1 (when K = N, $dN/dt = 0$)

Competition – Two Species Logistic Model, Equations Linked

Population 1:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

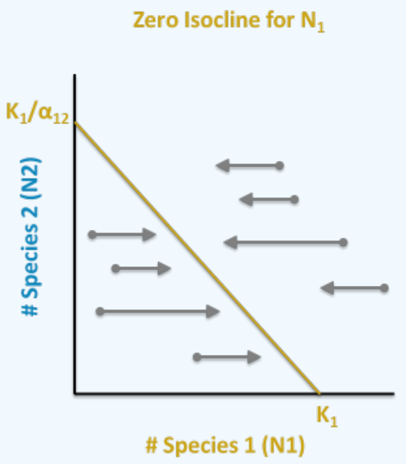
Population 2:

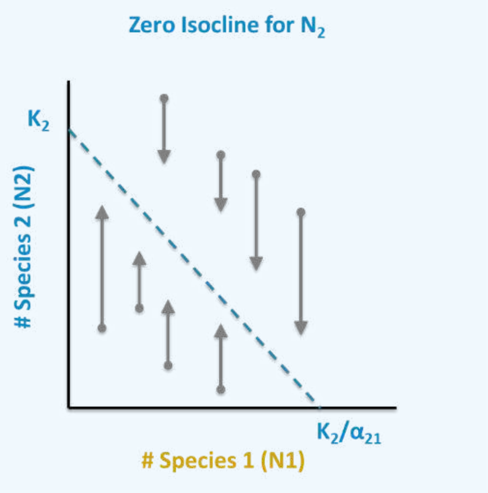
$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

α_{12} or α = a measure of the per capita effect of species 2 on the growth of species 1

α_{21} or β = a measure of the per capita effect of species 1 on the growth of species 2

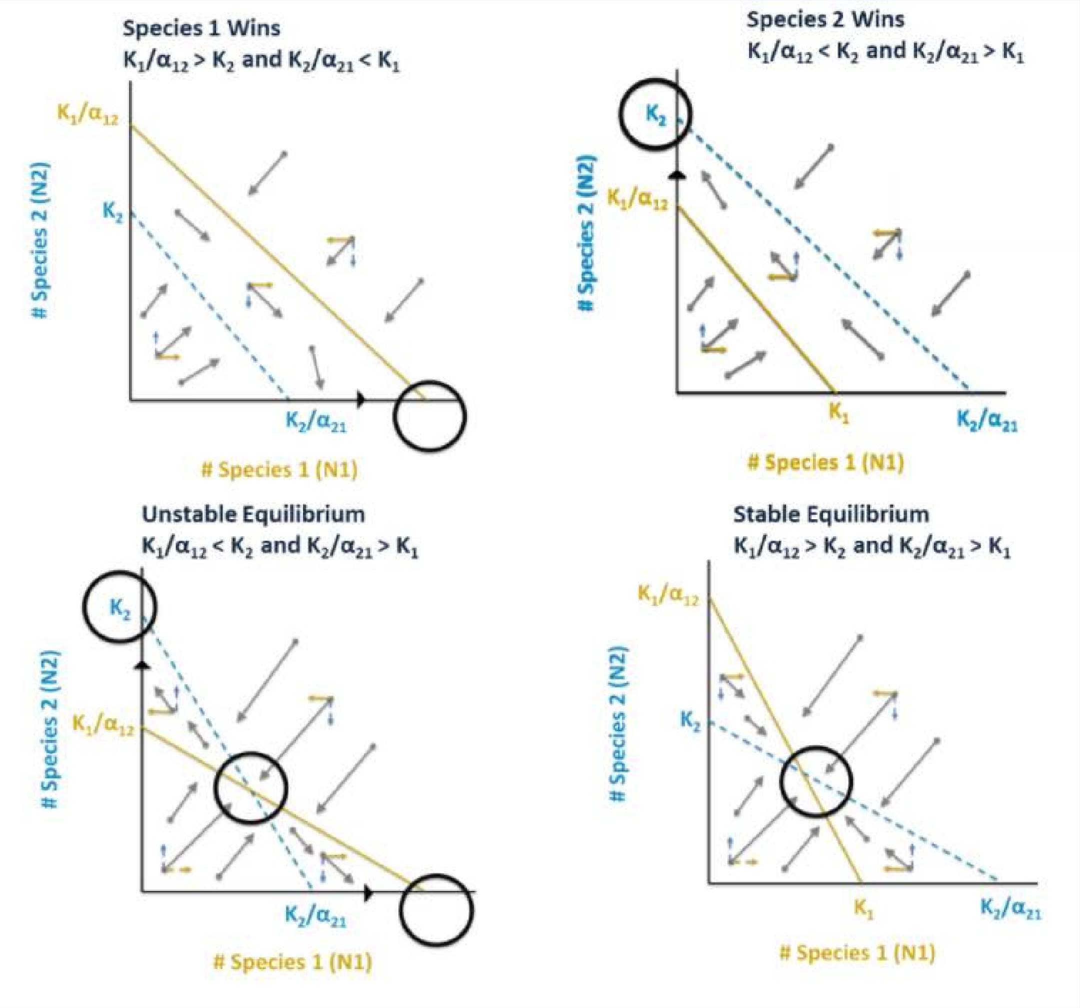
Species 1 and Species 2 Isoclines





$$N_1 = K_1 - a_{12}N_2 \quad N_2 = K_2 - a_{21}N_1$$

Species 1 and Species 2 Outcomes



? Predator/Prey Relations Exercise 15.5.1

Blue crabs have a death rate of 0.005 and an initial population size of 50. Oysters have an intrinsic growth rate of 0.1 and an initial population size of 200. For each 50 oysters a crab consumes, they can produce one additional baby blue crab. For every 400 additional oysters added to the population, each crab can consume one more oyster per unit time.

1) Where are the crab and oyster isoclines?

2) Draw a phase diagram with the isoclines. Note where the starting populations of both species are, as well as the directions of the vectors of the population changes in each quadrant.

3) Draw the boom-and-bust oscillations for these species.

4) If oysters evolved to have thicker and harder to open shells, which term of the predator-prey model would be impacted, and in what direction?

5) Although the oyster population has crashed due to overfishing, the blue crab population continues to increase. What might have caused this dynamic?

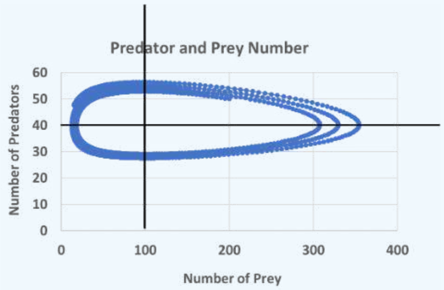
6) The oyster's predators and competitors have been eradicated, but their population stops growing after a long period of increase. Why has their population stopped growing?

Answer

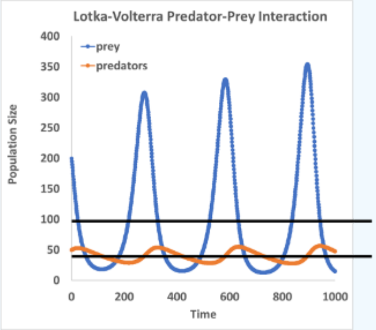
1) Isocline for predators (0 growth rate of predators): $N_(prey) = d/cp$ = 0.005/(0.02*0.0025) = 100

Isocline for prey (0 growth rate for prey): $N_pred = r/p$ = 0.1/0.0025 = 40

2)



3)



4) Handing time would increase, so p would decrease.

5) Prey-switching is a possible explanation.

6) The population has reached their carrying capacity.

❓ Phase Diagram Exercise 15.5.2

Two species of monkey in West Africa, putty-nosed monkeys (Species 1) and Diana monkeys (Species 2), have nearly identical niches and breed at the same time annually. Diana monkeys eat insects and fruit, but the putty-nosed monkey eats only insects. A team of ecologists conducting a study on competition between these two species find that:

> For the putty-nosed monkey population, Diana monkeys have a per capita impact equivalent to 0.8 putty-nosed monkeys.
>
> For the Diana monkey population, putty-nosed monkeys have a per capita impact equivalent to 0.6 Diana monkeys.
>
> Putty-nosed monkeys have a carrying capacity of 300 and starting population of 250.
>
> Diana monkeys have a carrying capacity of 500 and starting population of 400.

1) Why does it make sense for both populations to have a competition coefficient of less than one?

2) What is a change that one of these populations could make to reduce competition?

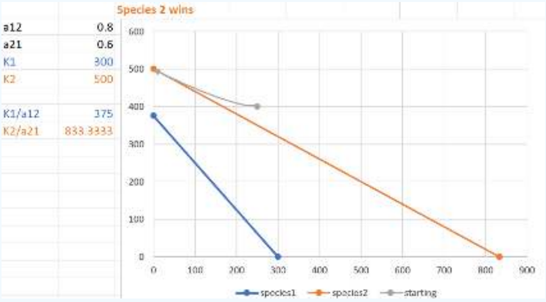
3) What are the isoclines for these competitors? Graph the isoclines. Which species wins, if any, and what is the name for this type outcome?

Answer

1) Since the two monkey species have differences in their diets, they are more likely to impact themselves than they are to impact each other—putty-nosed monkeys will not take fruit from Diana monkeys. For both species, intraspecific competition is stronger than interspecific competition.

2) One of the populations could change the time of year that they breed; the Diana monkeys can focus their diets on fruit; the populations could focus their diets on different types of insects.

3)



a12	0.8
a21	0.6
K1	300
K2	500
K1/a12	375
K2/a21	833.3333

References

Lotka, A.J. (1932). The growth of mixed populations: Two species competing for a common food supply. *Journal of the Washington Academy of Sciences*, *22*, pp. 461 469.

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

15.6: Sources and Attributions

Full Chapter Sources

Angert, A.L., Huxman, T.E., Chesson, P., & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences, 106*(28), pp. 11641–11645. doi:10.1073/pnas.0904512106

Barton, K.E., Sanders, N.J., & Gordon, D.M. (2002). The effects of proximity and colony age on interspecific interference competition between the desert ants *Pogonomyrmex barbatus* and *Aphaenogaster cockerelli*. *The American Midland Naturalist, 148*(2), pp. 376–382. doi:10.1674/0003-0031

Begon, M., Harper, J.L., & Townsend, C.R. (1996). Ecology: Individuals, populations and communities. *Blackwell Science*.

Bhuyain, M.M.H., & Lim, U.T. (2019). Interference and exploitation competition between *Frankliniella occidentalis* and *F. intonsa* (Thysanoptera: Thripidae) in laboratory assays. *Florida Entomologist, 102*(2), pp. 322–328. doi:10.1653/024.102.0206

Brown, W.L., & Wilson, E.O. (1956). Character displacement. *Systematic Zoology, 5*, pp.49–65.

Case, T.J., & Gilpin, M.E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America, 71*(8), pp. 3073–3077. doi:10.1073/pnas.71.8.3073

Caldwell, J.P., & Vitt, L.J. (1999). Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. *Oikos, 84*(3), pp. 383–397. doi:10.2307/3546419

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M., & Case, T.J. (2002). The interaction between predation and competition: A review and synthesis. *Ecology Letters, 5*(2), pp. 302–315. doi:10.1046/j.1461-0248.2002.00315.x

Chesson, P., & Warner, R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist, 117*(6), pp. 923–943. doi:10.1086/283778

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics, 31*, pp. 343–366. doi:10.1146/annurev.ecolsys.31.1.343

Chesson, P., & Kuang, J.J. (2008). The interaction between predation and competition. *Nature, 456*(7219), pp. 235–238. doi:10.1038/nature07248

Connell, J. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist, 122*(5), pp. 661–696. doi:10.1086/284165

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., & York, E.C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia, 125*, pp. 258-270. doi:10.1016/0040-5809(77)90042-9

Grover, J.P. (1994). Assembly rules for communities of nutrient-limited plants and specialist herbivores. *The American Naturalist, 143*(2), pp. 258–82. doi:10.1086/285603

Grover, J.P. (1997). Resource competition (1st ed.). *London: Chapman & Hall*. ISBN 978-0412749308

Hanson, F. (1981). Logistic growth with random density independent disasters. *Theoretical Population Biology, 19*(1), pp. 1–18. doi:10.1016/0040-5809(81)90032-0

Hardin, G. (1960). The competitive exclusion principle. *Science, 131*(3409), pp. 1292–1297. doi:10.1126/science.131.3409.1292

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology, 12*(2), pp. 197–229.

Holt, R.D., Grover, J., & Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *The American Naturalist, 144*(5), pp. 741–771. doi:10.1086/285705

Hutchinson, G.E. (1961). The paradox of the plankton. *The American Naturalist, 95*(882), pp. 137–145. doi:10.1086/282171

Jensen, A.L. (1987). Simple models for exploitative and interference competition. *Ecological Modelling, 35*(1), pp. 113–121. doi:10.1016/0304-3800(87)90093-7

Lang, J.M. & Benbow, M.E. (2013). Species interactions and competition. *Nature Education Knowledge, 4*(4), pp. 8.

Le Bourlot, V., Tully, T., & Claessen, D. (2014). Interference versus exploitative competition in the regulation of size-structured populations. *The American Naturalist, 184*(5), pp. 609–623. doi:10.1086/678083

Lotka, A.J. (1932). The growth of mixed populations: Two species competing for a common food supply. *Journal of the Washington Academy of Sciences, 22*, pp. 461 469.

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology, 39*(4), pp. 599-619.

Pacala, S.W., & Roughgarden, J. (1985). Population experiments with the Anolis lizards of St. Maarten and St. Eustatius. *Ecology, 66*(1), pp. 129–141. doi:10.2307/1941313

Sedio, B.E., Ostling, A.M. (2013). How specialised must natural enemies be to facilitate coexistence among plants? *Ecology Letters, 16*(8), pp. 995–1003. doi:10.1111/ele.12130

Schenk, H.J. (2006). Root competition: Beyond resource depletion. *Journal of Ecology, 94*(4), pp. 725–739. doi:10.1111/j.1365-2745.2006.01124.x

Schoener, T. (1973). Population growth regulated by intraspecific competition for energy or time: Some simple representations. *Theoretical Population Biology, 4*(1), pp. 56–84. doi:10.1016/0040-5809(73)90006-3

Stone, D.B., Martin, J.A., Cohen, B.S., Prebyl, T.J., Killmaster, C., & Miller, K.V. (2018). Intraspecific temporal resource partitioning at white-tailed deer feeding sites. *Current Zoology, 65*(2), pp. 139–146. doi:10.1093/cz/zoy05

Tilman, D. (1980). Resources: A graphical-mechanistic approach to competition and predation. *The American Naturalist, 116*(3), pp. 362–393. doi:10.1086/283633

Tilman, D. (1982). Resource competition and community structure. *Princeton: Princeton University Press*. ISBN 9780691083025.

Townsend. (2008). Essentials of Ecology. pp. 103–105. ISBN 978-1-4051-5658-5

Young, K.D., Ferreira, S.M., & Van Aarde, R.J. (2009). The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology, 34*(3), pp. 329–342. doi:10.1111/j.1442-9993.2009.01934.x

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Competition_biology by Wikipedia, the free encyclopedia
- Interspecific competition by Wikipedia, the free encyclopedia
- Intraspecific competition by Wikipedia, the free encyclopedia
- R*_rule_(ecology) by Wikipedia, the free encyclopedia
- Coexistence theory by Wikipedia, the free encyclopedia
- Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

CHAPTER OVERVIEW

16: Antagonistic Interactions

Learning Objectives

- Differentiate between the various types of antagonistic interactions
- Understand how antagonistic interactions drive evolution in the positively impacts species (predator, parasite, herbivore) and in the negatively impacted species (prey, host, plant)
- Predict fluctuations in populations of predators and prey (or parasites and hosts) using a modification of the exponential growth model, the Lotka-Volterra predator-prey model.

Summary

Antagonistic interactions involve interactions in which one individual or species benefits, while the other individual or species is harmed. These interactions include predation, herbivory, and parasitism. These type of interactions exert immense evolutionary pressure on the individuals involved as they are required to obtain energy (predators, parasites, herbivores) for one of the species involved and to avoid loss of energy or death (prey, host, plant) for the second species involved. As a result, antagonistic interactions often drive an "evolutionary arms race", a cycle of adaptations and counter-adaptations. Ecologists model interactions among predators and their prey using the Lotka-Volterra model, which builds on the exponential growth model to link predator population growth and prey population decline.

16.1: Predation

Figure 16.1.1: Polar bears (top photo) are solitary predators, here shown feeding on a beaded seal. Other species, like meat ants (photo below), cooperate to feed and are called social predators. Here, meat ants feed socially on a cicada far larger than themselves.

Predation is a biological interaction where one organism, the **predator**, kills and eats another organism, its **prey**. It is one of a family of common feeding behaviors that includes parasitism and micropredation (which usually do not kill the host) and parasitoidism (which always does, eventually). It is distinct from scavenging on dead prey, though many predators also scavenge. Predation and herbivory overlap because seed predators and destructive frugivores kill their "prey".

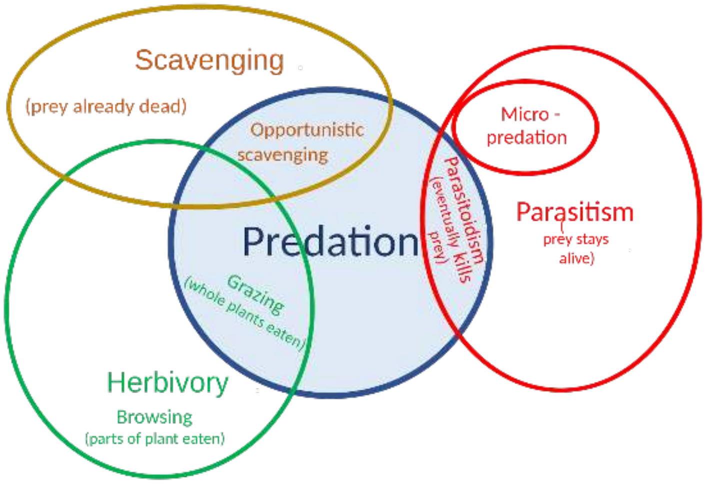


Figure 16.1.2: The relationship of predation to other feeding strategies.

The concept of predation is broad, defined differently in different contexts, and includes a wide variety of feeding methods; and some relationships that result in the prey's death are not generally called predation. A parasitoid, such as an ichneumon wasp, lays its eggs in or on its host; the eggs hatch into larvae, which eat the host, and it inevitably dies. Zoologists generally call this a form of parasitism, though conventionally parasites are thought not to kill their hosts. A predator can be defined to differ from a parasitoid in that it has many prey, captured over its lifetime, where a parasitoid's larva has just one, or at least has its food supply provisioned for it on just one occasion (Lafferty & Kuris, 2002; Gurr & Wratten, 2012).

Figure 16.1.3: Spider wasps paralyze and eventually kill their hosts, but are considered parasitoids, not predators.

There are other difficult and borderline cases. Micropredators are small animals that, like predators, feed entirely on other organisms; they include fleas and mosquitoes that consume blood from living animals, and aphids that consume sap from living plants. However, since they typically do not kill their hosts, they are now often thought of as parasites (Poulin et al., 2011; Poulin & Randhawa, 2015). Animals that graze on phytoplankton or mats of microbes are predators, as they consume and kill their food organisms; but herbivores that browse leaves are not, as their food plants usually survive the assault (Bengston 2002). Scavengers, organisms that only eat organisms found already dead, are not predators, but many predators such as the jackal and the hyena scavenge when the opportunity arises (Kruuk, 1972; Kane et al., 2017). Among invertebrates, social wasps (yellowjackets) are both hunters and scavengers of other insects (Schmidt, 2009).

Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency.

When prey is detected, the predator assesses whether to attack it. Predators may actively search for or pursue prey (**pursuit predation**) or sit and wait for prey (**ambush predation**), often concealed, prior to attack. If the attack is successful, the predator kills the prey, removes any inedible parts like the shell or spines, and eats it.

Predation has a powerful selective effect on prey, and the prey develop antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage, mimicry of well-defended species, and defensive spines and chemicals. Sometimes predator and prey find themselves in an **evolutionary arms race**, a cycle of adaptations and counter-adaptations.

16.1.1 Foraging

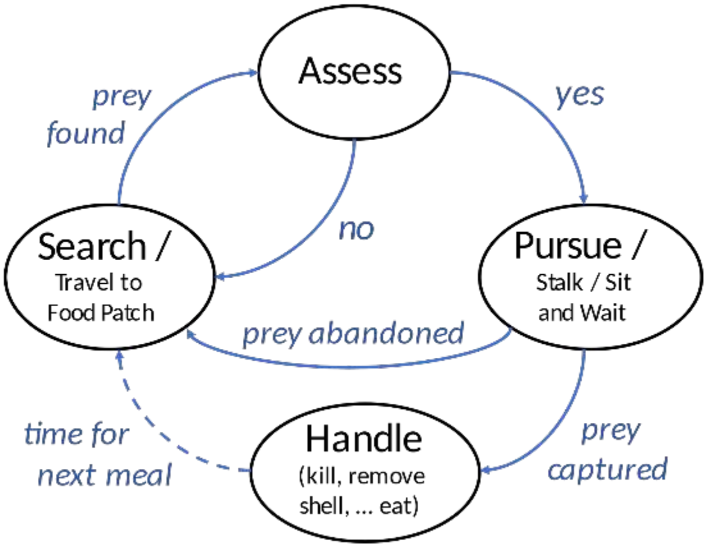


Figure 16.1.4: A basic foraging cycle for a predator, with some variations indicated (Kramer, 2001).

To feed, a predator must search for, pursue and kill its prey. These actions form a foraging cycle (Griffiths, 1980; Wetzel & Liken, 2000). The predator must decide where to look for prey based on its geographical distribution; and once it has located prey, it must assess whether to pursue it or to wait for a better choice. If it chooses pursuit, its physical capabilities determine the mode of pursuit (e.g., ambush or pursuit) (MacArthur, 1984; Pianka, 2011). Having captured the prey, it may also need to expend energy *handling* it (e.g., killing it, removing any shell or spines, and ingesting it) (Griffiths, 1980; Kramer, 2001).

Search

Predators have a choice of search modes ranging from *sit-and-wait* to *active* or *widely foraging* (Perry, 1999; Kramer, 2011; Bell, 2012; Eastman & Thiel, 2015). The sit-and-wait method is most suitable if the prey are dense and mobile, and the predator has low energy requirements (Bell, 2012). Wide foraging expends more energy, and is used when prey is sedentary or sparsely distributed (Pianka, 2011; Bell, 2012). There is a continuum of search modes with intervals between periods of movement ranging from seconds to months. Sharks, sunfish, insectivorous birds and shrews are almost always moving while web-building spiders, aquatic invertebrates, praying mantises and kestrels rarely move. In between, plovers and other shorebirds, freshwater fish including crappies, and the larvae of coccinellid beetles (ladybirds), alternate between actively searching and scanning the environment (Bell, 2012).

Figure 16.1.5: The black-browed albatross regularly flies hundreds of kilometers across the nearly empty ocean to find patches of food.

Prey distributions are often clumped, and predators respond by looking for *patches* where prey is dense and then searching within patches (Kramer, 2001). Where food is found in patches, such as rare shoals of fish in a nearly empty ocean, the search stage requires the predator to travel for a substantial time, and to expend a significant amount of energy, to locate each food patch (Bell, 2012). For example, the black-browed albatross regularly makes foraging flights to a range of around 700 kilometers (430 miles), up to a maximum foraging range of 3,000 kilometers (1,860 miles) for breeding birds gathering food for their young (Gremillet et al., 2000). With static prey, some predators can learn suitable patch locations and return to them at intervals to feed (Bell, 2012).

Assessment

Figure $16.1.6$: Seven-spot ladybirds select plants of good quality for their aphid prey.

Having found prey, a predator must decide whether to pursue it or keep searching. The decision depends on the costs and benefits involved. A bird foraging for insects spends a lot of time searching but capturing and eating them is quick and easy, so the efficient strategy for the bird is to eat every palatable insect it finds. By contrast, a predator such as a lion or falcon finds its prey easily but capturing it requires a lot of effort. In that case, the predator is more selective (Pianka, 2011).

One of the factors to consider is size. Prey that is too small may not be worth the trouble for the amount of energy it provides. Too large, and it may be too difficult to capture. For example, a mantid captures prey with its forelegs and they are optimized for grabbing prey of a certain size. Mantids are reluctant to attack prey that is far from that size. There is a positive correlation between the size of a predator and its prey (Pianka, 2011).

Capture

To capture prey, predators have a spectrum of pursuit modes that range from overt chase (pursuit predation) to a sudden strike on nearby prey (ambush predation) (Stevens, 2010; Kramer, 2011; Williams et al., 2012)

Ambush

Figure 16.1.7: A western green lizard ambushes its grasshopper prey (top photo) and a trapdoor spider waits in its burrow to ambush its prey (bottom photo).

Ambush or sit-and-wait predators are carnivorous animals that capture prey by stealth or surprise. In animals, ambush predation is characterized by the predator's scanning the environment from a concealed position until a prey is spotted, and then rapidly executing a fixed surprise attack (deVries et al., 2012; Moore & Biewener, 2015). Vertebrate ambush predators include frogs, fish such as the angel shark, the northern pike and the eastern frogfish (Canadian Wildlife Service, 2007; Bray, 2014; Moore & Biewener, 2015; Indiana Division of Fish and Wildlife, 2018). Among the many invertebrate ambush predators are trapdoor spiders and Australian Crab spiders on land and mantis shrimps in the sea (deVries et al., 2012; BBC, 2014; Arizona-Sonora Desert Museum). Ambush predators often construct a burrow in which to hide, improving concealment at the cost of reducing their field of vision. Some ambush predators also use lures to attract prey within striking range (Moore & Biewener, 2015). The capturing movement has to be rapid to trap the prey, given that the attack is not modifiable once launched (Moore & Biewener, 2015).

Pursuit

Figure 16.1.8: Humpback whales (top photo) are lunge feeders, filtering thousands of krill from seawater and swallowing them alive. Dragonflies (bottom photo), like this common clubtail with captured prey, are invertebrate pursuit predators.

In pursuit predation, predators chase fleeing prey. If the prey flees in a straight line, capture depends only on the predator's being faster than the prey (Moore & Biewener, 2015). If the prey maneuvers by turning as it flees, the predator must react in real time to calculate and follow a new intercept path as it closes on the prey (Moore & Biewener, 2015). Many pursuit predators use camouflage to approach the prey as close as possible unobserved (stalking) before starting the pursuit (Moore & Biewener, 2015). Pursuit predators include terrestrial mammals such as humans, African wild dogs, spotted hyenas and wolves; marine predators such as dolphins, orcas and many predatory fishes, such as tuna (Gazda et al., 2005; Tyus, 2011); predatory birds (raptors) such as falcons; and insects such as dragonflies (Combes et al., 2013). Pursuit predators may be social, like the lion and wolf that hunt in groups, or solitary (Lafferty & Kuris, 2002).

An extreme form of pursuit is endurance or persistence hunting, in which the predator tires out the prey by following it over a long distance, sometimes for hours at a time. The method is used by human hunter-gatherers and by canids such as African wild dogs and domestic hounds. The African wild dog is an extreme persistence predator, tiring out individual prey by following them for many miles at relatively low speed (Hubel et al., 2016).

A specialized form of pursuit predation is the lunge feeding of baleen whales. These very large marine predators feed on plankton, especially krill, diving and actively swimming into concentrations of plankton, and then taking a huge gulp of water and filtering it through their feathery baleen plates (Goldbogen et al., 2006; Sanders et al., 2015).

Handling

Figure 16.1.9: Catfish has sharp dorsal and pectoral spines which it holds erect to discourage predators such as herons which swallow prey whole (top photo). Osprey tears its fish prey apart, avoiding dangers such as sharp spines.

Once the predator has captured the prey, it has to handle it: very carefully if the prey is dangerous to eat, such as if it possesses sharp or poisonous spines, as in many prey fish. Some catfish such as the Ictaluridae have spines on the back (dorsal) and belly (pectoral) which lock in the erect position; as the catfish thrashes about when captured, these could pierce the predator's mouth, possibly fatally. Some fish-eating birds like the osprey avoid the danger of spines by tearing up their prey before eating it (Forbes, 1989). Some prey may also be time-consuming to handle, such as clams or other bivalves that are difficult for predators to crush or open.

16.1.2 Predator Adaptations

Physical adaptations

Under the pressure of natural selection, predators have evolved a variety of physical adaptations for detecting, catching, killing, and digesting prey. These include speed, agility, stealth, sharp senses, claws, teeth, filters, and suitable digestive systems (Bar-Yam, 2018).

For detecting prey, predators have well-developed vision, smell, or hearing (Stevens et al., 2010). Predators as diverse as owls and jumping spiders have forward-facing eyes, providing accurate binocular vision over a relatively narrow field of view, whereas prey animals often have less acute all-round vision. Animals such as foxes can smell their prey even when it is concealed under 2 feet (60 cm) of snow or earth. Many predators have acute hearing, and some such as echolocating bats hunt exclusively by active or passive use of sound (Royal Saskatchewan Museum, 2012).

Predators including big cats, birds of prey, and ants share powerful jaws, sharp teeth, or claws which they use to seize and kill their prey. Some predators such as snakes and fish-eating birds like herons and cormorants swallow their prey whole; some snakes can unhinge their jaws to allow them to swallow large prey, while fish-eating birds have long spear-like beaks that they use to stab and grip fast-moving and slippery prey (Royal Saskatchewan Museum, 2012). Fish and other predators have developed the ability to crush or open the armored shells of molluscs (Vermeij, 1993).

Many predators are powerfully built and can catch and kill animals larger than themselves; this applies as much to small predators such as ants and shrews as to big and visibly muscular carnivores like the cougar and lion (Lafferty & Kuris, 2002; Getz, 2011;

Royal Saskatchewan Museum, 2012).

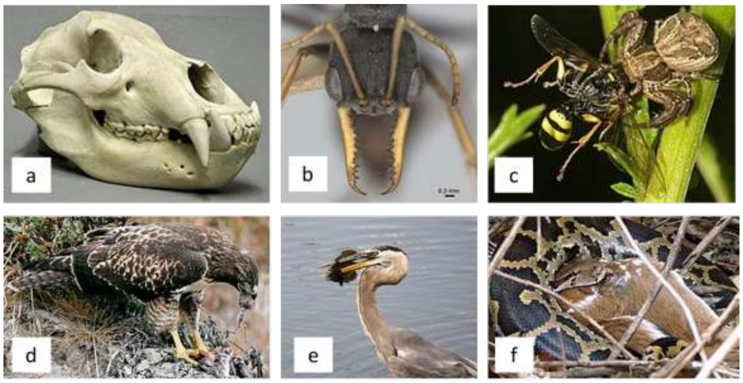


Figure 16.1.10: a) Skull of brown bear has large pointed canines for killing prey, and self-sharpening carnassial teeth at rear for cutting flesh with a scissor-like action, b) Large compound eyes, sensitive antennae, and powerful jaws (mandibles) of jack jumper ant, c) Crab spider, an ambush predator with forward-facing eyes, catching another predator, a field digger wasp, d) Red-tailed hawk uses sharp hooked claws and beak to kill and tear up its prey, e) Specialist: a great blue heron with a speared fish, f) Indian python unhinges its jaw to swallow large prey like this chital.

Camouflage and mimicry

Figure 16.1.11: A camouflaged snow leopard in Ladakh (top photo). Striated frogfish uses camouflage and aggressive mimicry in the form of a fishing rod-like lure on its head to attract prey (bottom photo).

Camouflage is the use of any combination of materials, coloration, or illumination for concealment, either by making animals or objects hard to see, or by disguising them as something else. Predators may use camouflage to more effectively capture prey, while prey may use camouflage to more effectively evade predation. Members of the cat family such as the snow leopard (treeless highlands), tiger (grassy plains, reed swamps), ocelot(forest), fishing cat (waterside thickets), and lion (open plains) are camouflaged with coloration and disruptive patterns suiting their habitats (Cott, 1940).

In aggressive mimicry, certain predators, including insects and fishes, make use of coloration and behavior to attract prey. Female *Photuris* fireflies, for example, copy the light signals of other species, thereby attracting male fireflies, which they capture and eat (Lloyd, 1965). Flower mantises are ambush predators; camouflaged as flowers, such as orchids, they attract prey and seize it when it is close enough (Forbes, 2009). Frogfishes are extremely well camouflaged, and actively lure their prey to approach using an esca, a bait on the end of a rod-like appendage on the head, which they wave gently to mimic a small animal, gulping the prey in an extremely rapid movement when it is within range (Bester, 2017).

Other Adaptations

- **Venom** - Many smaller predators such as the box jellyfish use venom to subdue their prey (Ruppert et al., 2005), and venom can also aid in digestion (as is the case for rattlesnakes and some spiders) (Cetaruk, 2005; Barceloux, 2008). The marbled sea snake that has adapted to egg predation has atrophied venom glands, and the gene for its three finger toxin contains a mutation (the deletion of two nucleotides) that inactives it. These changes are explained by the fact that its prey does not need to be subdued (Li et al., 2005).
- **Electric fields** - Several groups of predatory fish have the ability to detect, track, and sometimes, as in the electric ray, to incapacitate their prey by generating electric fields using electric organs (Castello et al., 2009; Feulner et al., 2009; Catania, 2015). The electric organ is derived from modified nerve or muscle tissue (Kramer, 1996).
- **Physiology** - Physiological adaptations to predation include the ability of predatory bacteria to digest the complex peptidoglycan polymer from the cell walls of the bacteria that they prey upon (Jurkevitch & Davidov, 2006). Carnivorous vertebrates of all five major classes (fishes, amphibians, reptiles, birds, and mammals) have lower relative rates of sugar to amino acid transport than either herbivores or omnivores, presumably because they acquire plenty of amino acids from the animal proteins in their diet (Karasov et al., 1988).

Predator/Prey Coevolution

Figure 16.1.12: Bats use echolocation to hunt moths at night.

To counter predation, prey have evolved defenses for use at each stage of an attack (Ruxton, 2004). They can try to avoid detection (Ruxton, 2004), such as by using camouflage and mimicry (Merilaita et al., 2017). They can detect predators (Caro, 2005) and warn others of their presence (Bergstrom & Lachmann, 2001; Getty, 2002). If detected, they can try to avoid being the target of an attack, for example, by signaling that they are toxic or unpalatable (Cott, 1940; Bowers et al., 1985), by forming groups (Beauchamp, 2012; Krause et al., 2002), or that a chase would be unprofitable (Ruxton et al., 2004; Caro, 2005). If they become a target, they can try to fend off the attack with defenses such as armor, quills, unpalatability, or mobbing (Dominey, 1983; Ruxton et al., 2004; Brodie, 2009) and they can escape an attack in progress by startling the predator (Cott, 1940; Merilaita et al., 2011; Edmunds, 2012), playing dead, shedding body parts such as tails, or simply fleeing (Caro, 2005).

Figure 16.1.13: Dead leaf mantis's camouflage makes it less visible to both predators and prey (top photo). Syrphid hoverfly misdirects predators by mimicking a wasp, but has no sting (bottom photo).

Predators and prey are natural enemies, and many of their adaptations seem designed to counter each other. For example, bats have sophisticated echolocation systems to detect insects and other prey, and insects have developed a variety of defenses including the ability to hear the echolocation calls (Jacobs & Bastian, 2017; Barbosa & Castellanos, 2005). Many pursuit predators that run on land, such as wolves, have evolved long limbs in response to the increased speed of their prey (Janis & Wilhelm, 1993). Their adaptations have been characterized as an **evolutionary arms race**, an example of the coevolution of two species (Dawkins & Krebs, 1979). In a gene centered view of evolution, the genes of predator and prey can be thought of as competing for the prey's body (Dawkins & Krebs, 1979). Though criticized, the "life-dinner" principle of Dawkins and Krebs predicts that this arms race is asymmetric: if a predator fails to catch its prey, it loses its dinner, while if it succeeds, the prey loses its life (Dawkins & Krebs, 1979).

Figure 16.1.14: Eastern coral snake, itself a predator, is venomous enough to kill predators that attack it, so when they avoid it, this behavior must be inherited, not learnt.

The metaphor of an arms race implies ever-escalating advances in attack and defense. However, these adaptations come with a cost; for instance, longer legs have an increased risk of breaking (Abrams, 1986), while the specialized tongue of the chameleon, with its ability to act like a projectile, is useless for lapping water, so the chameleon must drink dew off vegetation (Brodie, 1999).

16.1.3 Consequences of Predation

Predators affect their ecosystems not only directly by eating their own prey, but by indirect means such as reducing predation by other species, or altering the foraging behavior of an herbivore, as with the biodiversity effect of wolves on riverside vegetation or sea otters on kelp forests. This may explain population dynamics effects such as the cycles observed in lynx and snowshoe hares (Preisser et al., 2005; Peckarsky et al., 2008; Sheriff et al., 2020).

Biodiversity maintained by apex predation

Predators may increase the biodiversity of communities by preventing a single species from becoming dominant. Such predators are known as keystone species and may have a profound influence on the balance of organisms in a particular ecosystem (Bond, 2012). Introduction or removal of this predator, or changes in its population density, can have drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, grazers of a grassland may prevent a single dominant species from taking over (Bond, 2012).

Figure 16.1.15: Riparian willow recovery at Blacktail Creek, Yellowstone National Park, after reintroduction of wolves, the local keystone species and apex predator (Ripple & Beschta, 2004). Left, in 2002; right, in 2015

The elimination of wolves from Yellowstone National Park had profound impacts on the entire ecosystem's structure and function. In Yellowstone, wolves are both keystone species and apex predators. Without predation, herbivores began to over-graze many woody browse species, affecting the area's plant populations. In addition, wolves often kept animals from grazing near streams, protecting the beavers' food sources. The removal of wolves had a direct effect on the beaver population, as their habitat became territory for grazing. Increased browsing on willows and conifers along Blacktail Creek due to a lack of predation caused channel incision because the reduced beaver population was no longer able to slow the water down and keep the soil in place. The predators were thus demonstrated to be of vital importance in the ecosystem (Ripple & Beschta, 2004).

Population dynamics

In the absence of predators, the population of a species can grow exponentially until it approaches the carrying capacity of the environment (Neal, 2004). Predators limit the growth of prey both by consuming them and by changing their behavior (Nelson et al., 2004). Increases or decreases in the prey population can also lead to increases or decreases in the number of predators, for example, through an increase in the number of young they bear.

Cyclical fluctuations have been seen in populations of predator and prey, often with offsets between the predator and prey cycles. A well-known example is that of the snowshoe hare and lynx. Over a broad span of boreal forests in Alaska and Canada, the hare populations fluctuate in near synchrony with a 10-year period, and the lynx populations fluctuate in response. This was first seen in historical records of animals caught by fur hunters for the Hudson Bay Company over more than a century (Krebs et al., 2001; Peckarsky et al., 2008; Krebs, 2014; BBC, 2015).

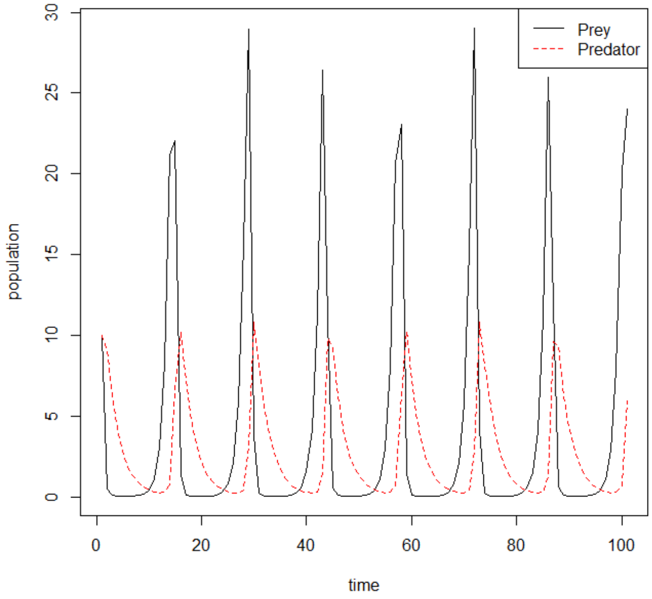


Figure 16.1.16: Predator-prey population cycles in a Lotka-Volterra model.

A simple model of a system with one species each of predator and prey, the Lotka–Volterra equations, predicts population cycles (Goel et al., 1971). However, attempts to reproduce the predictions of this model in the laboratory have often failed; for example, when the protozoan *Didinium nasutum* is added to a culture containing its prey, *Paramecium caudatum*, the latter is often driven to extinction (Levin et al., 2009).

The Lotka-Volterra equations rely on several simplifying assumptions, and they are structurally unstable, meaning that any change in the equations can stabilize or destabilize the dynamics (Murdoch et al., 2009; Nowak & May, 2000). For example, one assumption is that predators have a linear functional response to prey: the rate of kills increases in proportion to the rate of encounters. If this rate is limited by time spent handling each catch, then prey populations can reach densities above which predators cannot control them (Levin et al., 2009). Another assumption is that all prey individuals are identical. In reality, predators tend to select young, weak, and ill individuals, leaving prey populations able to regrow (Genovart et al., 2010).

Many factors can stabilize predator and prey populations (Rockwood, 2009). One example is the presence of multiple predators, particularly generalists that are attracted to a given prey species if it is abundant and look elsewhere if it is not (Rockwood, 2009). As a result, population cycles tend to be found in northern temperate and subarctic ecosystems because the food webs are simpler (Rockwood, 2009). The snowshoe hare-lynx system is subarctic, but even this involves other predators, including coyotes, goshawks and great horned owls, and the cycle is reinforced by variations in the food available to the hares (Rockwood, 2009).

A range of mathematical models have been developed by relaxing the assumptions made in the Lotka-Volterra model; these variously allow animals to have geographic distributions, or to migrate; to have differences between individuals, such as sexes and an age structure, so that only some individuals reproduce; to live in a varying environment, such as with changing seasons (Cushing, 2005; Thieme, 2003); and analyzing the interactions of more than just two species at once. Such models predict widely differing and often chaotic predator-prey population dynamics (Cushing, 2005; Kozlov & Vakulenko, 2013). The presence of refuge areas, where prey are safe from predators, may enable prey to maintain larger populations but may also destabilize the dynamics (Sih, 1987; McNair, 1986; Berryman et al., 2006; Ross & Garay, 2009).

✓ Alternative Stable States and Predator-Prey Dynamics 16.1.1

Case study based on the CC-BY Paper By:
Glaspie, C. N., Seitz, R. D., & Lipcius, R. N. (2020). Are predator-prey model predictions supported by empirical data? Evidence for a storm-driven shift to an alternative stable state in a crab-clam system. *Marine Ecology Progress Series*, *645*, 83-90.

Predators play a key role in ecosystem stability and function by consuming dominant competitors (Lubchenco & Gaines, 1981; Boudreau & Worm. 2012). Predators can also destabilize ecosystems or collapse food webs if they become too abundant (Estes et al., 2009), or if their prey do not have natural defenses against predation (Johnston et al., 2015). One of the ways the balance between predator and prey adaptations manifests itself in nature is through density-dependent predation. Predators can exhibit a numerical response to prey densities by increasing reproduction rates due to an overabundance of prey (demographic response) or by gathering in areas with relatively high densities of prey (aggregative response) (Holling, 1959). An individual predator may also adjust its predation rate to prey density through a ‘functional response’ (changes in a predator’s consumption rate in response to prey density).

Many mathematical models can be used to predict predator−prey dynamics (Briggs & Hoopes, 2004). These models contain nonlinear functions describing the density-dependent interactions between predator and prey. Due to nonlinearities, model behavior often includes shifts to alternative stable states (Drake & Griffen, 2010). The states may include extinction of one or both species, or coexistence steady states where both predator and prey are able to coexist at densities predicted by the model. The theory of **alternative stable states** predicts that ecosystems can exist under multiple "states" (sets of unique biotic and abiotic conditions). These alternative states are non-transitory and therefore considered stable over ecologically-relevant timescales. Ecosystems may transition from one stable state to another, in what is known as a state shift or regime shift, when perturbed. Due to ecological feedbacks, ecosystems display resistance to state shifts and therefore tend to remain in one state unless perturbations are large enough.

In their study, Glaspie et al. (2020) examined evidence for a storm-driven shift to a low-density state for the soft-shell clam *Mya arenaria*, which was once a biomass-dominant species in Chesapeake Bay, USA, in the face of predation by the blue crab *Callinectes sapidus*. Tropical Storm Agnes, which reached and remained in the Chesapeake Bay watershed from 21 to 23 June 1972, has long been suspected of causing long-term changes to the Bay (Orth & Moore, 1983). Tropical Storm Agnes was a ‘100-year storm’ that caused sustained, extremely low salinities and increased sedimentation throughout Chesapeake Bay (Schubel, 1976, Schubel et al., 1976). This storm has been blamed for accelerating the loss of seagrass *Zostera marina* (Orth & Moore, 1983) and oysters *Crassostrea virginica* (Haven et al. 1976) in Chesapeake Bay, although these losses were already in motion before the storm occurred. Unlike seagrass and oysters, declines in abundance of the soft-shell clam *M. arenaria* were uniquely related to the storm. *M. arenaria* was abundant enough to support a major commercial fishery throughout Chesapeake

Bay prior to 1972 (Haven, 1970). Widespread mass mortality of *M. arenaria* occurred after the storm (Cory & Redding, 1976), and the fishery never recovered in lower Chesapeake Bay (Virginia) (Glaspie et al., 2018).

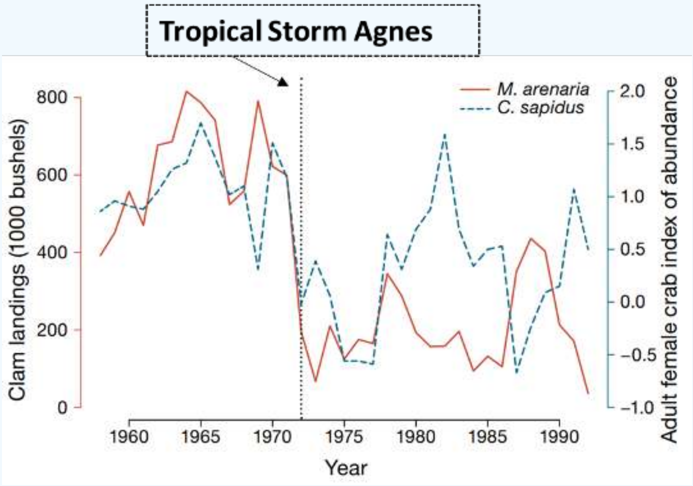


Figure $16.1.17$: Though the boom-and-bust cycle of the species continued after the Tropical Storm Agnes, the storm clearly impacted the abundance of the populations and disrupted the pattern of their population cycles.

Using a 30-year dataset on soft-shell clams and blue crabs, Glaspie et al. (2020) found that *Mya arenaria* was subjected to a storm-driven shift to a low-density alternative stable state, which has been maintained by blue crab predation in Chesapeake Bay. Before the storm, clams were likely prey for juvenile crabs that entered the fishery at 1 yr of age, resulting in a positive correlation between crab and clam abundance with a lag of 1 yr (Figure $16.1.2a$). After the storm, crabs were likely consuming juvenile clams that would have been large enough to enter the fishery a year later, resulting in a negative correlation between clams and crab abundance with a lag of 1 yr (Figure $16.1.2b$). Both *M. arenaria* and *Callinectes sapidus* enter their respective fisheries after $1-1.5$ yr (Newell & Hidu, 1986; Lipcius & van Engel, 1990), providing an explanation for the 1 yr lag. This is consistent with a shift from a system controlled from the bottom up (i.e., by the abundance of prey resources), to a system controlled from the top down by predation pressure on bivalves.

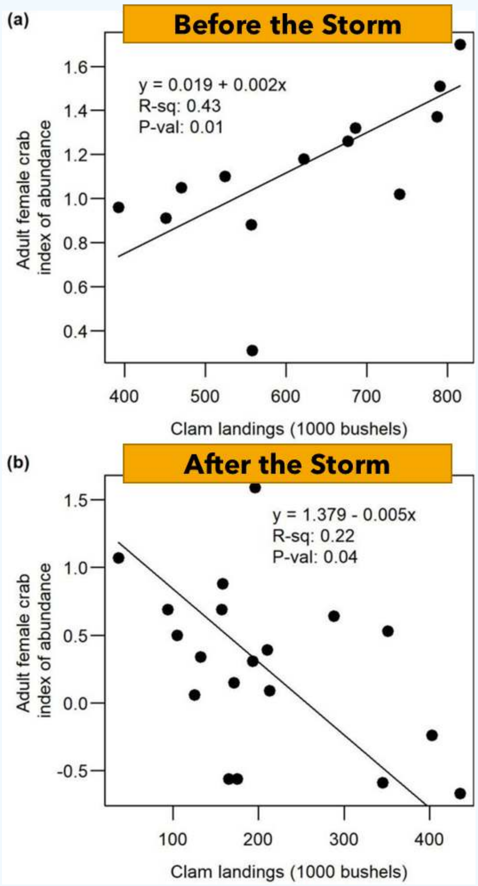


Figure 16.1.18: The change in trendlines from a positive correlation before the storm to a negative correlation after the storm again shows the impact natural disasters can have on the patterns of population cycles.

16.2: Quantifying Predator-Prey Dynamics

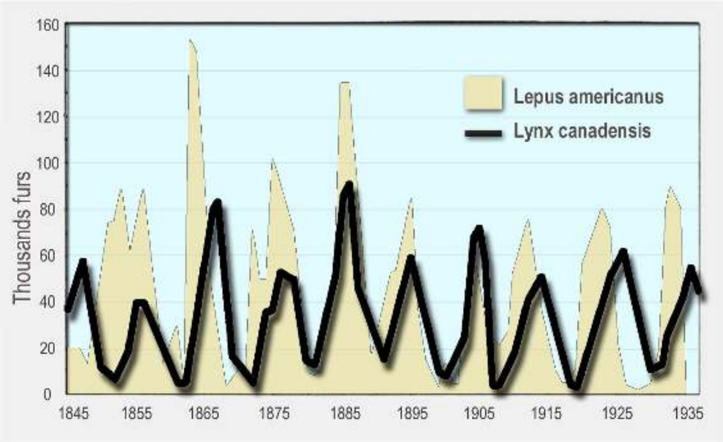


Figure 16.2.1 : Numbers of snowshoe hare (*Lepus americanus*) (yellow background) and Canada lynx (black line, foreground) furs sold to the Hudson's Bay Company from 1845 to 1935. Image by Lamiot is licensed under CC BY-SA 4.0.

In the classic Lotka-Volterra model of predator-prey dynamics, both predators and prey are modeled using a modified version of the equation for exponential growth, so neither population has an explicit carrying capacity. However, either or both may have an implicit carrying capacity imposed by the interaction between the two populations.

To model the prey population, we begin with a basic exponential model with some additional terms. Here, the prey population is growing at their intrinsic growth rate $\mathrm{r_{prey}}$, but is also declining due to predation.

The number of prey killed will depend on the number of predators: the greater the number of predators, the more prey they will kill ($\mathrm{N_{pred}}$). It will also depend on the number of prey available: the more prey, the more successful the predators ($\mathrm{N_{prey}}$). Finally, it will depend on the **attack rate**: the ability of a predator to find and consume prey (p). The number of prey killed in one time interval will be the product of these, $pN_{prey}N_{pred}$. The resulting equation for prey growth is:

$$\mathrm{dN_{prey}}/\mathrm{dt} = \mathrm{r_{prey}}\,\mathrm{N_{prey}} - \mathrm{pN_{prey}}\,\mathrm{N_{pred}}$$

In words, the prey population grows according to its per capita growth rate minus losses to predators. Losses are determined by attack rate, predator population, and prey population.

To model the predator population, we also begin with an exponential model, in concept. However, there is a wrinkle in this model, because we cannot assume a constant per capita rate of population growth. There is no simple *r* for the predator population because its growth rate will depend on how many prey are caught. As in the prey model, the number of prey caught will be $pN_{prey}N_{pred}$. The growth of the predator population will depend on this number, and on the efficiency with which predators convert consumed prey into predator offspring (*c* for conversion).

We will represent this conversion efficiency with the parameter *c*, so the per capita population growth of predators will be $cpN_{prey}N_{pred}$. We should reduce this predator population growth by some quantity to represent the starvation rate of predators who fail to consume prey. This will be the product of the per capita starvation rate times the predator population: dN_{pred}. Taking all this into account, we can write an equation for the predator population:

$$\mathrm{dN_{pred}/dt = cpN_{prey}\,N_{pred} - d_{pred}\,N_{pred}}$$

In words, the predator population grows according to the attack rate, conversion efficiency, and prey population, minus losses to starvation.

Predator-Prey Model Parameters

dN_{prey}/dt = rate of change in prey population (change in number over change in time)

dN_{pred}/dt = rate of change in predator population (change in number over change in time)

c = rate at which prey are converted into offspring (a slope: predators produced per predator per time as a function of prey consumed per unit time)

p = attack rate efficiency (a slope: the change in prey consumed per predator per time as a function of the number of prey); higher search or handling time leads to a lower p

d_{pred} = predator death rate

r_{prey} = prey per capita rate of increase

N_{prey} = number of prey

N_{pred} = number of predators

It's important to note that the prey and predator equations above are **coupled equations**. In other words, the equation for prey includes a term for N_{pred} and the equation for predators includes the term N_{prey} and changes in one population will always impact the other population. Specifically, these equations lead to oscillations between the populations of predators and their prey.

We can ask several questions about the interaction between predators and their prey using these equations:

- Under what conditions (i.e., parameter values) will the predator population drive the prey to extinction?
- Under what conditions will the predator population die off, leaving the prey population to expand unhindered?
- Under what conditions will predator and prey populations both persist indefinitely? What will be their population dynamics while they coexist? In other words, will one or both populations stabilize, or will they continue to change over time?

Equilibrium Solutions

We will examine these questions by seeking equilibrium solutions to the coupled predator and prey equations we introduced above. For the prey population, we want to find values of predator and prey population sizes at which the prey population remains stable. In other words, we want to solve for $dN_{pred}/dt = 0$ and $dN_{prey}/dt = 0$. Though we will not go through the derivations here, you can try them out on your own by replacing these terms with 0 then solving for N_{prey} and N_{pred}, respectively.

In words, the prey population reaches equilibrium when the predator population equals the prey's per capita growth rate divided by the predator's attack rate. Note that this is a constant. Strangely, the equilibrium size of the prey population is not determined by this solution, which says, in effect, that the prey population can be stable at any size as long as the predator population is at the specified size.

The isocline of Zero Growth for Prey occurs at $N_{pred} = r_{prey}/p$

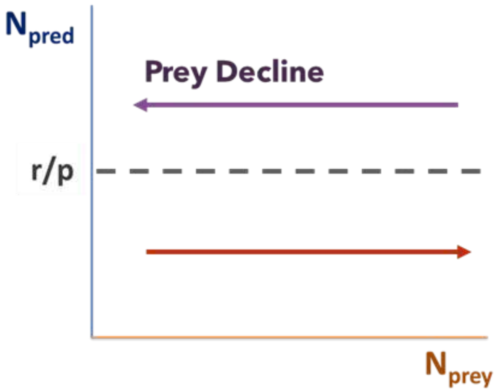


Figure 16.2.2: The dotted line (r/p) shows the isocline of zero growth for prey. They purple and orange lines show the direction of the prey and predator populations.

In words, the predator population reaches equilibrium when the prey population equals the predator's starvation rate over the product of attack rate times conversion efficiency. Note that this is also a constant, and like the solution for the prey population, it does not specify the equilibrium size of the predator population, only the size of the prey population at which the predators are at equilibrium.

The isocline of Zero Growth for Predator occurs at $N_{prey} = d/cp$

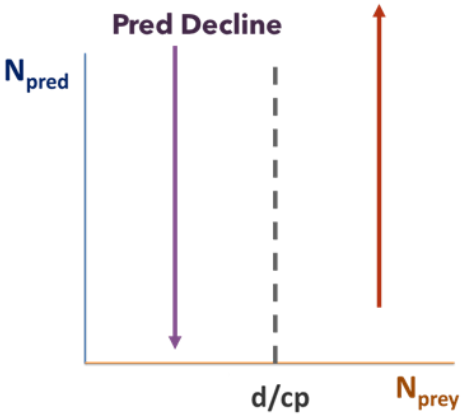


Figure 16.2.3: The dotted line shows the isocline of zero growth for predators (d/cp), while the purple and orange lines describe the direction the predator and prey populations will trend towards.

Now that we have solved for these isoclines, we can plot the population sizes of the two interacting populations on the two axes of a graph. The equilibrium solutions then become straight-line zero net growth isoclines (ZNGIs).

On this graph, the ZNGI for the prey population is a horizontal line at r_{prey}/p (orange line), below which the prey population increases, and above which it decreases. The ZNGI for the predator population is a vertical line at d/cp (blue line), to the left of which the predator population decreases, and to the right of which it increases (dashed arrows).

Where the two lines cross—at the point [d/cp, r_{prey}/p]—the two populations are at equilibrium. The continuous-time Lotka-Volterra model predicts that the point representing the two populations will cycle endlessly around the point where the two ZNGIs cross.

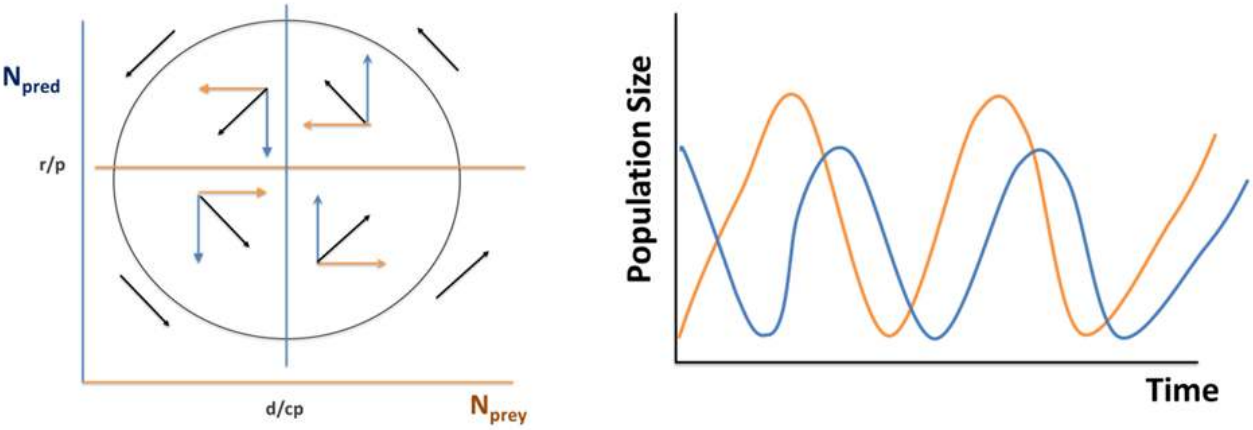


Figure 16.2.4: To the left, the isoclines for zero predator and prey growth are plotted. The vector arrows in each quadrant describe the counter-clockwise trends of the populations based on the movement from their initial populations to the point of equilibrium created by the isoclines. To the right, the boom-and-bust cycle of the populations are shown.

A Quick Summary - Coupled Predator-Prey Models

Based on the Exponential Model:

- Predators decline exponentially without food (prey)
- Prey increase exponentially without predation

Outcomes Depend on:

- Predator functional (p) and numerical (c) response
- Predator and prey birth/death rate
- Predator and prey initial population size

Steps for Finding the Oscillations:

- Find and plot d/cp
- Find and plot and r/p
- Plot initial population
- At isoclines, either predator or prey change trajectory

16.3: Herbivory

Herbivory is a form of consumption in which an organism principally eats autotrophs (Abraham 2006) such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs are known as **primary consumers.** Herbivory is usually limited to animals that eat plants. Fungi, bacteria, and protists that feed on living plants are usually termed plant pathogens (plant diseases), while fungi and microbes that feed on dead plants are described as saprotrophs. Flowering plants that obtain nutrition from other living plants are usually termed parasitic plants.

16.3.1 Feeding Strategies

Two herbivore feeding strategies are grazing (e.g. cows) and browsing (e.g. moose). For a terrestrial mammal to be called a grazer, at least 90% of the forage has to be grass, and for a browser at least 90% tree leaves and twigs. An intermediate feeding strategy is called "mixed-feeding" (Janis, 1990). In their daily need to take up energy from forage, herbivores of different body mass may be selective in choosing their food (Belovsky, 1997). "Selective" means that herbivores may choose their forage source depending on, e.g., season or food availability, but also that they may choose high quality (and consequently highly nutritious) forage before lower quality. The latter especially is determined by the body mass of the herbivore, with small herbivores selecting for high-quality forage, and with increasing body mass animals are less selective (Belovsky, 1997).

Feeding Strategy	Diet	Example
Algivores	Algae	krill, crabs, sea snail, sea urchin, parrotfish, surgeonfish, flamingo
Frugivores	Fruit	Ruffed lemurs, orangutans
Folivores	Leaves	Koalas, gorillas, red colobuses
Nectarivores	Nectar	Honey possum, hummingbirds
Granivores	Seeds	Hawaiian honeycreepers
Graminivores	Grass	Horses
Palynivores	Pollen	Bees
Mucivores	Plant fluids, i.e. sap	Aphids
Xylophages	Wood	Termites

Figure 16.3.1 : Herbivores employ numerous types of feeding strategies. Many herbivores do not fall into one specific feeding strategy, but employ several strategies and eat a variety of plant parts.

16.3.2 Plant-herbivore interactions

Interactions between plants and herbivores can play a prevalent role in ecosystem dynamics such community structure and functional processes (Sandsen & Klaassen, 2008; Descombes et al., 2016). Plant diversity and distribution is often driven by herbivory, and it is likely that trade-offs between plant competitiveness and defensiveness, and between colonization and mortality allow for coexistence between species in the presence of herbivores (Lubchenco, 1978; Gleeson & Wilson, 1986; Olff & Ritchie, 1998; Hidding et al., 2009). However, the effects of herbivory on plant diversity and richness is variable. For example, increased abundance of herbivores such as deer decrease plant diversity and species richness (Arcese et al., 2014), while other large mammalian herbivores like bison control dominant species, which allows other species to flourish (Collins 1998). Plant-herbivore interactions can also operate so that plant communities mediate herbivore communities (Pellissier et al., 2013). Plant communities that are more diverse typically sustain greater herbivore richness by providing a greater and more diverse set of resources (Tilman, 1997).

Coevolution and phylogenetic correlation between herbivores and plants are important aspects of the influence of herbivore and plant interactions on communities and ecosystem functioning, especially in regard to herbivorous insects (Descombes et al., 2016; Pellissier et al., 2013; Mitter et al., 1991). This is apparent in the adaptations plants develop to tolerate and/or defend from insect herbivory and the responses of herbivores to overcome these adaptations. The evolution of antagonistic and mutualistic plant-herbivore interactions are not mutually exclusive and may co-occur (de Mazancourt et al., 2001). Plant phylogeny has been found to facilitate the colonization and community assembly of herbivores, and there is evidence of phylogenetic linkage between plant beta diversity and phylogenetic beta diversity of insect clades such as butterflies. These types of eco-evolutionary feedbacks between plants and herbivores are likely the main driving force behind plant and herbivore diversity (Pellissier et al., 2013; Mitter et al., 1991).

Abiotic factors such as climate and biogeographical features also impact plant-herbivore communities and interactions. For example, in temperate freshwater wetlands herbivorous waterfowl communities change according to season, with species that eat above-ground vegetation being abundant during summer, and species that forage below-ground being present in winter months (Sansten & Klaassen, 2008; Hidding et al., 2009). These seasonal herbivore communities differ in both their assemblage and functions within the wetland ecosystem (Hidding et al., 2009). Such differences in herbivore modalities can potentially lead to trade-offs that influence species traits and may lead to additive effects on community composition and ecosystem functioning (Sansten & Klaassen, 2008; Hidding et al., 2009). Seasonal changes and environmental gradients such as elevation and latitude often affect the palatability of plants which in turn influences herbivore community assemblages and vice versa (Descombes et al., 2016; Hidding et al., 2009). Examples include a decrease in abundance of leaf-chewing larvae in the fall when hardwood leaf palatability decreases due to increased tannin levels which results in a decline of arthropod species richness (Futuyma & Gould, 1979) and increased palatability of plant communities at higher elevations where grasshoppers abundances are lower (Descombes et al., 2016). Climatic stressors such as ocean acidification can lead to responses in plant-herbivore interactions in relation to palatability as well (Poore et al., 2013).

Herbivore Offense

Figure 16.3.2: Aphids are fluid feeders on plant sap.

The myriad defenses displayed by plants means that their herbivores need a variety of skills to overcome these defenses and obtain food. These allow herbivores to increase their feeding and use of a host plant. Herbivores have three primary strategies for dealing with plant defenses: choice, herbivore modification, and plant modification.

Feeding choice involves which plants a herbivore chooses to consume. It has been suggested that many herbivores feed on a variety of plants to balance their nutrient uptake and to avoid consuming too much of any one type of defensive chemical. This involves a tradeoff however, between foraging on many plant species to avoid toxins or specializing on one type of plant that can be detoxified (Dearing et al., 2000).

Herbivore modification is when various adaptations to body or digestive systems of the herbivore allow them to overcome plant defenses. This might include detoxifying secondary metabolites (Karban & Agrawal, 2002), sequestering toxins unaltered (Nishida, 2002), or avoiding toxins, such as through the production of large amounts of saliva to reduce effectiveness of defenses. Herbivores may also utilize symbionts to evade plant defenses. For example, some aphids use bacteria in their gut to provide essential amino acids lacking in their sap diet (Douglas, 1998).

Plant modification occurs when herbivores manipulate their plant prey to increase feeding. For example, some caterpillars roll leaves to reduce the effectiveness of plant defenses activated by sunlight (Sagers, 1992).

Plant Defense

A plant defense is a trait that increases plant fitness when faced with herbivory. This is measured relative to another plant that lacks the defensive trait. Plant defenses increase survival and/or reproduction (fitness) of plants under pressure of predation from herbivores.

Defense can be divided into two main categories, tolerance and resistance. Tolerance is the ability of a plant to withstand damage without a reduction in fitness (Call & St. Clair, 2018). This can occur by diverting herbivory to non-essential plant parts, resource allocation, compensatory growth, or by rapid regrowth and recovery from herbivory (Hawkes & Sullivan, 2001). Resistance refers to the ability of a plant to reduce the amount of damage it receives from herbivores (Call & St. Clair, 2018). This can occur via avoidance in space or time (Milchunas & Noy-Meir, 2002), physical defenses, or chemical defenses. Defenses can either be constitutive, always present in the plant, or induced, produced or translocated by the plant following damage or stress (Edwards & Wratten, 1985).

Physical, or mechanical, defenses are barriers or structures designed to deter herbivores or reduce intake rates, lowering overall herbivory. Thorns such as those found on roses or acacia trees are one example, as are the spines on a cactus. Smaller hairs known as trichomes may cover leaves or stems and are especially effective against invertebrate herbivores (Pillemer & Tingey, 1976). In addition, some plants have waxes or resins that alter their texture, making them difficult to eat. Also the incorporation of silica into cell walls is analogous to that of the role of lignin in that it is a compression-resistant structural component of cell walls; so that plants with their cell walls impregnated with silica are thereby afforded a measure of protection against herbivory (Epstein, 1994).

Chemical defenses are secondary metabolites produced by the plant that deter herbivory. There are a wide variety of these in nature and a single plant can have hundreds of different chemical defenses. Chemical defenses can be divided into two main groups, carbon-based defenses and nitrogen-based defenses.

1. Carbon-based defenses include terpenes and phenolics. Terpenes are derived from 5-carbon isoprene units and comprise essential oils, carotenoids, resins, and latex. They can have several functions that disrupt herbivores such as inhibiting adenosine triphosphate (ATP) formation, molting hormones, or the nervous system (Langenheim, 1994). Phenolics combine an aromatic carbon ring with a hydroxyl group. There are several different phenolics such as lignins, which are found in cell walls and are very indigestible except for specialized microorganisms; tannins, which have a bitter taste and bind to proteins making them indigestible; and furanocumerins, which produce free radicals disrupting DNA, protein, and lipids, and can cause skin irritation.
2. Nitrogen-based defenses are synthesized from amino acids and primarily come in the form of alkaloids and cyanogens. Alkaloids include commonly recognized substances such as caffeine, nicotine, and morphine. These compounds are often bitter and can inhibit DNA or RNA synthesis or block nervous system signal transmission. Cyanogens get their name from the cyanide stored within their tissues. This is released when the plant is damaged and inhibits cellular respiration and electron transport.

Plants have also changed features that enhance the probability of attracting natural enemies to herbivores. Some emit semiochemicals, odors that attract natural enemies, while others provide food and housing to maintain the natural enemies' presence, e.g. ants that reduce herbivory (Heil et al., 2001). A given plant species often has many types of defensive mechanisms, mechanical or chemical, constitutive or induced, which allow it to escape from herbivores.

16.4: Parasitism

Figure 16.4.1: A fish parasite, the isopod *Cymothoa exigua*, replacing the tongue of a *Lithognathus.*

Parasitism is a close relationship between species, where one organism, the parasite, lives on or inside another organism, the host, causing it some harm, and is adapted structurally to this way of life (Poulin, 2007). Like predation, parasitism is a type of consumer-resource interaction (Getz, 2011), but unlike predators, parasites, with the exception of parasitoids, are typically much smaller than their hosts, do not kill them, and often live in or on their hosts for an extended period. Parasites of animals are highly specialized, and reproduce at a faster rate than their hosts. Classic examples include interactions between vertebrate hosts and tapeworms, flukes, the malaria-causing *Plasmodium* species, and fleas.

Parasites reduce host fitness by general or specialized pathology, from parasitic castration to modification of host behavior. Parasites increase their own fitness by exploiting hosts for resources necessary for their survival, in particular by feeding on them and by using intermediate (secondary) hosts to assist in their transmission from one definitive (primary) host to another. Although parasitism is often unambiguous, it is part of a spectrum of interactions between species, grading via parasitoidism into predation, through evolution into mutualism, and in some fungi, shading into being saprophytic.

Within that scope are many possible strategies. Taxonomists classify parasites in a variety of overlapping schemes, based on their interactions with their hosts and on their life-cycles, which are sometimes very complex. An **obligate** parasite depends completely on the host to complete its life cycle, while a **facultative** parasite does not. Parasite life-cycles involving only one host are called **"direct"**; those with a definitive host (where the parasite reproduces sexually) and at least one intermediate host are called **"indirect"** (Garcia, 1999). An **endoparasite** lives inside the host's body; an **ectoparasite** lives outside, on the host's surface (Australian Society of Parasitology, 2010). **Mesoparasites**—like some copepods, for example—enter an opening in the host's body and remain partly embedded there (Vecchione & Aznar, 2008). Some parasites can be **generalists,** feeding on a wide range of hosts, but many parasites, and the majority of protozoans and helminths that parasitise animals, are **specialists** and extremely host-specific (Australian Society of Parasitology, 2010). The microorganisms and viruses that can reproduce and complete their life cycle within the host are known as **microparasites**. **Macroparasites** are the multicellular organisms that reproduce and complete their life cycle outside of the host or on the host's body (Poulin, 2011; Blackwell Science, 2018).

16.4.1 Strategies

There are six major parasitic strategies, namely parasitic castration; directly transmitted parasitism; trophically-transmitted parasitism; vector-transmitted parasitism; parasitoidism; and micropredation. These apply to parasites whose hosts are plants as well as animals (Poulin, 2011; Poulin, 2015). These strategies represent adaptive peaks; intermediate strategies are possible, but organisms in many different groups have consistently converged on these six, which are evolutionarily stable (Poulin, 2011).

A perspective on the evolutionary options can be gained by considering four key questions: the effect on the fitness of a parasite's hosts; the number of hosts they have per life stage; whether the host is prevented from reproducing; and whether the effect depends on intensity (number of parasites per host). From this analysis, the major evolutionary strategies of parasitism emerge, alongside predation (Lafferty & Kuris, 2002).

Host fitness	Single host, stays alive	Single host, dies	Multiple hosts
Able to reproduce (fitness > 0)	Conventional parasite *Pathogen*	Trophically-transmitted parasite *Trophically-transmitted pathogen*	Micropredator *Micropredator*
Unable to reproduce (fitness = 0)	----- *Parasitic castrator*	Trophically-transmitted parasitic castrator *Parasitoid*	Social predator *Solitary predator*

Figure 16.4.2: Major parasitic strategies categorized by host fitness and survival and by the number of hosts.

Parasitic castrators

Figure 16.4.3: The parasitic castrator *Sacculina carcini* (highlighted) attached to its crab host.

Parasitic castrators partly or completely destroy their host's ability to reproduce, diverting the energy that would have gone into reproduction into host and parasite growth, sometimes causing gigantism in the host. The host's other systems remain intact, allowing it to survive and to sustain the parasite (Poulin, 2015; Poulin, 2007). Parasitic crustaceans such as those in the specialized barnacle genus *Sacculina* specifically cause damage to the gonads of their many species (Elumalai et al., 2013) of host crabs. In the case of *Sacculina*, the testes of over two-thirds of their crab hosts degenerate sufficiently for these male crabs to develop female secondary sex characteristics such as broader abdomens, smaller claws and egg-grasping appendages. Various species of helminth castrate their hosts (such as insects and snails). This may happen directly, whether mechanically by feeding on their gonads, or by secreting a chemical that destroys reproductive cells; or indirectly, whether by secreting a hormone or by diverting nutrients. For example, the trematode *Zoogonus lasius*, whose sporocysts lack mouths, castrates the intertidal marine snail *Tritia obsoleta* chemically, developing in its gonad and killing its reproductive cells (Poulin, 2007; Cheng, 2012).

Directly transmitted

Figure 16.4.4: Human head-lice exemplify directly transmitted obligate ectoparasites.

Directly transmitted parasites, not requiring a vector to reach their hosts, include such parasites of terrestrial vertebrates as lice and mites; marine parasites such as copepods and cyamid amphipods; monogeneans; and many species of nematodes, fungi, protozoans, bacteria, and viruses. Whether endoparasites or ectoparasites, each has a single host-species. Within that species, most individuals are free or almost free of parasites, while a minority carry a large number of parasites; this is known as an aggregated distribution (Poulin, 2015).

Trophically transmitted

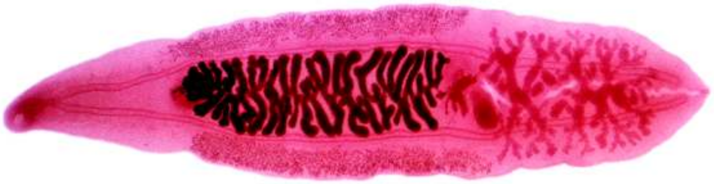


Figure 16.4.5: *Clonorchis sinensis*, the Chinese liver fluke, is trophically transmitted.

Trophically-transmitted parasites are transmitted by being eaten by a host. They include trematodes (all except schistosomes), cestodes, acanthocephalans, pentastomids, many round worms, and many protozoa such as *Toxoplasma* (Poulin, 2015). They have complex life-cycles involving hosts of two or more species. In their juvenile stages they infect and often encyst in the intermediate host. When the intermediate-host animal is eaten by a predator, the definitive host, the parasite survives the digestion process and matures into an adult; some live as intestinal parasites. Many trophically-transmitted parasites modify the behavior of their intermediate hosts, increasing their chances of being eaten by a predator. As with directly transmitted parasites, the distribution of trophically transmitted parasites among host individuals is aggregated (Poulin, 2015). Coinfection by multiple parasites is common (Cox, 2001). Autoinfection, where (by exception) the whole of the parasite's life-cycle takes place in a single primary host, can sometimes occur in helminths such as *Strongyloides stercoralis* (Australian Society of Parasitology, 2017).

Vector-transmitted

Figure 16.4.6: The vector-transmitted protozoan endoparasite *Trypanosoma* among human red blood cells.

Vector-transmitted parasites rely on a third party, an intermediate host, where the parasite does not reproduce sexually (Australian Society of Parasitology, 2010) to carry them from one definitive host to another (Poulin & Randhawa, 2015). These parasites are microorganisms, namely protozoa, bacteria, or viruses, often intracellular pathogens (disease-causers) (Poulin & Randhawa, 2015). Their vectors are mostly hematophagic arthropods such as fleas, lice, ticks, and mosquitoes (Poulin & Randhawa, 2015; PEOI, 2013). For example, the deer tick *Ixodes scapularis* acts as a vector for diseases including Lyme disease, babesiosis, and anaplasmosis (Steere, 2001). Protozoan endoparasites, such as the malarial parasites in the genus *Plasmodium* and sleeping-sickness parasites in the genus *Trypanosoma*, have infective stages in the host's blood which are transported to new hosts by biting insects (Pollitt et al., 2011).

Parasitoids

Parasitoids are insects which sooner or later kill their hosts, placing their relationship close to predation (Stevens, 2010). Most parasitoids are parasitoid wasps or other hymenopterans; others include dipterans such as phorid flies. They can be divided into two groups, idiobionts and koinobionts, differing in their treatment of their hosts (Gullan & Cranston, 2010).

Idiobiont parasitoids sting their often large prey on capture, either killing them outright or paralyzing them immediately. The immobilized prey is then carried to a nest, sometimes alongside other prey if it is not large enough to support a parasitoid throughout its development. An egg is laid on top of the prey and the nest is then sealed. The parasitoid develops rapidly through its larval and pupal stages, feeding on the provisions left for it (Gullan & Cranston, 2010).

Figure 16.4.7: Idiobiont parasitoid wasps immediately paralyze their hosts for their larvae (*Pimplinae*, pictured) to eat (Poulin & Randhawa, 2015).

Koinobiont parasitoids, which include flies as well as wasps, lay their eggs inside young hosts, usually larvae. These are allowed to go on growing, so the host and parasitoid develop together for an extended period, ending when the parasitoids emerge as adults, leaving the prey dead, eaten from inside. Some koinobionts regulate their host's development, for example preventing it from pupating or making it molt whenever the parasitoid is ready to molt. They may do this by producing hormones that mimic the host's molting hormones (ecdysteroids), or by regulating the host's endocrine system (Gullan & Cranston, 2010).

Figure 16.4.8: Koinobiont parasitoid wasps like this braconid lay their eggs inside their hosts, which continue to grow and moult.

Figure 16.4.9: Phorid fly (center left) is laying eggs in the abdomen of a worker honey-bee, altering its behavior.

Micropredators

Figure 16.4.10: Mosquitoes are micropredators, and important vectors of disease.

A micropredator attacks more than one host, reducing each host's fitness by at least a small amount, and is only in contact with any one host intermittently. This behavior makes micropredators suitable as vectors, as they can pass smaller parasites from one host to another (Poulin & Randhawa, 2015; Lafferty & Kuris, 2002; Wilson et al., 2017). Most micropredators are hematophagic, feeding on blood. They include annelids such as leeches, crustaceans such as branchiurans and gnathiid isopods, various dipterans such as mosquitoes and tsetse flies, other arthropods such as fleas and ticks, vertebrates such as lampreys, and mammals such as vampire bats (Poulin & Randhawa, 2015).

16.4.2 Variations on Parasitism

Hyperparasitism

Hyperparasites feed on another parasite, as exemplified by protozoa living in helminth parasites (Dissanaike, 1957), or facultative or obligate parasitoids whose hosts are either conventional parasites or parasitoids (Poulin & Randhawa, 2015; Gullan & Cranston, 2010). Levels of parasitism beyond secondary also occur, especially among facultative parasitoids. In oak gall systems, there can be up to five levels of parasitism (Askew, 1951).

Hyperparasites can control their hosts' populations, and are used for this purpose in agriculture and to some extent in medicine. The controlling effects can be seen in the way that the CHV1 virus helps to control the damage that chestnut blight, *Cryphonectria parasitica*, does to American chestnut trees, and in the way that bacteriophages can limit bacterial infections. It is likely, though little researched, that most pathogenic microparasites have hyperparasites which may prove widely useful in both agriculture and medicine (Parratt & Laine, 2016).

Figure 16.4.11: A hyperparasitoid pteromalid wasp on the cocoons of its host, itself a parasitoid braconid wasp.

Social parasitism

Social parasites take advantage of interspecific interactions between members of eusocial animals such as ants, termites, and bumblebees. Examples include the large blue butterfly, *Phengaris arion*, its larvae employing ant mimicry to parasitise certain ants (Thomas et al., 2010), *Bombus bohemicus*, a bumblebee which invades the hives of other bees and takes over reproduction while their young are raised by host workers, and *Melipona scutellaris*, a eusocial bee whose virgin queens escape killer workers and invade another colony without a queen (Van Oystaeyen et al., 2013). An extreme example of interspecific social parasitism is found in the ant *Tetramorium inquilinum*, an obligate parasite which lives exclusively on the backs of other *Tetramorium* ants (Antkeepers, 2016).

Figure 16.4.12: The large blue butterfly is an ant mimic and social parasite.

Brood parasitism

In brood parasitism, the hosts act as parents as they raise the young as their own. Brood parasites include birds in different families such as cowbirds, whydahs, cuckoos, and black-headed ducks. These do not build nests of their own, but leave their eggs in nests of other species. The eggs of some brood parasites mimic those of their hosts, while some cowbird eggs have tough shells, making them hard for the hosts to kill by piercing, both mechanisms implying selection by the hosts against parasitic eggs (Payne, 1997; Rothstein, 1990; De Marsico et al., 2013). The adult female European cuckoo further mimics a predator, the European sparrowhawk, giving her time to lay her eggs in the host's nest unobserved (Welbergen & Davies, 2011).

Figure 16.4.13: In brood parasitism, the host raises the young of another species, here a cowbird's egg, that has been laid in its nest.

Kleptoparasitism

In kleptoparasitism (from Greek κλέπτης (*kleptēs*), "thief"), parasites steal food gathered by the host. The parasitism is often on close relatives, whether within the same species or between species in the same genus or family. For instance, the many lineages of cuckoo bees lay their eggs in the nest cells of other bees in the same family (Slater et al., 2005). Kleptoparasitism is uncommon generally but conspicuous in birds; some such as skuas are specialized in pirating food from other seabirds, relentlessly chasing them down until they disgorge their catch (Furness, 1978).

Figure 16.4.14: The great skua is a powerful kleptoparasite, relentlessly pursuing other seabirds until they disgorge their catches of food.

Sexual parasitism

A unique approach is seen in some species of anglerfish, such as *Ceratias holboelli*, where the males are reduced to tiny sexual parasites, wholly dependent on females of their own species for survival, permanently attached below the female's body, and unable to fend for themselves. The female nourishes the male and protects him from predators, while the male gives nothing back except the sperm that the female needs to produce the next generation (Pietsch, 2005).

Figure 16.4.15: The male anglerfish *Ceratias holboelli* lives as a tiny sexual parasite permanently attached below the female's body.

Adelphoparasitism

Adelphoparasitism, (from Greek ἀδελφός (*adelphós*), brother – Maggenti et al., 2005), also known as sibling-parasitism, occurs where the host species is closely related to the parasite, often in the same family or genus (Rochat & Gutierrez, 2001). In the citrus blackfly parasitoid, *Encarsia perplexa*, unmated females of which may lay haploid eggs in the fully developed larvae of their own species, producing male offspring (University of Florida, 2018), while the marine worm *Bonellia viridis* has a similar reproductive strategy, although the larvae are planktonic (Berec et al., 2005).

Figure 16.4.16: *Encarsia perplexa* (center), a parasitoid of citrus blackfly (lower left), is also an adelphoparasite, laying eggs in larvae of its own species.

16.5: Infection

An **infection** is the invasion of an organism's body tissues by disease-causing agents, their multiplication, and the reaction of host tissues to the infectious agents and the toxins they produce. An **infectious disease**, also known as a **transmissible disease** or **communicable disease**, is an illness resulting from an infection.

Infections can be caused by a wide range of pathogens, most prominently bacteria and viruses (Sehgal & Ladd, 2020). Hosts can fight infections using their immune system. Mammalian hosts react to infections with an innate response, often involving inflammation, followed by an adaptive response.

16.5.1 Pathophysiology

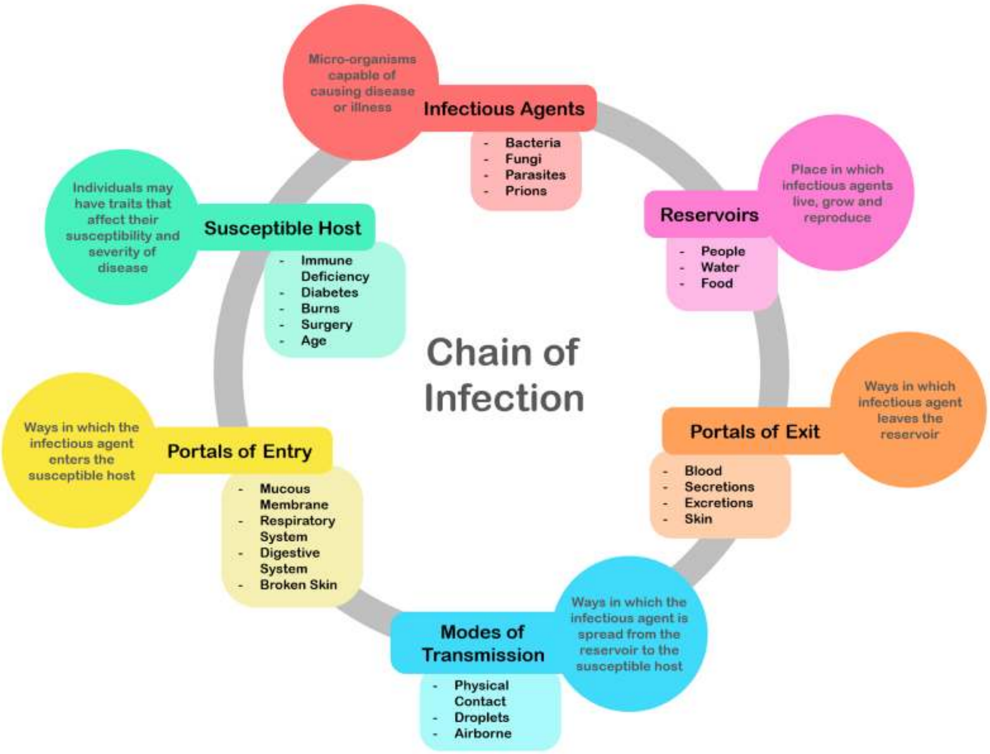


Figure 16.5.1 : Chain of infection; the chain of events that lead to infection.

There is a general chain of events that applies to infections, sometimes called the **chain of infection**. The chain of events involves several steps – which include the infectious agent, reservoir, entering a susceptible host, exit and transmission to new hosts. Each of the links must be present in a chronological order for an infection to develop. Understanding these steps helps health care workers target the infection and prevent it from occurring in the first place.

Colonization

Infection begins when an organism successfully enters the body, grows and multiplies. This is referred to as **colonization**. Individuals with compromised or weakened immune systems have an increased susceptibility to chronic or persistent infections.

Individuals who have a suppressed immune system are particularly susceptible to opportunistic infections. Entrance to the host at host-pathogen interface, generally occurs through the mucosa in orifices like the oral cavity, nose, eyes, genitalia, anus, or the microbe can enter through open wounds. While a few organisms can grow at the initial site of entry, many migrate and cause systemic infection in different organs. Some pathogens grow within the host cells (intracellular) whereas others grow freely in bodily fluids.

Wound colonization refers to non-replicating microorganisms within the wound, while in infected wounds, replicating organisms exist and tissue is injured (Negut et al., 2020). All multicellular organisms are colonized to some degree by extrinsic organisms, and the vast majority of these exist in either a mutualistic or commensal relationship with the host. An example of the former is the anaerobic bacteria species, which colonizes the mammalian colon, and an example of the latter are the various species of staphylococcus that exist on human skin. Neither of these colonizations are considered infections. The difference between an infection and a colonization is often only a matter of circumstance. Non-pathogenic organisms can become pathogenic given specific conditions, and even the most virulent organism requires certain circumstances to cause a compromising infection. Some colonizing bacteria, such as *Corynebacteria sp.* and *viridans streptococci*, prevent the adhesion and colonization of pathogenic bacteria and thus have a symbiotic relationship with the host, preventing infection and speeding wound healing.

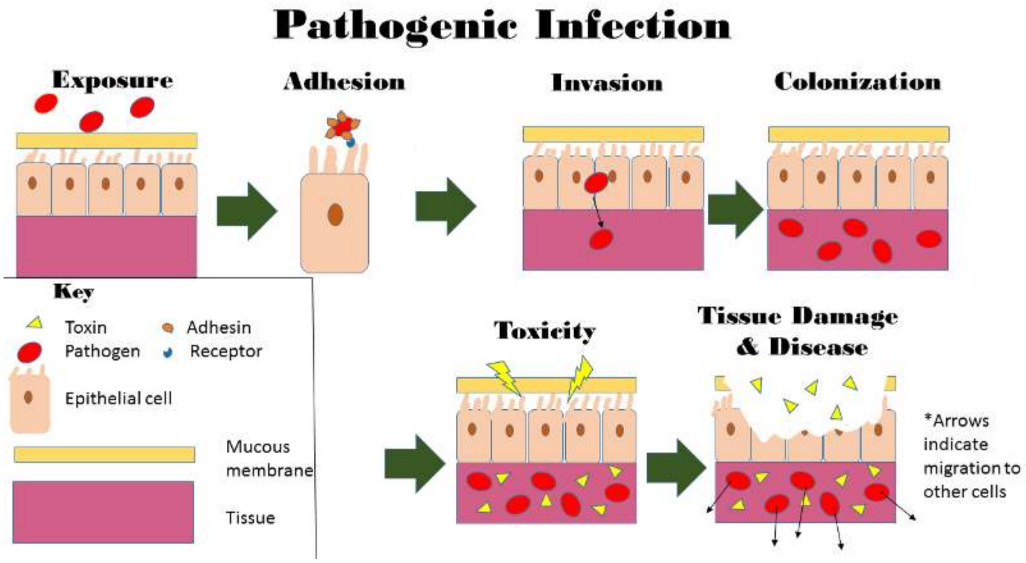


Figure 16.5.2: This image depicts the steps of pathogenic infection.

The variables involved in the outcome of a host becoming inoculated by a pathogen and the ultimate outcome include:

- the route of entry of the pathogen and the access to host regions that it gains
- the intrinsic virulence of the particular organism
- the quantity or load of the initial inoculant
- the immune status of the host being colonized

As an example, several staphylococcal species remain harmless on the skin, but, when present in a normally sterile space, such as in the capsule of a joint or the peritoneum, multiply without resistance and cause harm.

Disease

Disease can arise if the host's protective immune mechanisms are compromised and the organism inflicts damage on the host. Microorganisms can cause tissue damage by releasing a variety of toxins or destructive enzymes. For example, *Clostridium tetani* releases a toxin that paralyzes muscles, and staphylococcus releases toxins that produce shock and sepsis. Not all infectious agents cause disease in all hosts. For example, less than 5% of individuals infected with polio develop disease. On the other hand, some infectious agents are highly virulent. The prion causing mad cow disease and Creutzfeldt–Jakob disease invariably kills all animals and people that are infected.

Persistent infections occur because the body is unable to clear the organism after the initial infection. Persistent infections are characterized by the continual presence of the infectious organism, often as latent infection with occasional recurrent relapses of active infection. There are some viruses that can maintain a persistent infection by infecting different cells of the body. Some viruses once acquired never leave the body. A typical example is the herpes virus, which tends to hide in nerves and become reactivated when specific circumstances arise.

Transmission

Figure 16.5.3: A southern house mosquito (*Culex quinquefasciatus*) is a vector that transmits the pathogens that cause West Nile fever and avian malaria among others.

For infecting organisms to survive and repeat the infection cycle in other hosts, they (or their progeny) must leave an existing reservoir and cause infection elsewhere. The relationship between *virulence versus transmissibility* is complex; if a disease is rapidly fatal, the host may die before the microbe can be passed along to another host. Infection transmission can take place via many potential routes:

- **Droplet contact**, also known as the *respiratory route*, and the resultant infection can be termed airborne disease. If an infected individual coughs or sneezes on another individual the microorganisms, suspended in warm, moist droplets, may enter the body through the nose, mouth or eye surfaces.
- **Fecal-oral transmission**, wherein food or water become contaminated and individuals who eat and drink them become infected. Common fecal-oral transmitted pathogens include *Vibrio cholerae*, *Giardia* species, rotaviruses, *Entameba histolytica*, *Escherichia coli*, and tapeworms. Most of these pathogens cause gastroenteritis.
- **Sexual transmission**, with the resulting disease being called sexually transmitted disease.
- **Oral transmission**, diseases that are transmitted primarily by oral means may be caught through direct or indirect oral contact between individuals.
- **Transmission by direct contact**, some diseases that are transmissible by direct contact include athlete's foot, impetigo and warts.
- **Vehicle transmission,** transmission by an inanimate reservoir (food, water, soil).
- **Vertical transmission**, directly from the mother to an embryo, fetus or offspring during pregnancy or birth. It can occur as a result of a pre-existing infection or one acquired during pregnancy.
- **Latrogenic transmission**, due to medical procedures such as injection or transplantation of infected material.
- **Vector-borne transmission**, transmitted by a vector, which is an organism that does not cause disease itself but that transmits infection by conveying pathogens from one host to another.

16.5.2 Modeling Infectious Disease

Mathematical modeling of infectious diseases often assigns individuals within populations to specific compartments – for example, **S**, **I**, or **R**, (**S**usceptible, **I**nfectious, or **R**ecovered). Individuals may progress between these compartments over time. The **SIR model** is one of the simplest compartmental models, and many models are derivatives of this basic form (Harko et al., 2014).

The flow of this model may be considered as follows:

S -> I -> R

Specifically, the three compartments represent:

S: The number of **s**usceptible individuals. When a susceptible and an infectious individual come into "infectious contact", the susceptible individual contracts the disease and transitions to the infectious compartment.

I: The number of **i**nfectious individuals. These are individuals who have been infected and are capable of infecting susceptible individuals.

R: The number of **r**ecovered (and immune) or deceased individuals. These are individuals who have been infected and have either recovered from the disease and entered the removed compartment, or died. It is assumed that the number of deaths is negligible with respect to the total population. This compartment may also be called "**r**emoved" or "**r**esistant".

These variables (**S**, **I**, and **R**) represent the number of people in each compartment at a particular time. To represent that the number of susceptible, infectious and recovered individuals may vary over time (even if the total population size remains constant), we make the precise numbers a function of *t* (time): **S**(*t*), **I**(*t*) and **R**(*t*). For a specific disease in a specific population, these functions may be worked out in order to predict possible outbreaks (Yang et al., 2020).

As implied by the variable function of *t*, the model is dynamic in that the numbers in each compartment may fluctuate over time. The importance of this dynamic aspect is most obvious in an endemic disease with a short infectious period, such as measles in the UK prior to the introduction of a vaccine in 1968. Such diseases tend to occur in cycles of outbreaks due to the variation in number of susceptibles (S(*t*)) over time. During an epidemic, the number of susceptible individuals falls rapidly as more of them are infected and thus enter the infectious and removed compartments. The disease cannot break out again until the number of susceptibles has built back up, e.g. as a result of offspring being born into the susceptible compartment. This model is reasonably predictive for infectious diseases that are transmitted from human to human, and where recovery confers lasting resistance, such as measles, mumps and rubella.

The dynamics of an epidemic, for example, the flu, are often much faster than the dynamics of birth and death, therefore, birth and death are often omitted in simple compartmental models. The SIR system without so-called vital dynamics (birth and death, sometimes called demography) described above can be expressed by the following system of ordinary differential equations (Hethcote, 2000), which include transition rates (described below):

$$\begin{cases} \frac{dS}{dt} = -\frac{\beta IS}{N}, \\ \frac{dI}{dt} = \frac{\beta IS}{N} - \gamma I, \\ \frac{dR}{dt} = \gamma I, \end{cases}$$

Transition rates

For the full specification of the SIR model, the arrows should be labeled with the transition rates between compartments. Between ***S*** and ***I***, the transition rate is assumed to be ***d(S/N)/dt = -βSI/N2***, where ***N*** is the total population, ***β*** is the average number of contacts per person per time, multiplied by the probability of disease transmission in a contact between a susceptible and an infectious subject, and ***SI/N2*** is the fraction of those contacts between an infectious and susceptible individual which result in the susceptible person becoming infected.

Between ***I*** and ***R***, the transition rate is assumed to be proportional to the number of infectious individuals which is ***γI***. This is equivalent to assuming that the probability of an infectious individual recovering in any time interval *dt* is simply ***γdt***. For the special case in which there is no recovery from the infectious compartment ($\gamma = 0$), the SIR model reduces to a very simple SI model, which has a logistic solution, in which every individual eventually becomes infected.

Each member of the population typically progresses from susceptible to infectious to recovered. This can be shown as a flow diagram in which the boxes represent the different compartments and the arrows the transition between compartments.

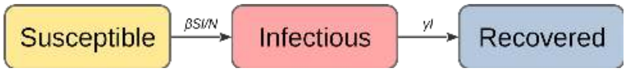


Figure 16.5.4: States in an SIR epidemic model and the rates at which individuals transition between them.

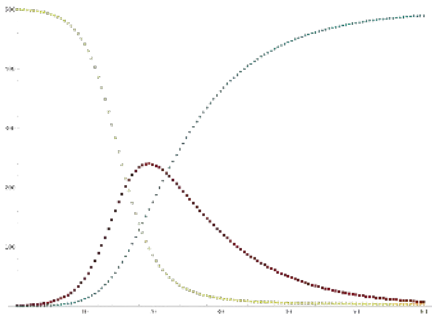


Figure 5: Dynamics of SIR model occurring over time. Yellow = Susceptible, Maroon = Infectious, Teal = Recovered

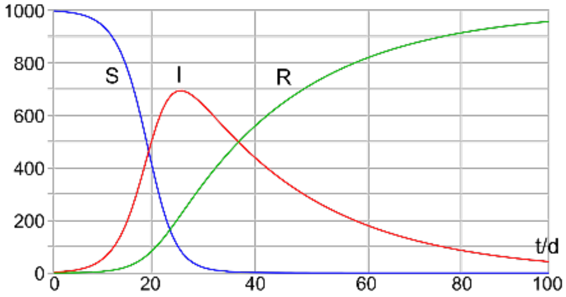


Figure 6: Diagram of the SIR model with initial values S(0) = 997, I(0) = 3, R(0) = 0 and rates for infection β = 0.4 and for recovery γ = 0.04.

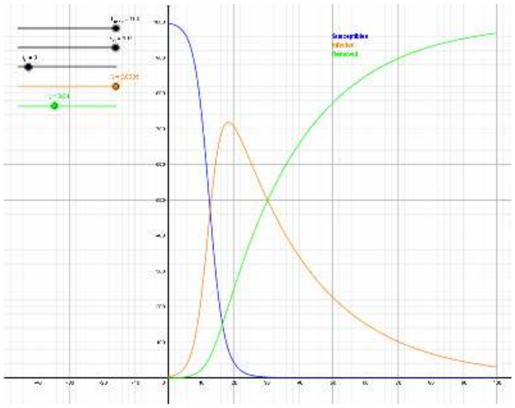


Figure 16.5.7: Animation of the SIR model with initial values S(0) = 997, I(0) = 3, R(0) = 0, and rate of recovery γ = 0.04. The animation shows the effect of reducing the rate of infection from β = 0.5 to β = 0.12. If there is no medicine or vaccination available, it is only possible to reduce the infection rate (often referred to as "flattening the curve") by appropriate measures such as social distancing.

Note that the dynamics of the infectious class depends on the following ratio:

$$R_0 = \frac{\beta}{\gamma}$$

The so-called **basic reproduction number** or **basic reproduction ratio** (denoted as *R0* - pronounced *R nought* or *R zero*) (Milligan & Barrett, 2015) is derived as the expected number of new infections (these new infections are sometimes called secondary infections) from a single infection in a population where all subjects are susceptible (Bailey, 1975). The most important uses of *R0* are determining if an emerging infectious disease can spread in a population and determining what proportion of the population should be immunized through vaccination to eradicate a disease. In commonly used infection models, when *R0* > 1 the infection will be able to start spreading in a population, but not if *R0* < 1. Generally, the larger the value of *R0*, the harder it is to control the epidemic. For simple models, the proportion of the population that needs to be effectively immunized (meaning not susceptible to infection) to prevent sustained spread of the infection has to be larger than 1 - 1/*R0* (Kröger, 2020). Conversely, the proportion of the population that remains susceptible to infection in the **endemic equilibrium** is 1/*R0*.

The basic reproduction number is affected by several factors, including the duration of infectivity of affected people, the infectiousness of the microorganism, and the number of susceptible people in the population that the infected people contact.

16.6: Sources and Attributions

Full Chapter Sources

Cougar. Hinterland Who's Who. *Canadian Wildlife Service and Canadian Wildlife Federation*. Archived from the original on 18 May 2007. Retrieved 22 May 2007.

Featured creatures. *Encarsia perplexa*. *University of Florida*. Retrieved 6 January 2018.

Helminth Parasites. *Australian Society of Parasitology*. Retrieved 9 October 2017.

Parasitism | The encyclopedia of ecology and environmental management. *Blackwell Science*. Retrieved 8 April 2018.

Pathogenic parasitic infections. *PEOI*. Retrieved 18 July 2013.

Pikes (*Esocidae*). *Indiana Division of Fish and Wildlife*. Retrieved 3 September 2018.

Predator & prey: Adaptations. (2012). *Royal Saskatchewan Museum*. Archived from the original (PDF) on 3 April 2018. Retrieved 19 April 2018.

Predators and their prey. *BBC*. Retrieved 7 October 2015.

Social parasites in the ant colony. *Antkeepers*. Retrieved 4 April 2016.

Trapdoor spider. (2014). *Arizona-Sonora Desert Museum*. Retrieved 12 December 2014.

Trapdoor spiders. *BBC*. Retrieved 12 December 2014.

Abraham, M.A.A. (2006). Sustainability science and engineering. *Elsevier, 1*, pp. 123. ISBN 978-0444517128

Abrams, P.A. (1986). Adaptive responses of predators to prey and prey to predators: The failure of the arms-race analogy. *Evolution, 40*(6), pp. 1229–1247. doi:10.1111/j.1558-5646.1986.tb05747.x. PMID 28563514. S2CID 27317468.

Arcese, P., Schuster, R., Campbell, L., Barber, A., & Martin, T.G. (2014). Deer density and plant palatability predict shrub cover, richness, diversity and aboriginal food value in a North American archipelago. *Diversity and Distributions, 20*(12), pp. 1368–1378. doi:10.1111/ddi.12241. ISSN 1366-9516.

Bailey, N.T.J. (1975). The mathematical theory of infectious diseases and its applications (2nd ed.). *London: Griffin*. ISBN 0-85264-231-8.

Barbosa, P., & Castellanos, I. (2005). Ecology of predator-prey interactions. *Oxford University Press*, p. 78. ISBN 9780199874545.

Barceloux, D.G. (2008). Medical toxicology of natural substances: Foods, fungi, medicinal herbs, plants, and venomous animals. *Wiley*, p. 1028. ISBN 978-0-470-33557-4.

Bar-Yam. Predator-prey relationships. *New England Complex Systems Institute*. Retrieved 7 September 2018.

Belovsky, G.E. (1997). Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evolutionary Ecology, 11*(6), pp. 641–672. doi:10.1023/A:1018430201230. S2CID 23873922.

Bengtson, S. (2002). Origins and early evolution of predation. In Kowalewski, M., & Kelley, P.H. (Eds.), *The fossil record of predation*. The Paleontological Society, pp. 289–317.

Berec, L., Schembri, P.J., & Boukal, D.S. (2005). Sex determination in *Bonellia viridis* (Echiura: Bonelliidae): Population dynamics and evolution. *Oikos, 108*(3), pp. 473–484. doi:10.1111/j.0030-1299.2005.13350.x.

Berenbaum, M.R. (1995). The chemistry of defense: Theory and practice. *Proceedings of the National Academy of Sciences of the United States of America, 92*(1), pp. 2–8. Bibcode:1995PNAS...92....2B. doi:10.1073/pnas.92.1.2. PMC 42807. PMID 7816816.

Bergstrom, C.T., & Lachmann, M. (2001). Alarm calls as costly signals of antipredator vigilance: The watchful babbler game. *Animal Behaviour, 61*(3), 535–543. CiteSeerX 10.1.1.28.773. doi:10.1006/anbe.2000.1636. S2CID 2295026.

Berryman, A.A., & Hawkins, Bradford A. (2006). The refuge as an integrating concept in ecology and evolution. *Oikos, 115*(1), 192–196. doi:10.1111/j.0030-1299.2006.15188.x.

Bester, C. (2017). *Antennarius striatus*. *University of Florida*. Retrieved 31 January 2018.

Bond, W.J. (2012). Keystone species. In Schulze, E.D., & Mooney, H.A. (Eds.), *Biodiversity and Ecosystem Function*. Springer. p. 237. ISBN 978-3642580017.

Boudreau, S.A., & Worm, B. (2012). Ecological role of large benthic decapods in marine ecosystems: A review. *Mar. Ecol. Prog. Ser., 469*, pp. 195−213

Bowers, M.D., Brown, I.L., & Wheye, D. (1985). Bird predation as a selective agent in a butterfly population. *Evolution, 39*(1), pp. 93–103. doi:10.1111/j.1558-5646.1985.tb04082.x. PMID 28563638. S2CID 12031679.

Bray, D. Eastern frogfish, *Batrachomoeus dubius*. *Fishes of Australia*. Archived from the original on 14 September 2014. Retrieved 14 September 2014.

Briggs, C.J., & Hoopes, M.F. (2004). Stabilizing effects in spatial parasitoid−host and predator−prey models: A review. *Theor. Popul. Biol., 65*, pp. 299−315

Brodie, E.D. (2009). Toxins and venoms. *Current Biology, 19*(20), R931–R935. doi:10.1016/j.cub.2009.08.011. PMID 19889364. S2CID 9744565.

Brodie, E.D. (1999). Predator-prey arms races. *BioScience, 49*(7), pp. 557–568. doi:10.2307/1313476. JSTOR 1313476.

Brousseau, D.J. (1978). Population dynamics of the soft-shell clam *Mya arenaria*. *Mar. Biol. 50*, pp. 63−71

Call, A., & St. Clair, S.B. (2018). In Ryan, M. (Eds.), Timing and mode of simulated ungulate herbivory alter aspen defense strategies. *Tree Physiology, 38*(10), pp. 1476–1485. doi:10.1093/treephys/tpy071. ISSN 1758-4469. PMID 29982736.

Castello, M.E., Rodriguez-Cattaneo, A., Aguilera, P.A., Iribarne, L., Pereira, A.C., & Caputi, A.A. (2009). Waveform generation in the weakly electric fish *Gymnotus coropinae* (Hoedeman): The electric organ and the electric organ discharge. *Journal of Experimental Biology, 212*(9), pp. 1351–1364. doi:10.1242/jeb.022566. PMID 19376956.

Catania, K.C. (2015). Electric eels use high-voltage to track fast-moving prey. *Nature Communications, 6*(1), pp. 8638. Bibcode:2015NatCo...6.8638C. doi:10.1038/ncomms9638. ISSN 2041-1723. PMC 4667699. PMID 26485580.

Cetaruk, E.W. (2005). Rattlesnakes and other Crotalids. In Brent, J. (Eds.), *Critical care toxicology: Diagnosis and management of the critically poisoned patient*. Elsevier Health Sciences. p. 1075. ISBN 978-0-8151-4387-1.

Cheng, T.C. (2012). General parasitology. *Elsevier Science*, pp. 13–15. ISBN 978-0-323-14010-2.

Collins, S.L. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science, 280*(5364), pp. 745–747. Bibcode:1998Sci...280..745C. doi:10.1126/science.280.5364.745. ISSN 0036-8075. PMID 9563952.

Combes, S.A., Salcedo, M.K., Pandit, M.M., & Iwasaki, J.M. (2013). Capture success and efficiency of dragonflies pursuing different types of prey. *Integrative and Comparative Biology, 53*(5), pp. 787–798. doi:10.1093/icb/ict072. PMID 23784698.

Cory, R.L., & Redding, M.J. (1976). Mortalities caused by Tropical Storm Agnes to clams and oysters in the Rhode River area of Chesapeake Bay. In Anderson, A.M. (Eds.), *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, MD, p 478-487.

Cott. (1940). pp. 368–389

Cox, F.E. (2001). Concomitant infections, parasites and immune responses. *Parasitology*. 122. Supplement: S23–38. doi:10.1017/s003118200001698x. PMID 11442193. S2CID 150432.

Cressman, R., & Garay, J. (2009). A predator–prey refuge system: Evolutionary stability in ecological systems. *Theoretical Population Biology, 76*(4), pp. 248–57. doi:10.1016/j.tpb.2009.08.005. PMID 19751753.

Cushing, J.M. (2005). Book reviews | Mathematics in population biology, by Horst R. Thiene. *Bulletin of the American Mathematical Society, 42*(4), pp. 501–505. doi:10.1090/S0273-0979-05-01055-4.

Dawkins, R., & Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society B: Biological Sciences*, *205*(1161), pp. 489–511. Bibcode:1979RSPSB.205..489D. doi:10.1098/rspb.1979.0081. PMID 42057. S2CID 9695900.

De Marsico, M.C., Gloag, R., Ursino, C.A., & Reboreda, J.C. (2013). A novel method of rejection of brood parasitic eggs reduces parasitism intensity in a cowbird host. *Biology Letters, 9*(3): 20130076. doi:10.1098/rsbl.2013.0076. PMC 3645041. PMID 23485877.

de Mazancourt, C., Loreau, M., & Dieckmann, U. (2001). Can the evolution of plant defense lead to plant-herbivore mutualism? *The American Naturalist, 158*(2), pp. 109–123. doi:10.1086/321306. ISSN 0003-0147. PMID 18707340. S2CID 15722747.

Dearing, M.D., Mangione, A.M., & Karasov, W.H. (2000). Diet breadth of mammalian herbivores: Nutrient versus detoxification constraints. *Oecologia, 123*(3), pp. 397–405. Bibcode:2000Oecol.123..397D. doi:10.1007/s004420051027. PMID 28308595. S2CID 914899.

Descombes, P., Marchon, J., Pradervand, J.N., Bilat, J., Guisan, A., Rasmann, S., & Pellissier, L. (2016). Community-level plant palatability increases with elevation as insect herbivore abundance declines. *Journal of Ecology, 105*(1), pp. 142–151. doi:10.1111/1365-2745.12664. ISSN 0022-0477.

deVries, M.S., Murphy, E.A.K., & Patek S.N. (2012). Strike mechanics of an ambush predator: The spearing mantis shrimp. *Journal of Experimental Biology, 215*(Pt 24), pp. 4374–4384. doi:10.1242/jeb.075317. PMID 23175528.

Dissanaike, A.S. (1957). On Protozoa hyperparasitic in Helminth, with some observations on *Nosema helminthorum Moniez*, 1887. *Journal of Helminthology, 31*(1–2), pp. 47–64. doi:10.1017/s0022149x00033290. PMID 13429025.

Dominey, W.J. (1983). Mobbing in colonially nesting fishes, especially the bluegill, *Lepomis macrochirus*. *Copeia*, (4), pp. 1086–1088. doi:10.2307/1445113. JSTOR 1445113.

Douglas, A.E. (1998). Nutritional interactions in insect–microbial symbioses: Aphids and their symbiotic bacteria buchnera. *Annual Review of Entomology, 43*, pp. 17–37. doi:10.1146/annurev.ento.43.1.17. PMID 15012383.

Drake, J.M., & Griffen, B.D. (2010). Early warning signals of extinction in deteriorating environments. *Nature, 467*, pp. 456−459

Eastman, L.B., & Thiel, M. (2015). Foraging behavior of crustacean predators and scavengers. In Thiel, M., & Watling, L. (Eds.), *Lifestyles and feeding biology*. Oxford University Press. pp. 535–556. ISBN 9780199797066.

Edmunds, M. (2012). Deimatic Behavior. *Springer*. Retrieved 31 December 2012.

Edwards, P.J., & Wratten, S.D. (1985). Induced plant defenses against insect grazing: Fact or artefact?. *Oikos, 44*(1), pp. 70–74. doi:10.2307/3544045. JSTOR 3544045.

Elumalai, V., Viswanathan, C., Pravinkumar, M., & Raffi, S.M. (2013). Infestation of parasitic barnacle *Sacculina spp.* in commercial marine crabs. *Journal of Parasitic Diseases, 38*(3), pp. 337–339. doi:10.1007/s12639-013-0247-z. PMC 4087306. PMID 25035598.

Estes, J.A., Doak, D.F., Springer, A.M., & Williams, T.M. (2009). Causes and consequences of marine mammal population declines in southwest Alaska: A food-web perspective. *Philos. Trans. R. Soc. B., 364*, pp. 1647−1658

Feulner, P. G., Plath, M., Engelmann, J., Kirschbaum, F., & Tiedemann, R. (2009). Electrifying love: Electric fish use species-specific discharge for mate recognition. *Biology Letters, 5*(2), pp. 225–228. doi:10.1098/rsbl.2008.0566. PMC 2665802. PMID 19033131.

Forbes, L.S. (1989). Prey defenses and predator handling behaviour: The dangerous prey hypothesis. *Oikos, 55*(2), pp. 155–158. doi:10.2307/3565418. JSTOR 3565418.

Forbes, P. (2009). Dazzled and deceived: Mimicry and camouflage. *Yale University Press*, p. 134. ISBN 978-0-300-17896-8.

Furness, R.W. (1978). Kleptoparasitism by great skuas (*Catharacta skua Brünn*.) and Arctic skuas (*Stercorarius parasiticus L*.) at a Shetland seabird colony. *Animal Behaviour, 26*, pp. 1167–1177. doi:10.1016/0003-3472(78)90107-0. S2CID 53155057.

Futuyma, D.J., & Gould, F. (1979). Associations of plants and insects in deciduous forest. *Ecological Monographs, 49*(1), pp. 33–50. doi:10.2307/1942571. ISSN 0012-9615. JSTOR 1942571.

Garcia, L.S. (1999). Classification of human parasites, vectors, and similar organisms. *Clinical Infectious Diseases, 29*(4), pp. 734–746. doi:10.1086/520425. PMID 10589879.

Gazda, S.K., Connor, R.C., Edgar, R.K., & Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society, 272*(1559), pp. 135–140. doi:10.1098/rspb.2004.2937. PMC 1634948. PMID 15695203.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: Evidence of natural selection by predation. *PLOS ONE, 5*(3): e9774. Bibcode:2010PLoSO...5.9774G. doi:10.1371/journal.pone.0009774. PMC

2841644. PMID 20333305.

Getty, T. (2002). The discriminating babbler meets the optimal diet hawk. *Anim. Behav., 63*(2), pp. 397–402. doi:10.1006/anbe.2001.1890. S2CID 53164940.

Getz, W.M. (2011). Biomass transformation webs provide a unified approach to consumer-resource modelling. *Ecology Letters, 14*(2), pp. 113–124. doi:10.1111/j.1461-0248.2010.01566.x. PMC 3032891. PMID 21199247.

Glaspie, C.N. (2019). Blue crab *Callinectes sapidus* and softshell clam *Mya arenaria* index of abundance time series 1958−1992. *Knowledge Network for Biocomplexity*. doi: 10.5063/F19S1PB9

Glaspie, C.N., & Seitz, R.D. (2018). Habitat complexity and benthic predator−prey interactions in Chesapeake Bay. *PLOS ONE*, 13: e0205162

Glaspie, C.N., Seitz, R.D., Ogburn, M.B., Dungan, C.F., & Hines, A.H. (2018). Impacts of habitat, predators, recruitment, and disease on soft-shell clams *Mya arenaria* and stout razor clams *Tagelus plebeius* in Chesapeake Bay. *Mar. Ecol. Prog. Ser., 603*, pp. 117−133

Gleeson, S.K., & Wilson, D.S. (1986). Equilibrium diet: Optimal foraging and prey coexistence. *Oikos, 46*(2), pp. 139. doi:10.2307/3565460. ISSN 0030-1299. JSTOR 3565460.

Goel, N.S., Maitra, S.C., & Montroll, E.W. (1971). On the Volterra and other non-linear models of interacting populations. *Academic Press*. ISBN 978-0122874505.

Goldbogen, J.A., Calambokidis, J., Shadwick, R.E., Oleson, E.M., McDonald, M.A., & Hildebrand, J.A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology, 209*(7), pp. 1231–1244. doi:10.1242/jeb.02135. PMID 16547295. S2CID 17923052. Archived from the original (PDF) on 13 August 2011. Retrieved 4 September 2018.

Gremillet, D., Wilson, R.P., Wanless, S., & Chater, T. (2000). Black-browed albatrosses, international fisheries and the Patagonian Shelf. *Marine Ecology Progress Series, 195*, pp. 69–280. Bibcode:2000MEPS..195..269G. doi:10.3354/meps195269.

Griffiths, D. (1980). Foraging costs and relative prey size. *The American Naturalist, 116*(5), pp. 743–752. doi:10.1086/283666. JSTOR 2460632. S2CID 85094710.

Gullan, P.J., & Cranston, P.S. (2010). The insects: An outline of entomology (4th ed.). *Wiley*, pp. 308, 365–367, 375, 440–441. ISBN 978-1-118-84615-5.

Gurr, G.M., Wratten, S.D., & Snyder, W.E. (2012). Biodiversity and insect pests: Key issues for sustainable management. *John Wiley & Sons*, pp. 105. ISBN 978-1-118-23185-2.

Harko, T., Lobo, F.S., & Mak, M.K. (2014). Exact analytical solutions of the Susceptible-Infected-Recovered (SIR) epidemic model and of the SIR model with equal death and birth rates. *Applied Mathematics and Computation, 236*, pp. 184–194. doi:10.1016/j.amc.2014.03.030

Haven, D.S. (1970). A study of the hard and soft clam resources of Virginia: Annual contract report for the period 1 July 1969 through 30 June 1970. *Virginia Institute of Marine Science, Gloucester Point, VA.*

Haven, D.S., Hargis, W.J., Loesch, J.G., & Whitcomb, J.P. (1976). The effect of Tropical Storm Agnes on oysters, hard clams, soft clams, and oyster drills in Virginia. In Anderson, A.M. (Eds.), *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, MD, pp. 488−508.

Hawkes, C.V., & Sullivan, J.J. (2001). The impact of herbivory on plants in different resource conditions: A meta-analysis. 82, pp. 2045–2058 – via Wiley.

Heil, M., Koch, T., Hilpert, A., Fiala, B., Boland, W., & Linsenmair, K.E. (2001). Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius*, is an induced, indirect, defensive response elicited by jasmonic acid. *Proceedings of the National Academy of Sciences, 98*(3), pp. 1083–1088. Bibcode:2001PNAS...98.1083H. doi:10.1073/pnas.031563398. PMC 14712. PMID 11158598.

Hethcote, H. (2000). The mathematics of infectious diseases. *SIAM Review, 42*(4), pp. 599–653. doi:10.1137/s0036144500371907

Hidding, B., Nolet, B.A., de Boer, T., de Vries, P.P., & Klaassen, M. (2009). Above- and below-ground vertebrate herbivory may each favour a different subordinate species in an aquatic plant community. *Oecologia, 162*(1), pp. 199–208. doi:10.1007/s00442-009-1450-6. ISSN 0029-8549. PMC 2776151. PMID 19756762.

Holling, C. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol., 91*, pp. 293−320

Hubel, T.Y., Myatt, J.P., Jordan, N.R., Dewhirst, O.P., McNutt, J.W., & Wilson, A.M. (2016). Energy cost and return for hunting in African wild dogs. *Nature Communications, 7*: 11034. doi:10.1038/ncomms11034. PMC 4820543. PMID 27023457.

Janis, C. (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In Damuth, J., & MacFadden, B.J. (Eds.), *Body size in mammalian paleobiology: Estimation and biological implications*. Cambridge University Press, pp. 255–299.

Janis, C.M., & Wilhelm, P.B. (1993). Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *Journal of Mammalian Evolution, 1*(2), pp. 103–125. doi:10.1007/bf01041590. S2CID 22739360.

Johnston, M.W., Purkis, S.J., & Dodge, R.E. (2015). Measuring Baha - mian lionfish impacts to marine ecological services using habitat equivalency analysis. *Mar. Biol., 162*, pp. 2501−2512

Jurkevitch, E., & Davidov, Y. (2006). Phylogenetic diversity and evolution of predatory prokaryotes. *Predatory Prokaryotes*. Springer. pp. 11–56. doi:10.1007/7171_052. ISBN 978-3-540-38577-6.

Kane, A., Healy, K., Guillerme, T., Ruxton, G.D., & Jackson, A.L. (2017). A recipe for scavenging in vertebrates – the natural history of a behaviour. *Ecography, 40*(2), pp. 324–334. doi:10.1111/ecog.02817

Karasov, W.H., & Diamond, J.M. (1988). Interplay between physiology and ecology in digestion. *BioScience, 38*(9), pp. 602–611. doi:10.2307/1310825. JSTOR 1310825.

Karban, R., & Agrawal, A.A. (2002). Herbivore offense. *Annual Review of Ecology and Systematics, 33*, pp. 641–664. doi:10.1146/annurev.ecolsys.33.010802.150443.

King, A.A., & Schaffer, W.M. (2001. The geometry of a population cycle: A mechanistic model of snowshoe hare demography. *Ecology, 82*, pp. 814–830.

Kozlov, V., & Vakulenko, S. (2013). On chaos in Lotka–Volterra systems: An analytical approach. *Nonlinearity, 26*(8), pp. 2299–2314. Bibcode:2013Nonli..26.2299K. doi:10.1088/0951-7715/26/8/2299.

Kramer, B. (1996). Electroreception and communication in fishes. *Progress in Zoology, 42*.

Kramer, D.L. (2001). Foraging behavior. In Fox, C.W., Roff, D.A., & Fairbairn, D.J. (Eds.), *Evolutionary ecology: Concepts and case studies*. Oxford University Press, pp. 232–238. ISBN 9780198030133. Archived from the original (PDF) on 12 July 2018. Retrieved 20 September 2018.

Krause, J., & Ruxton, G.D. (2002). Living in groups. *Oxford University Press*, pp. 13–15. ISBN 9780198508182.

Krebs, C.J., Boonstra, R., Boutin, S., & Sinclair, A.R.E. (2001). What drives the 10-year cycle of snowshoe hares?. *BioScience, 51*(1), pp. 25. doi:10.1641/0006-3568(2001)051[0025:WDTYCO]2.0.CO;2.

Krebs, C., & Myers, J. (2014). The snowshoe hare 10-year cycle – a cautionary tale. Ecological rants. *University of British Columbia*. Retrieved 2 October 2018.

Kröger, M., & Schlickeiser, R. (2020). Analytical solution of the SIR-model for the temporal evolution of epidemics. Part A: Time-independent reproduction factor. *Journal of Physics A, 53*(50): 505601. doi:10.1088/1751-8121/abc65d

Kruuk, H. (1972). The spotted hyena: A study of predation and social behaviour. *University of California Press*, pp. 107–108. ISBN 978-0226455082.

Lafferty, K.D., & Kuris, A.M. (2002). Trophic strategies, animal diversity and body size. *Trends in Ecology and Evolution, 17*(11), pp. 507–513. doi:10.1016/s0169-5347(02)02615-0. Archived from the original (PDF) on 3 October 2019.

Langenheim, J.H. (1994). Higher plant terpenoids: A phytocentric overview of their ecological roles. *Journal of Chemical Ecology, 20*,(6), pp. 1223–1280. doi:10.1007/BF02059809. PMID 24242340. S2CID 25360410.

Levin, S.A., Carpenter, S.R., Godfray, H.C.J., Kinzig, A.P., Loreau, M., Losos, J.B., Walker, B., & Wilcove, D.S. (2009). The Princeton guide to ecology. *Princeton University Press*, pp. 204–209. ISBN 9781400833023.

Li, M., Fry, B.G., & Kini, R.M. (2005). Eggs-only diet: Its implications for the toxin profile changes and ecology of the marbled sea snake (*Aipysurus eydouxii*). *Journal of Molecular Evolution, 60*(1), pp. 81–89. Bibcode:2005JMolE..60...81L.

doi:10.1007/s00239-004-0138-0. PMID 15696370. S2CID 17572816.

Lipcius, R.N., & van Engel, W.A. (1990). Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River 1972−1988) and stock−recruit functions. *Bull Mar. Sci.*, *46*, pp. 180−194

Lloyd J.E. (1965). Aggressive mimicry in Photuris: Firefly femmes fatales. *Science*, *149*(3684), pp. 653–654. Bibcode:1965Sci...149..653L. doi:10.1126/science.149.3684.653. PMID 17747574. S2CID 39386614.

Pellissier, L., Ndiribe, C., Dubuis, A., Pradervand, J.N., Salamin, N., Guisan, A., & Rasmann, S. (2013). Turnover of plant lineages shapes herbivore phylogenetic beta diversity along ecological gradients. *Ecology Letters*, *16*(5), pp. 600–608. doi:10.1111/ele.12083. PMID 23448096.

Lubchenco, J., & Gaines, S.D. (1981). A unified approach to marine plant−herbivore interactions. I. Populations and communities. *Annu. Rev. Ecol. Syst.*, *12*, pp. 405−437

Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *The American Naturalist*, *112*(983), pp. 23–39. doi:10.1086/283250. ISSN 0003-0147. S2CID 84801707.

MacArthur, R.H. (1984). The economics of consumer choice. Geographical ecology: Patterns in the distribution of species. *Princeton University Press*, pp. 59–76. ISBN 9780691023823.

Maggenti, A.R., Maggenti, M.A., & Gardner, S.L. (2005). Online dictionary of invertebrate zoology. *University of Nebraska*, p. 22. Archived from the original (PDF) on 18 April 2018.

McNair, J.N. (1986). The effects of refuges on predator-prey interactions: A reconsideration. *Theoretical Population Biology*, *29*, (1), pp. 38–63. doi:10.1016/0040-5809(86)90004-3. PMID 3961711.

Merilaita, S., Scott-Samuel, N.E., & Cuthill, I.C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1724): 20160341. doi:10.1098/rstb.2016.0341. PMC 5444062. PMID 28533458.

Merilaita, S., Vallin, A., Kodandaramaiah, U., Dimitrova, M., Ruuskanen, S., & Laaksonen, T. (2011). Number of eyespots and their intimidating effect on naïve predators in the peacock butterfly. *Behavioral Ecology*, *22*(6), pp. 1326–1331. doi:10.1093/beheco/arr135.

Milchunas, D.G., & Noy-Meir, I. (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, *99*(1), pp. 113–130. doi:10.1034/j.1600-0706.2002.990112.x.

Milligan, G.N., & Barrett, A.D. (2015). Vaccinology: An essential guide. *Chichester, West Sussex: Wiley Blackwell*, p. 310. ISBN 978-1-118-63652-7.

Mitter, C., Farrell, B., & Futuyma, D.J. (1991). Phylogenetic studies of insect-plant interactions: Insights into the genesis of diversity. *Trends in Ecology & Evolution*, *6*(9), pp. 290–293. doi:10.1016/0169-5347(91)90007-k. ISSN 0169-5347. PMID 21232484.

Moore, T.Y., & Biewener, A.A. (2015). Outrun or outmaneuver: Predator–prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integrative and Comparative Biology*, *55*(6), pp. 1188–97. doi:10.1093/icb/icv074. PMID 26117833.

Murdoch, W.W., Briggs, C.J., & Nisbet, R.M. (2013). Consumer-resource dynamics. *Princeton University Press*, p. 39. ISBN 9781400847259.

Neal, D. (2004). Introduction to population biology. *Cambridge University Press*, pp. 68–69. ISBN 9780521532235.

Negut, I., Grumezescu, V., & Grumezescu, A.M. (2018). Treatment strategies for infected wounds. *Molecules*, *23*(9), pp. 2392. doi:10.3390/molecules23092392

Nelson, E.H., Matthews, C.E., & Rosenheim, J.A. (2004). Predators reduce prey population growth by inducing changes in prey behavior. *Ecology*, *85*(7), pp. 1853–1858. doi:10.1890/03-3109. JSTOR 3450359.

Newell, C.R., & Hidu, H. (1986). Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—softshell clam. *US Fish Wildl. Serv. Biol. Rep.*, *82*(11.53). US Army Corps of Engineers, TR EL-82-4. https: //apps.dtic.mil/dtic/tr/fulltext/ u2/ a174837. Pdf

Nishida, R. (2002). Sequestration of defensive substances from plants by Lepidoptera. *Annual Review of Entomology*, *47*, pp. 57–92. doi:10.1146/annurev.ento.47.091201.145121. PMID 11729069.

Nowak, M., & May, R.M. (2000). Virus dynamics: Mathematical principles of immunology and virology. *Oxford University Press*, p. 8. ISBN 9780191588518.

Olff, H., & Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, *13*(7), pp. 261–265. doi:10.1016/s0169-5347(98)01364-0. hdl:11370/3e3ec5d4-fa03-4490-94e3-66534b3fe62f. ISSN 0169-5347. PMID 21238294.

Orth, R.J., & Moore, K.A. (1983). Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science*, *222*, pp. 51−53

Overview of parasitology. Australian Society of Parasitology and Australian Research Council/National Health and Medical Research Council) Research Network for Parasitology. July 2010. ISBN 978-1-8649999-1-4.

Parratt, S.R., & Laine, A.L. (2016). The role of hyperparasitism in microbial pathogen ecology and evolution. *The ISME Journal*, *10*(8), pp. 1815–1822. doi:10.1038/ismej.2015.247. PMC 5029149. PMID 26784356.

Payne, R.B. (1997). Avian brood parasitism. In Clayton, D.H., & Moore, J. (Eds.), *Host–parasite evolution: General principles and avian models*. Oxford University Press. pp. 338–369. ISBN 978-0198548928.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J., & Trussell, G.C. (2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, *89*(9), pp. 2416–2425. doi:10.1890/07-1131.1. PMID 18831163.

Perry, G. (1999). The evolution of search modes: Ecological versus phylogenetic perspectives. *The American Naturalist*, *153*(1), pp. 98–109. doi:10.1086/303145. PMID 29578765. S2CID 4334462.

Pianka, E.R. (2011). Evolutionary ecology (7th (eBook) ed.). pp. 78–83.

Pietsch, T.W. (2005). Dimorphism, parasitism, and sex revisited: Modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). *Ichthyological Research*, *52*(3), pp. 207–236. doi:10.1007/s10228-005-0286-2. S2CID 24768783.

Pillemer, E.A., & Tingey, W.M. (1976). Hooked trichomes: A physical plant barrier to a major agricultural pest. *Science*, *193*(4252), pp. 482–484. Bibcode:1976Sci...193..482P. doi:10.1126/science.193.4252.482. PMID 17841820. S2CID 26751736.

Epstein, E. (1994). A review. *PNAS*, *91*.

Pollitt, L.C., MacGregor, P., Matthews, K., & Reece, S.E. (2011). Malaria and trypanosome transmission: Different parasites, same rules? *Trends in Parasitology*, *27*(5), pp. 197–203. doi:10.1016/j.pt.2011.01.004. PMC 3087881. PMID 21345732.

Poore, A.G.B., Graba-Landry, A., Favret, M., Sheppard Brennand, H., Byrne, M., & Dworjanyn, S.A. (2013). Direct and indirect effects of ocean acidification and warming on a marine plant–herbivore interaction. *Oecologia*, *173*(3), pp. 1113–1124. Bibcode:2013Oecol.173.1113P. doi:10.1007/s00442-013-2683-y. ISSN 0029-8549. PMID 23673470. S2CID 10990079.

Poulin, R. (2011). The many roads to parasitism: A tale of convergence. In Rollinson, D., & Hay, S.I. (Eds.), *Advances in parasitology*, *74*. Academic Press. pp. 27–28. doi:10.1016/B978-0-12-385897-9.00001-X. ISBN 978-0-12-385897-9. PMID 21295676.

Poulin, R., & Randhawa, H.S. (2015). Evolution of parasitism along convergent lines: From ecology to genomics. *Parasitology*, *142*(Suppl 1): S6–S15. doi:10.1017/S0031182013001674. PMC 4413784. PMID 24229807.

Preisser, E.L., Bolnick, D.I., & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*(2), pp. 501–509. doi:10.1890/04-0719. ISSN 0012-9658.

Ripple, W.J., & Beschta, R.L. (2004). Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience*, *54*(8), pp. 755. doi:10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2.

Rochat, J., & Gutierrez, A.P. (2001). Weather-mediated regulation of olive scale by two parasitoids. *Journal of Animal Ecology*, *70*(3), pp. 476–490. doi:10.1046/j.1365-2656.2001.00505.x. S2CID 73607283.

Rothstein, S.I. (1990). A model system for coevolution: Avian brood parasitism. *Annual Review of Ecology and Systematics*, *21*, pp. 481–508. doi:10.1146/annurev.ecolsys.21.1.481.

Rosenzweig, M.L., & MacArthur, R.H. (1963). Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, *97*, pp. 209–223.

Ruppert, E.E., Fox, R.S., & Barnes, R.D. (2004). Invertebrate zoology, 7th edition. *Cengage Learning*. pp. 153–154. ISBN 978-81-315-0104-7.

Ruxton, Sherratt & Speed 2004, pp. vii–xii

Sagers, C.L. (1992). Manipulation of host plant quality: Herbivores keep leaves in the dark. *Functional Ecology, 6*(6), pp. 741–743. doi:10.2307/2389971. JSTOR 2389971.

Sanders, J.G., Beichman, A.C., Roman, J., Scott, J.J., Emerson, D., McCarthy, J.J., & Girguis, P.R. (2015). Baleen whales host a unique gut microbiome with similarities to both carnivores and herbivores. *Nature Communications, 6*, pp. 8285. Bibcode:2015NatCo...6.8285S. doi:10.1038/ncomms9285. PMC 4595633. PMID 26393325.

Sandsten, H., & Klaassen, M. (2008). Swan foraging shapes spatial distribution of two submerged plants, favouring the preferred prey species. *Oecologia, 156*(3), pp. 569–576. Bibcode:2008Oecol.156..569S. doi:10.1007/s00442-008-1010-5. ISSN 0029-8549. PMC 2373415. PMID 18335250.

Schmidt, J.O. (2009). Wasps. ScienceDirect. Encyclopedia of Insects (Second ed.). pp. 1049–1052. doi:10.1016/B978-0-12-374144-8.00275-7

Schubel, J.R. (1976). Effects of Agnes on the suspended sediment on the Chesapeake Bay and contiguous shelf waters. In Schubel, J.R. (Eds.), *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, MD, p 179−200

Schubel, J.R., Carter, H.H., & Cronin, W.B. (1976). Effects of Agnes on the distribution of salinity along the main axis of the Bay and in contiguous shelf waters. In Ruzecki, E.P. (Eds.), *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, MD, p 33−65

Sehgal, M., Ladd, H.J., & Totapally, B. (2020). Trends in epidemiology and microbiology of severe sepsis and septic shock in children. *Hospital Pediatrics, 10*(12), pp. 1021–1030. doi:10.1542/hpeds.2020-0174

Sheriff, M.J., Peacor, S.D., Hawlena, D., Thaker, M., & Gaillard, J.M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology, 89*(6), pp. 1302–1316. doi:10.1111/1365-2656.13213. PMID 32215909.

Sih, A. (1987). Prey refuges and predator-prey stability. *Theoretical Population Biology, 31*, pp. 1–12. doi:10.1016/0040-5809(87)90019-0.

Slater, P.J.B., Rosenblatt, J.S., Snowdon, C.T., Roper, T.J., Brockmann, H.J., & Naguib, M. (2005). Advances in the study of behavior. *Academic Press*, p. 365. ISBN 978-0-08-049015-1.

Steere, A.C. (2001). Lyme disease. *New England Journal of Medicine, 345*(2), pp. 115–125. doi:10.1056/NEJM200107123450207. PMID 11450660.

Stevens, A.N.P. (2010). Predation, herbivory, and parasitism. *Nature Education Knowledge, 3*(10), pp. 36. Retrieved 12 February 2018.

Thieme, H.R. (2003). Mathematics in population biology. *Princeton University Press*. ISBN 978-0-691-09291-1.

Thomas, J.A., Schönrogge, K., Bonelli, S., Barbero, F., & Balletto, E. (2010). Corruption of ant acoustical signals by mimetic social parasites: Maculinea butterflies achieve elevated status in host societies by mimicking the acoustics of queen ants. *Commun Integr Biol., 3*(2), pp. 169–171. doi:10.4161/cib.3.2.10603. PMC 2889977. PMID 20585513.

Tyus, H.M. (2011). Ecology and conservation of fishes. *CRC Press*, p. 233. ISBN 978-1-4398-9759-1.

Van Oystaeyen, A., Araujo Alves, D., Caliari Oliveira, R., Lima do Nascimento, D., Santos do Nascimento, F., Billen, J., & Wenseleers, T. (2013). Sneaky queens in Melipona bees selectively detect and infiltrate queenless colonies. *Animal Behaviour, 86*(3), pp. 603–609. CiteSeerX 10.1.1.309.6081. doi:10.1016/j.anbehav.2013.07.001. S2CID 12921696.

Vermeij, G.J. (1993). Evolution and escalation: An ecological history of life. *Princeton University Press*, pp. 11 and passim. ISBN 978-0-691-00080-0.

Wetzel, R.G., & Likens, G.E. (2000). Predator-prey interactions. Limnological Analyses. Springer. pp. 257–262. doi:10.1007/978-1-4757-3250-4_17. ISBN 978-1-4419-3186-3.

Williams, A.C., & Flaxman, S.M. (2012). Can predators assess the quality of their prey's resource? *Animal Behaviour, 83*(4), pp, 883–890. doi:10.1016/j.anbehav.2012.01.008. S2CID 53172079.

Wilson, A.J., et al. (2017). What is a vector? *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1719): 20160085. doi:10.1098/rstb.2016.0085. PMC 5352812. PMID 28289253.

Wilson, E.O. (2014). The meaning of human existence. *W. W. Norton & Company,* p. 112. ISBN 978-0-87140-480-0.

Yang, W., Zhang, D., Peng, L., Zhuge, C., & Hong, L. (2020). Rational evaluation of various epidemic models based on the COVID-19 data of China. arXiv:2003.05666v1

Contributors and Attributions

This chapter was written by N. Gownaris and T. Zallek, with text taken from the following CC-BY resources:

- Predation by Wikipedia, the free Encyclopedia
- Herbivore by Wikipedia, the free Encyclopedia
- Parasitism by Wikipedia, the free Encylopedia
- Infection by Wikipedia, the free Encyclopedia
- Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

CHAPTER OVERVIEW

17: Mutualism and Commensalism

Learning Objectives

- Introduce and explore the types of mutualisms and commensalisms
- Explore theories that explain the evolution of mutualisms
- Discuss hypotheses regarding the maintenance of mutualistic relationships

Summary

A commensal relationship occurs when one species benefits from a close prolonged interaction, while the other neither benefits nor is harmed. Commensal relationships come many forms including: phoresis, inquilinism, and metabiosis. A mutualism occurs when two species benefit from their interaction, and can be generalized into three types: resource-resource, service-resource, and service-service. Many mutualisms are thought to have evolved from antagonistic interactions, such as parasite-host relationships. Reciprocal evolutionary responses are most likely important to the evolution of symbiotic mutualisms, like some plant-pollinator interactions, and may be important mechanisms for diversification, though evidence for this is mixed. The maintenance of mutualisms can be undermined by cheating, however, the destabilizing effect of cheating can be minimized by host sanctioning.

17.1: Introduction

Commensalism

A commensal relationship occurs when one species benefits from a close prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 17.1.1). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Many potential commensal relationships are difficult to identify because it is difficult to prove that one partner does not derive some benefit from the presence of the other.

Figure 17.1.1: The southern masked-weaver is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. "African Masked Weaver" by Hanay is licensed under CC BY 3.0.

Mutualism

A mutualism occurs when two species benefit from their interaction. For example, termites have a mutualistic relationship with protists that live in the insect's gut (Figure 17.1.2**a**). The termite benefits from the ability of the protists to digest cellulose. However, the protists are able to digest cellulose only because of the presence of symbiotic bacteria within their cells that produce the cellulase enzyme. The termite itself cannot do this: without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. In turn, the protists benefit from the enzymes provided by their bacterial endosymbionts, while the bacteria benefit from a doubly protective environment and a constant source of nutrients from two hosts. Lichen are a mutualistic relationship between a fungus and photosynthetic algae or cyanobacteria (Figure 17.1.2**b**). The glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae. The algae of lichens can live independently given the right environment, but many of the fungal partners are unable to live on their own.

Figure 17.1.2: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living in close association. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Contributors and Attributions

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

17.2: Types of Mutualisms

Resource-resource relationships

Mutualistic relationships can be thought of as a form of "biological barter" (Ollerton, 2016). For example, in mycorrhizal associations between plant roots and fungi, with the plant providing food resources (ie, carbohydrates) to the fungus in return for other important nutrients (eg, nitrogen and phosphorous). Other examples include rhizobia bacteria that fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates (Denison & Kiers, 2004).

Service-resource relationships

A few birds are perched, eating ticks off of various body parts of an impala standing in a field.

Figure 17.2.1 : The red-billed oxpecker eats ticks on the impala's coat, in a cleaning symbiosis. Photograph by Muhammad Mahdi Karim.

Service-resource relationships are common. Three important types are pollination, cleaning symbiosis, and zoochory. In pollination, a plant trades food resources in the form of nectar or pollen for the service of pollen dispersal. Cleaning symbioses are carried out by Phagophiles, animals that feed on ectoparasites, thereby providing anti-pest service, as in cleaning symbiosis. *Elacatinus* and *Gobiosoma*, genera of gobies, feed on ectoparasites of their clients while cleaning them (Soares et al., 2008). Zoochory is the dispersal of the seeds of plants by animals. This is similar to pollination in that the plant produces food resources (for example, fleshy fruit, overabundance of seeds) for animals that disperse the seeds (service). Plants may advertise these resources using color (Lim & Burns, 2021) and a variety of other fruit characteristics. Another example is ant protection of aphids, where the aphids trade sugar-rich honeydew (a by-product of their mode of feeding on plant sap) in return for defense against predators such as ladybugs.

Service-service relationships

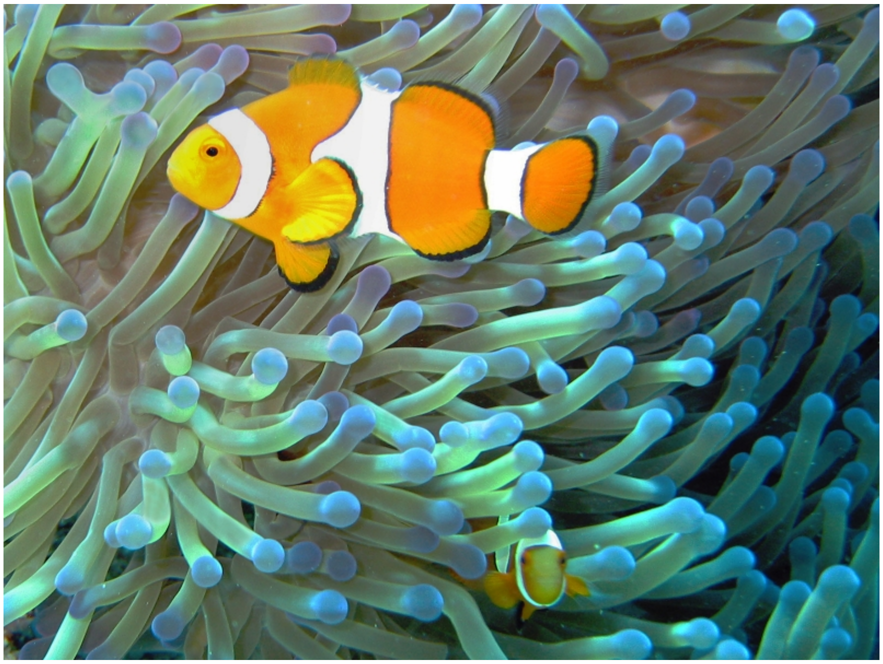


Figure 17.2.2 : Ocellaris clownfish and Ritter's sea anemones live in a mutual service-service symbiosis, the fish driving off butterflyfish and the anemone's tentacles protecting the fish from predators. Photograph by Jan Derk is available in the public domain.

Strict service-service interactions are very rare, for reasons that are far from clear (Ollerton, 2006). One example is the relationship between sea anemones and anemone fish in the family Pomacentridae: the anemones provide the fish with protection from predators (which cannot tolerate the stings of the anemone's tentacles) and the fish defend the anemones against butterflyfish (family Chaetodontidae), which eat anemones. However, in common with many mutualisms, there is more than one aspect to it: in the anemonefish-anemone mutualism, waste ammonia from the fish feeds the symbiotic algae that are found in the anemone's tentacles (Porat & Chadwick-Furman, 2004; Porat & Chadwick-Furman, 2005). Therefore, what appears to be a service-service mutualism in fact has a service-resource component. A second example is that of the relationship between some ants in the genus *Pseudomyrmex* and trees in the genus *Acacia*, such as the whistling thorn and bullhorn acacia. The ants nest inside the plant's thorns. In exchange for shelter, the ants protect acacias from attack by herbivores (which they frequently eat when those are small enough, introducing a resource component to this service-service relationship) and competition from other plants by trimming back vegetation that would shade the acacia. In addition, another service-resource component is present, as the ants regularly feed on lipid-rich food-bodies called Beltian bodies that are on the *Acacia* plant (Palomar College, 2019).

References

Denison, R.F., & Kiers, E.T. (2004). Why are most rhizobia beneficial to their plant hosts, rather than parasitic. *Microbes and Infection*, *6*(13), pp. 1235–1239. doi:10.1016/j.micinf.2004.08.005. PMID 15488744.

Soares, M.C., Côté, I.M., Cardoso, S.C., & Bshary, R. (2008). The cleaning goby mutualism: A system without punishment, partner switching or tactile stimulation. *Journal of Zoology, 276*(3), pp. 306–312. doi:10.1111/j.1469-7998.2008.00489.x.

Lim, G., & Burns, K.C. (2021). Do fruit reflectance properties affect avian frugivory in New Zealand? *New Zealand Journal of Botany*, pp. 1–11. doi:10.1080/0028825X.2021.2001664. ISSN 0028-825X. S2CID 244683146.

Ollerton, J. (2006). 'Biological barter': Interactions of specialization compared across different mutualisms. In Waser, N.M., & Ollerton, J. (Eds.), *Plant-pollinator interactions: From specialization to generalization* (pp. 411-435). University of Chicago Press.

Porat, D., & Chadwick-Furman, N.E. (2004). Effects of anemonefish on giant sea anemones: Expansion behavior, growth, and survival. *Hydrobiologia*, *530*(1–3), pp. 513–520. doi:10.1007/s10750-004-2688-y. S2CID 2251533.

Porat, D., & Chadwick-Furman, N.E. (2005). Effects of anemonefish on giant sea anemones: Ammonium uptake, zooxanthella content and tissue regeneration. *Mar. Freshw.Behav. Phys*., *38*, pp. 43–51.

"Swollen Thorn Acacias". *www2.palomar.edu*. Retrieved 22 February 2019.

Contributors and Attributions

This chapter was written by Aaron Howard with text taken from the following CC-BY resources:

- **Mutualism (biology) by Wikipedia, the free encyclopedia**

17.3: Evolution of Mutualisms

Evolution of Mutualisms

Many mutualisms are thought to have evolved from antagonistic interactions. Several studies have determined ecological or evolutionary conditions driving transitions from mutualism to antagonism (mutualism breakdown) (Kiers et al., 2010; Sachs & Simms, 2000), yet limited theory has been developed to mechanistically explain the evolutionary transitions from antagonism to mutualism (de Mazancourt et al., 2001; deMazancourt et al., 2005). Models of virulence predict evolution of reduced antagonism, perhaps toward mutualism, in cases of parasitism where host fidelity is high and availability of alternate hosts is low (Yamamura, 1993; Yamamura, 1996). In these models, host fidelity is achieved when lineages of parasites and their host are tightly linked through vertical transmission from parent to offspring.

Compelling evidence for the ‘virulence theory’ comes from interactions involving microbial parasites (Weeks et al., 2007; Sachs et al., 2014). For example, *Wolbachia* are endosymbiotic bacteria that live inside the cells of their invertebrate hosts. They are transmitted directly from mother to offspring, and spread through populations by manipulating the reproduction of their hosts. The most common reproductive manipulation responsible for the spread of these bacteria, called “cytoplasmic incompatibility,” arises when infected males mate with uninfected females, resulting in fewer offspring than normal. There are fitness costs for the hosts associated with *Wolbachia* infections, most commonly involving a reduction in egg production. The virulence theory predicts and evidence suggests that there is selection for the bacteria to evolve a more benign lifestyle, changing the bacterium from being parasitic to more mutualistic, where *Wolbachia*-infected hosts have higher rates of egg production than their uninfected counterparts (Weeks et al., 2007).

Reciprocal evolutionary responses are most likely important to the evolution of symbiotic mutualisms, and subsequent diversification may be the result of the mutualism improving niche width, population size, or transition into adaptive zones (Hembry et al., 2014). However, with the exception of plant-pollinator interactions, it is unclear how important mutualistic coevolution is as a driving force of diversification, especially as compared to the well-established mechanisms associated with competitive and antagonistic coevolution.

Plant-pollinator interactions are powerful tools of evolution because pollinators transport gametes (via pollen) between flowers. Plant-pollinator relationships are thought to be critical to the historical diversification of angiosperm flowers. In fact, up to 25% of plant speciation events could be as a result of interactions with pollinators (van der Niet & Johnson, 2012).

The obligate pollinating seed-predation mutualisms of the yucca and yucca moth and fig and fig wasps are attributed to coevolution diversification because the intimacy of the association may prevent species from making phylogenetically drastic switches to new partners. Interacting with a distant relative of your partner may not be an option if coevolution has created incompatibilities in specialized traits required for the interaction (Figure 17.3.1). For instance, if laying eggs into yucca flowers requires a particular complement of ovipositor traits and moth behaviors, we might predict to find host switches only between closely related yuccas. Initial analyses of yucca and yucca moth phylogenies suggest that the trees are somewhat congruent, although there have been at least two instances of moths switching hosts to quite distantly related yuccas (Pellmyr, 2003). The interaction between yuccas and yucca moths is clearly one that is highly specialized and coevolved, yet we do not find a phylogenetic pattern of perfect matching between plant and insect.

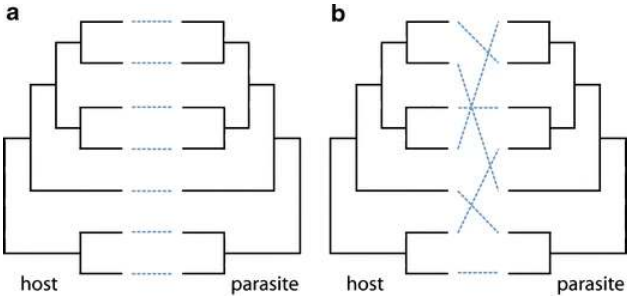


Figure 17.3.1: Comparison of host and parasite phylogenetic trees. The *dotted lines* indicate host associations of the parasites. a) Matching speciation events between host and parasite show a strict pattern of cospeciation. b) Host switches to distant relatives are shown by the crossing lines. Some parasites use closely related hosts, but most have jumped to a distant relative. *Source: Segraves, 2010.*

However, there is also evidence opposing the primacy of mutualistic coevolution in these relationships. Figs have been shown to be successfully pollinated regardless of pollinator species (Moe & Weiblen, 2012) and pollinator host-switch may be more frequent than co-speciation events (Wang et al., 2021; Figure 17.3.2). There is also evidence that geographic isolation plays a significant role in yucca diversification (Althoff et al., 2012; Smith et al., 2008). These together suggest that while coevolution plays a role in the emergence of these mutualisms, it is not the exclusive mechanism and may not even be the primary one.

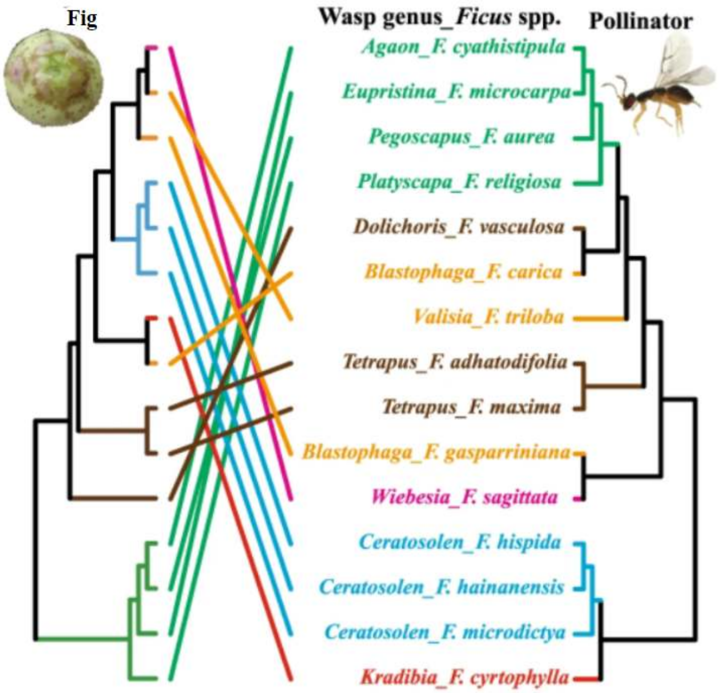


Figure 17.3.2: Cophylogenetic comparison of the pollinators associated with the 15 fig species studied. *Ficus* and pollinator phylogenies used were indicated with symbol of figs and wasp separately. Tip-name colors indicate subgeneric classification. Extensive phylogenetic incongruence is shown for each pair of phylogenies (credit: modified from Wang et al. 2021).

References

Althoff, D.M., Segraves, K.A., Smith, C.I., Leebens-Mack, J., & Pellmyr, O. (2012). Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification. *Molecular Phylogenetics and Evolution, 62,* pp. 898–906.

de Mazancourt, C., Loreau, M., & Dieckmann, U. (2001). Can the evolution of plant defense lead to plant-herbivore mutualism? *Am. Nat.*, *158*, pp. 09–123.

de Mazancourt, C., Loreau, M., & Dieckmann, U. (2005). Understanding mutualism when there is adaptation to the partner. *J. Ecol.*, *93*, pp. 305–314.

Hembry, D.H., Yoder, J.B., & Goodman, K.R. (2014). Coevolution and the diversification of Llfe. *The American Naturalist*, *184*(4), pp. 425–38. https://doi.org/10.1086/677928.

Kiers, T.E., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010). Mutualisms in a changing world: An evolutionary perspective. *Ecol. Lett.*, *13*, pp. 1459–1474.

Moe, A.M., & Weiblen., G.D. (2012). Pollinator-mediated reproductive isolation among dioecious fig species *(Ficus, Moraceae). Evolution, 66*, pp. 3710–3721.

Pellmyr, O. (2003). Yuccas, yucca moths, and coevolution: A review. *Ann. Mo. Bot. Gard.*, 90, pp. 35–55.

Sachs, J. & Simms, E. (2006). Pathways to mutualism breakdown. *Trends Ecol. Evol.*, *21*, pp. 585–592.

Sachs, J., Skophammer, R., Bansal, N. & Stajich, J. (2014). Evolutionary origins and diversification of proteobacterial mutualists. *Proc. R. Soc. B Biol. Sci.*, *281*, 20132146.

Smith, C.I., Pellmyr, O., Althoff, D.M., Balcázar-Lara, M., Leebens-Mack, K., & Segraves, K.A. (2008). Pattern and timing of diversification in Yucca *(Agavaceae)*: Specialized pollination does not elevate rates of diversification. *Proceedings of the Royal Society B: Biological Sciences, 275,* pp. 249–258.

van der Niet, T., & Johnson, S.D. (2012). Phylogenetic evidence for pollinator-driven diversification of angiosperms. *Trends in Ecology and Evolution, 27,* pp. 353–361.

Weeks, A., Turelli, M., Harcombe, W., Reynolds, K. & Hoffmann, A. (2007). From parasite to mutualist: Rapid evolution of Wolbachia in natural populations of Drosophila. *PLoS Biol., 5,* e114.

Yamamura, N. (1993). Vertical transmission and evolution of mutualism from parasitism. *Theor. Popul. Biol., 44,* pp. 95–109.

Yamamura, N. (1996). Evolution of mutualistic symbiosis: A differential equation model. *Res. Popul. Ecol., 38,* pp. 211–218.

Contributors and Attributions

This chapter was written by Aaron Howard with text taken from the following CC-BY resources:

- Johnson, C.A., Smith, G.P., Yule, K. *et al.* (2021). Coevolutionary transitions from antagonism to mutualism explained by the Co-Opted Antagonist Hypothesis. *Nat Commun*, *12*, 2867. https://doi.org/10.1038/s41467-021-23177-x
- Segraves, K.A. (2010). Branching out with coevolutionary trees. *Evo. Edu. Outreach*, *3*, pp. 62–70. https://doi.org/10.1007/s12052-009-0199-z
- Wang, G., Zhang, X., Herre, E.A. *et al.* (2021). Genomic evidence of prevalent hybridization throughout the evolutionary history of the fig-wasp pollination mutualism. *Nat Commun.*, *12*, 718. https://doi.org/10.1038/s41467-021-20957-3
- Weeks, A., Turelli, M., Harcombe, W., Reynolds, K. & Hoffmann, A. (2007). From parasite to mutualist: Rapid evolution of Wolbachia in natural populations of Drosophila. *PLoS Biol*., *5*, e114.

17.4: Maintenance of Mutualisms

Maintenance of mutualism

The stability of mutualisms can be undermined by cheating. Cheating is a behavior whereby organisms receive a benefit at the cost of other organisms. Cheating is common in many mutualistic and altruistic relationships (Ferriere et al., 2002). A cheater is an individual who does not cooperate (or cooperates less than their fair share) but can potentially gain the benefit from others cooperating (West et al., 2006). Cheaters are also those who selfishly use common resources to maximize their individual fitness at the expense of a group (McLean & Gudelj, 2006). Simple two-player game theory and the associated evolutionary theory indicate that cheating can be evolutionarily stable, but there are mechanisms to regulate it (Foster & Kokko, 2006).

The mutualism between legume plants and rhizobia (nitrogen-fixing soil bacteria) is an example where this regulation occurs. Rhizobia establish symbiotic organs termed root nodules on the roots of their host, and proliferate by extracting nutrients from the host plant. In turn, they supply their host plants with nitrogen resources produced by nitrogen gas fixation. This mutual nutrient exchange should promote the fitness of both organisms and thereby strengthen the symbiotic relationship. This beneficial effect, known as “partner fidelity feedback”, is assumed as a stabilizing factor for the mutualistic relationship (Sachs et al., 2004; Weyl et al., 2010; Friesen & Jones, 2012; Friesen, 2012).

On the other hand, naturally occurring rhizobium strains vary in their nitrogen fixation activity, and ineffective rhizobia that colonize their host plants without undertaking nitrogen fixation in their root nodules are ubiquitous (Gibson et al., 1975; Bottomly & Jenkins, 1983; Moawad, 1998; Burdon et al., 1999). Because the nitrogen fixation reaction consumes much energy (or costs), such parasitic cheaters could use surplus energy for their own growth or for synthesizing storage substances. Consequently, they are likely to proliferate more efficiently than nitrogen-fixing cooperators, posing a risk to the symbiotic interaction. Rhizobia are therefore exposed to two opposite effects that simultaneously promote (by providing benefit) and destabilize (by incurring cost) the mutualistic relationship.

Figure 17.4.1: Nitrogen-fixing nodules in legumes. Image by Terraprima is licensed under CC BY-SA 3.0.

Despite the widespread presence of ineffective rhizobia, the legume–rhizobia symbiosis is evolutionarily stable. Host sanctioning is a potential mechanism that stabilizes the symbiotic interaction, where plants punish more parasitic cheaters by reducing nutrient supply based on their symbiotic performance (Friesen & Jones, 2012; Friesen, 2012; Kiers & Denison, 1998).

Another example is found within the yucca-yucca moth mutualisms. "Cheating" sometimes happens when the yucca moth deposits too many eggs in one plant. In this case, the yucca plant has little to no benefits from this interaction. However, the plant has a unique way of sanctioning this behavior. While the sanctions against cheating often occurs directly to the individual, in this case, the constraint occurs to the individual's offspring. The yucca plant can "abort" the moths by aborting the flowers. Pellmyr and

Huth (1994) found that there is selective maturation for flowers that have low egg loads and high number of scars (and therefore a high amount of pollen). In this way, there is selection against the "cheaters" who try to use the yucca plant without providing the benefits of pollination.

Figure 17.4.2: Two yucca moth females in a yucca flower. The female on the right is laying an egg and clearly shows the pollen ball on the underside of her head. The female on the left is actively pollinating with her maxillary tentacles. Photograph by Olle Pellmyr.

Exercise 17.4.1: When should you sanction a cheater?

Yucca plants will drop flowers if their obligate pollinators, the yucca moths, lay too many eggs. This reduces fitness for both the plant and the moth that laid the egg, and is a form of sanctioning by the plant. However, devoting resources to growing a fruit with too many yucca moth larvae on it would reduce the plant's fitness even more than aborting the flower does. If the flower is aborted, the cost to fitness for the pollinator is very high, making this an effective sanction against moths that try to "cheat" the plant by laying too many eggs.

Neither option is great for the plant - but at what point is it worse for the plant's fitness to retain and invest resources in a flower with too many eggs, rather than dropping the flower and sacrificing any possible surviving seeds? It turns out that most yucca fruits that are retained by the plant contain about 130 seeds, but about 20% of those seeds (26 seeds) are eaten by larvae (Alexander et al.). Therefore, plants begin to drop flowers when the number of larvae present are likely to consume more than 20% of the seeds! In the graph below, you can see the probability of retaining versus dropping a flower based on the number of larvae present. This graph was simulated from the real values found by Pellmyr and Huth in their groundbreaking 1994 paper, which showed that mutualisms are not always strictly collaborative, but can involve tension between opposing forces (the plant needs pollination, but doesn't 'want' seeds eaten, the moth needs to lay as many eggs as it can) held in check by natural selection.

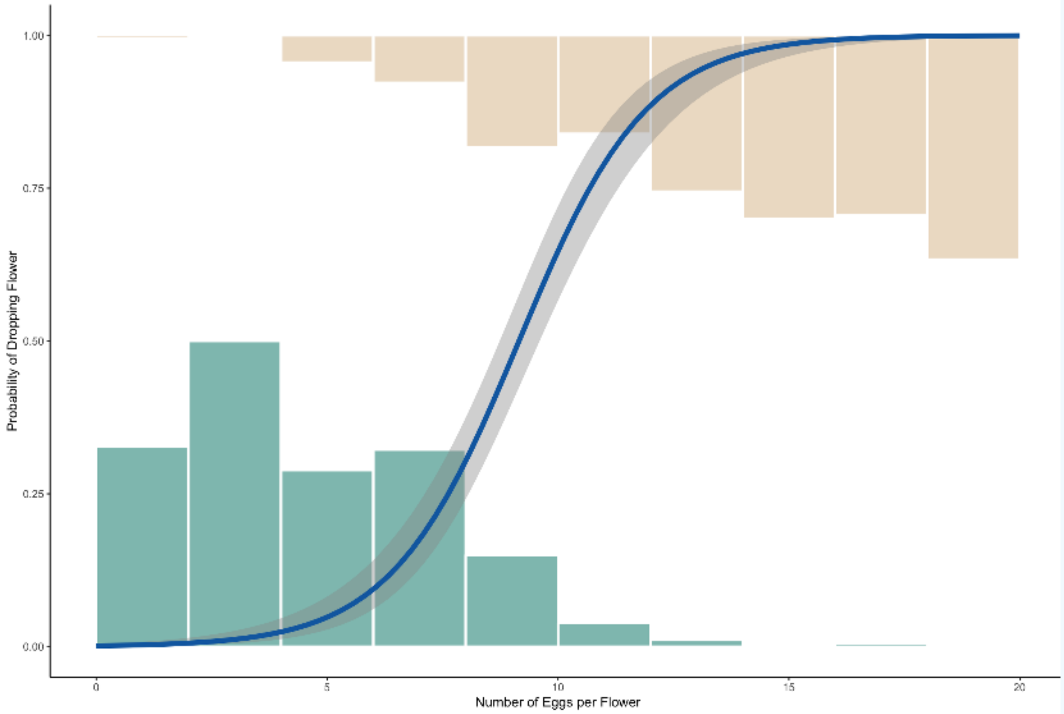


Figure 17.4.3: This graph shows the probability of retaining a flower (0) versus aborting a flower (1) based on the number of eggs laid on that flower. As the number of eggs increases, the plant becomes more likely to abort the flower, beginning to switch when there are ~6.5 larvae, meaning that most larvae eat ~4 seeds. However, as you can see from the green (retained) and tan (dropped) histograms, not every plant responds in the same way. Some plants retain flowers even with over 15 eggs laid, while others will drop flowers with only 2 eggs.

1. How many larvae could a flower tolerate if each flower had 250 seeds, instead of 130?
2. How many larvae could a flower tolerate if each larva had to eat 10 seeds, instead of 4?

Answer

1. 12.5 larvae
2. 2.6 larvae

References

Alexander, R.R., Pond, F.W., & Rodgers, J.E. (n.d.). Yucca (L.). *Forest Service Handbooks.* https://www.fs.fed.us/rm/pubs_other/wo_AgricHandbook727/wo_AgricHandbook727_1175_1177.pdf

Bottomley. P, & Jenkins, M. (1983). Some characteristic of Rhizobium meliloti isolates from alfalfa fields in Oregon. *Soil Sci. Soc. Am.*, J 47, pp. 1153–1157.

Burdon, J., Gibson, A., Searle, S., Woods, M., & Brockwell, J. (1999). Variation in the effectiveness of symbiotic associations between native rhizobia and temperate Australian Acacia: Within-species interactions. *J. Appl. Ecol.*, *36*, pp. 398–408.

Ferriere, R., Bronstein, J.L., Rinaldi, S., Law, R., & Gauduchon, M. (2002). Cheating and the evolutionary stability of mutualisms. *Proc. R. Soc. Lond.*, *269*(1493), pp. 773–780. doi:10.1098/rspb.2001.1900. PMC 1690960. PMID 11958708.

Foster, K.R., & Kokko, H. (2006). Cheating can stabilize cooperation in mutualisms. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), pp. 2233-2239. *doi:10.1098/rspb.2006.3571. PMC 1635526. PMID 16901844.*

Friesen, M.L., & Jones, E.I. (2012). Modelling the evolution of mutualistic symbioses. *Methods Mol. Biol.*, *804*, pp. 481–499.

Friesen, M.L. (2012). Widespread fitness alignment in the legume-rhizobium symbiosis. *New Phytol.*, *194*, pp. 1096–1111.

Gibson, A., Curnow, B., Bergersen, F., Brockwell, J., & Robinson, A. (1975). Studies of field populations of Rhizobium: Effectiveness of strains of Rhizobium trifolii associated with Trifolium subterraneum L. pastures in South-Eastern Australia. *Soil Biol. Biochem.*, *7*, pp. 95–102.

Kiers, E., & Denison, R. (2008). Sanctions, cooperation, and the stability of plant Rhizosphere mutualisms. *Annu. Rev. Ecol. Evol. Syst.*, *39*, pp. 215–236.

MacLean, R.C., & Gudelj, I. (2006). Resource competition and social conflict in experimental populations of yeast. *Nature*, *441*(7092), 498-501. *Bibcode:2006Natur.441..498M*. *doi:10.1038/nature04624*. *PMID 16724064*. *S2CID 4419943*.

Moawad, H., El-Din, S., & Abdel-Aziz, R. (1998). Improvement of biological nitrogen fixation in Egyptian winter legumes through better management of Rhizobium. *Plant Soil*, *204*, pp. 95–106.

Pellmyr, O., & Huth, C.J. (1994). Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, *372*(6503), pp. 257–260. Bibcode:1994Natur.372..257P. doi:10.1038/372257a0. S2CID 4330563.

Sachs, J., Mueller, U., Wilcox, T., & Bull, J. (2004). The evolution of cooperation. *Quart. Rev. Biol.*, *79*, pp. 135–160.

West, S.A., Griffin, A.S., Gardner, A., & Diggle, S.P. (2006). Social evolution theory for microorganisms. *Nature Reviews Microbiology*, *4*(8), pp. 597-607. *doi:10.1038/nrmicro1461*. *PMID 16845430*. *S2CID 18451640*.

Weyl, E.G., Frederickson, M.E., Yu, D.W., & Pierce, N.E. (2010). Economic contract theory tests models of mutualism. *Proc. Natl. Acad. Sci. USA.*, *107*, pp. 15712–15716.

Contributors and Attributions

This chapter was written by Aaron Howard with text taken from the following CC-BY resources. Exercise text, data simulation, and code written by Castilleja Olmsted:

- **Cheating (biology) by Wikipedia, the free encyclopedia**
- Fujita H, Aoki S, Kawaguchi M (2014) Evolutionary Dynamics of Nitrogen Fixation in the Legume–Rhizobia Symbiosis. PLoS ONE 9(4): e93670. doi:10.1371/journal.pone.0093670

17.5: Types of Commensalisms

Phoresis

Phoresis or **phoresy** is a non-permanent, commensalistic interaction in which one organism (a phoront or phoretic) attaches itself to another (the host) solely for the purpose of travel (White et al., 2017). Phoresis has been observed directly in ticks and mites since the 18th century (Houck & O'Connor, 1991), and indirectly in fossils 320 million years old (White et al., 2017). It is not restricted to arthropods or animals; plants with seeds that disperse by attaching themselves to animals are also considered to be phoretic (Houck, 2009).

Figure 17.5.1: Male *Bombus hypnorum* with phoretic mites. Photograph by Dimităr Boevski.

The strict definition of phoresis excludes cases in which the relationship is permanent (e.g. that of a barnacle surviving on a whale) or those in which the phoront gains any kind of advantage from the host organism (e.g. remoras attaching to sharks for transportation and food) (Houck & O'Connor, 1991). Phoresis is a commensal relationship and deviations result in mutualistic or parasitic relationships. Phoretic relationships can become parasitic if a cost is inflicted upon the host, such as if the number of mites on a host begins impeding its movement. Parasitic relationships could also evolve for from phoretic ones if the phoront gains a fitness advantage from the death of a host (e.g. nutrition). Mutualistic relationships could also evolve if the phoront began to confer a benefit to the host (e.g. predator defense) (White et al., 2017). The evolutionary plasticity of phoretic relationships allow them to potentially add to the complexity and diversity of ecosystems (Houck, 2009).

Cases in which the phoront parasitizes or preys upon the host organism after travel are still considered phoresis, as long as the travel behavior and the feeding or parasitizing behavior are separate (White et al., 2017). Similarly, some pseudoscorpions prey upon the same species that act as their phoretic host. The behaviors are completely separate, however, since the pseudoscorpion uses anatomical features specifically for predation when treating the host as prey, but employs anatomical features used for phoresis when travelling (Poinar et al., 1998).

Inquilinism

An **inquiline** is an animal that lives commensally in the nest, burrow, or dwelling place of an animal of another species. For example, some organisms such as insects may live in the homes of gophers or the garages of human beings and feed on debris, fungi, and roots. The most widely distributed types of inquiline are those found in association with the nests of social insects, especially ants and termites – a single colony may support dozens of different inquiline species. The distinctions between parasites, social parasites, and inquilines are subtle, and many species may fulfill the criteria for more than one of these, as inquilines do exhibit many of the same characteristics as parasites. However, parasites are specifically *not* inquilines, because by definition they have a deleterious effect on the host species (Nash & Boomsma, 2008), while inquilines have not been confirmed to do so.

In the specific case of termites, the term "*inquiline*" is restricted to termite species that inhabit other termite species' nests (Florencio et al., 2013; Cunha et al., 2003; Hugo et al., 2019), whereas other arthropods cohabiting termitaria are called "*termitophiles*" (Rosa et al., 2018; Oliveira, 2018). It is important to reiterate that inquilinism in termites (*Blattodea*, formerly *Isoptera*) contrasts with the inquilinism observed in other eusocial insects such as ants and bees (*Hymenoptera*), even though the term "*inquiline*" has been adopted in both cases. A major distinction is that, while in the former the species mostly resemble forms of commensalism, the latter includes species currently confirmed as social parasites, thus, being closely related to parasitism.

Inquilines are known especially among the gall wasps (*Cynipidae* family). In the sub-family *Synerginae*, this mode of life predominates. These insects are similar in structure to the true gall-inducing wasp but do not produce galls, instead, they deposit their eggs within those of other species. They infest certain species of galls, such as those of the blackberry and some oak galls, in large numbers, and sometimes more than one kind occur in a single gall. Perhaps the most remarkable feature of these inquilines is their frequent close resemblance to the insect that produces the gall they infest (Rines, 2020; Discover Life, 2011).

The term *inquiline* has also been applied to aquatic invertebrates that spend all or part of their life cycles in phytotelmata, water-filled structures produced by plants (Cronk & Fennessy, 2001). For example, *Wyeomyia smithii*, *Metriocnemus knabi*, and *Habrotrocha rosa* are three invertebrates that make up part of the microecosystem within the pitchers of *Sarracenia purpurea* (Cochran-Stafira & von Ende, 1998). Some species of pitcher plants like the *Nepenthes* and *Cephalotus* produce acidic, toxic or digestive fluids and host a limited diversity of inquilines. Other pitcher plant species like the *Sarracenia* or *Heliamphora* host diverse organisms and depend to a large extent on their symbionts for prey utilization (Adkassnig et al., 2011).

Figure 17.5.2: *Wyeomyia smithii* larva is an inquiline species in the pitcher leaves of *Sarracenia purpurea*. "Wyeomyia smithii" by Rkitko is licensed under CC BY-SA 3.0.

Metabiosis

Metabiosis is a more indirect dependency, in which one organism creates or prepares a suitable environment for a second. Examples include maggots, which develop on and infest corpses, and hermit crabs, which use gastropod shells to protect their bodies.

References

Adlassnig, W., Peroutka, M., & Lendl, T. (2011). Traps of carnivorous pitcher plants as a habitat: Composition of the fluid, biodiversity and mutualistic activities. *Annals Of Botany*, *107*(2).

Cochran-Stafira, D.L., & von Ende, C.N. (1998). Integrating bacteria into food webs: Studies with *Sarracenia purpurea* inquilines. *Ecology*, *79*(3), pp. 880–898.

Cunha, H.F.D., Andrade Costa, D., Espirito Santo Filho, K.D., Silva, L.O., & Brandão, D. (2003). Relationship between Constrictotermes cyphergaster and inquiline termites in the Cerrado (Isoptera: Termitidae). *Sociobiology, 42*(3), pp. 761-770.

Cronk, J.K., & Fennessy, M.S. (2001).Wetland plants: Biology and ecology, p. 45.

Discover Life: Family Cynipidae: Subfamily Synerginae visited 1 January 2011

Florencio, D.F., Marins, A., Rosa, C.S., Cristaldo, P.F., Araújo, A.P.A., Silva, I.R., & DeSouza, O. (2013). Diet segregation between cohabiting builder and inquiline termine species. *PLOS ONE*, *8*(6), *Bibcode:2013PLoSO...866535F*. *doi:10.1371/journal.pone.0066535*. *PMC 3689842*. *PMID 23805229*.

Houck, M.A., & O'Connor, B.M. (1991). Ecoological and evolutionary significance of Phoresy in the Astigmata. *Annual Review of Entomology, 36(1), pp. 611–636. doi:10.1146/annurev.en.36.010191.003143. ISSN 0066-4170.*

Houck, M.A. (2009). Phoresy, encyclopedia of insects. *Elesvier*, pp. 772-774. *doi:10.1016/b978-0-12-374144-8.00205-8*, *ISBN 9780123741448*, *retrieved 2018-10-14*

Hugo, H., Cristaldo, P. F., & DeSouza, O. (2019). Peaceful behaviour: A strategy employed by an obligate nest invader to avoid conflict with its host species. *bioRxiv*, 587592. https://doi.org/10.1101/587592

Nash, D.R., & Boomsma, J.J. (2008). Communication between hosts and social parasites. In D'Ettore, P., & Hughes, D.P. (Eds.), *Sociobiology of communication: An interdisciplinary perspective* , pp. 1-55, e80. Oxford: Oxford University Press.

Oliveira, M.H., Da Silva Vieira, R.V., Moreira, I.E., Pires-Silva, C.M., De Lima, H.V.G., De Lima Andrade, M.R., & Bezerra-Gusmão, M.A. (2018). The road to reproduction: Foraging trails of Constrictotermes cyphergaster (Termitidae: Nasutitermitinae) as maternities for Staphylinidae beetles. *Sociobiology, 65*(3), pp. 531-533.

Poinar Jr., G.O., Curcic, B.P.M., & Cokendolpher, J.C. (1998). Arthropod Phoresy involving pseudoscorpions in the past and present. *Acta Arachnologica*, *47*(2), pp. 79–96. doi:10.2476/a

Rines, G.E. (1920). Inquiline. Encyclopedia Americana.

Rosa, C.S., Cristaldo, P.F., Florencio, D.F., Marins, A., Lima, E.R. & DeSouza, O. (2018). On the chemical disguise of a physogastric termitophilous rove beetle. *Sociobiology, 65*, pp. 38-47.

White, P., Morran, L., & de Roode, J. (2017). Phoresy. Current Biology, 27(12), R578-R580. *doi:10.1016/j.cub.2017.03.073*. *PMC 5749251*. *PMID 28633022*.

Contributors and Attributions

This chapter was written by Aaron Howard with text taken from the following CC-BY resources:

- **Commensalism by Wikipedia, the free encyclopedia**
- **Phoresis by Wikipedia, the free encyclopedia**
- **Inquiline by Wikipedia, the free encyclopedia**

CHAPTER OVERVIEW

18: Ecological Succession

Learning Objectives

- Introduce succession by exploring the history of its theory
- Describe role of disturbance and expected outcomes regarding diversity
- Summarize important models of successional change
- Go beyond plants by investigating the roles of consumers in succession

Summary

Succession, or the process of change in the species composition of a community over time, was one of the first theories developed in ecology. Succession is brought about by environmental disturbances, and generally speaking, disturbance increases biodiversity. However, the level of disturbance significantly influences species diversity and may be maximized at intermediate levels. The patterns of successional change in biodiversity are scale dependent and must be quantified appropriately using alpha, beta, and gamma diversities. There are three common models used to explain the dynamics of community development through succession. In these models pioneer species facilitate, inhibit, or can be tolerated by later successional organisms. Succession is commonly framed within plant communities. However, animal communities affect succession through phenomena like the redirection of successional trajectories and the development of alternative stable states.

18.1: Introduction

Ecological succession is the process of change in the species composition of an ecological community over time. It is a process by which an ecological community undergoes more or less orderly and predictable changes following a disturbance or the initial colonization of a new habitat. Succession may be initiated either by formation of new, unoccupied habitat, such as from a lava flow or a severe landslide, or by some form of disturbance of a community, such as from a fire, severe windthrow, or logging. Succession that begins in new habitats, uninfluenced by pre-existing communities is called primary succession, whereas succession that follows disruption of a pre-existing community is called secondary succession.

18.1.1: **History of succession**

Succession was among the first theories advanced in the ecological literature. Ecological succession was first documented in the Indiana Dunes of Northwest Indiana and remains an important ecological topic of study.[1]

Between 1899-1910, Henry Chandler Cowles, at the University of Chicago, developed a more formal concept of succession. Inspired by studies of Danish dunes by Eugen Warming, Cowles studied vegetation development on sand dunes on the shores of Lake Michigan (the Indiana Dunes). He recognized that vegetation on dunes of different ages might be interpreted as different stages of a general trend of vegetation development on dunes (an approach to the study of vegetation change later termed space-for-time substitution, or chronosequence studies).

From about 1900 to 1960, however, understanding of succession was dominated by the theories of Frederic Clements, a contemporary of Cowles, who held that **seres** were highly predictable and deterministic series of successional plant communities that converged on a climatically determined stable climax community regardless of starting conditions. Clements explicitly analogized the successional development of ecological communities with ontogenetic development of individual organisms, and his model is often referred to as the pseudo-organismic theory of community ecology. Clements and his followers developed a complex taxonomy of communities and successional pathways.

Henry Gleason offered a contrasting framework as early as the 1920s. The Gleasonian model was more complex and much less deterministic than the Clementsian. It differs most fundamentally from the Clementsian view in suggesting a much greater role of chance factors and in denying the existence of coherent, sharply bounded community types. Gleason argued that species distributions responded individualistically to environmental factors, and communities were best regarded as artifacts of the juxtaposition of species distributions. Gleason's ideas, first published in 1926, were largely ignored until the late 1950s.

Two quotes illustrate the contrasting views of Clements and Gleason. Clements wrote in 1916:

> *The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development.*
>
> *— Frederic Clements*[2]

while Gleason, in his 1926 paper, said:

> *An association is not an organism, scarcely even a vegetational unit, but merely a coincidence.*
>
> *— Henry Gleason*[3]

Gleason's ideas were, in fact, more consistent with Cowles' original thinking about succession. About Clements' distinction between primary succession and secondary succession, Cowles wrote (1911):

> *This classification seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and it places together such unlike things as human agencies and the subsidence of land.*
>
> *— Henry Cowles*[4]

Succession theory was developed primarily by botanists. The study of succession applied to whole ecosystems initiated in the writings of Ramon Margalef, while Eugene Odum's publication of *The Strategy of Ecosystem Development* is considered its formal starting point.[5]

Animal life also exhibits changes with changing communities. In the lichen stage fauna is sparse. It comprises a few mites, ants and spiders living in cracks and crevices. The fauna undergoes a qualitative increase during the herb grass stage. The animals found during this stage include nematodes, insects larvae, ants, spiders, mites, etc. The animal population increases and diversifies with the development of the forest climax community. The fauna consists of invertebrates like slugs, snails, worms, millipedes, centipedes, ants, bugs; and vertebrates such as squirrels, foxes, mice, moles, snakes, various birds, salamanders and frogs.

A more rigorous, data-driven testing of successional models and community theory generally began with the work of Robert Whittaker and John Curtis in the 1950s and 1960s. Succession theory has since become less monolithic and more complex. J. Connell and R. Slatyer attempted a codification of successional processes by mechanism. Among British and North American ecologists, the notion of a stable climax vegetation has been largely abandoned, and successional processes have come to be seen as much less deterministic, with important roles for historical contingency and for alternate pathways in the actual development of communities. Debates continue as to the general predictability of successional dynamics and the relative importance of equilibrial vs. non-equilibrial processes. Former Harvard professor Fakhri A. Bazzaz introduced the notion of *scale* into the discussion, as he considered that at local or small area scale the processes are stochastic and patchy, but taking bigger regional areas into consideration, certain tendencies can not be denied.[6]

18.1.2: Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) and Kyle Whittinghill (University of Vermont) from the following sources:

- https://en.wikipedia.org/wiki/Ecological_succession

1. Smith, S., & Mark, S. (2009). The historical roots of the nature conservancy in the Northwest Indiana/Chicagoland region: From science to preservation. *The South Shore Journal*, *3*. *"Archived copy". Archived from the original on 2016-01-01. Retrieved 2015-11-22.*
2. Clements, F.E. (1916). Plant succession: an analysis of the development of vegetation.
3. Gleason, H.A. (1926). The individualistic concept of the plant association. *The Bulletin of the Torrey Botanical Club*.
4. Cowles, H.C. (1911). The causes of vegetational cycles. *Annals of the Association of American Geographers, 1*(1), pp. 3-20.
5. The succession of forest trees, and wild apples. Archive.org. Retrieved on 2014-04-12.
6. Bazzaz, F.A. (1996). Plants in changing environments. UK: Cambridge University Press. pp. 4–5. ISBN 9-780521-398435.

18.2: What are the Effects of Disturbance?

Changes in community structure and composition over time are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain. Thus, disturbance can initiate successional change.

Species that are well adapted for exploiting disturbance sites are referred to as pioneers or early successional species. These shade-intolerant species are able to photosynthesize at high rates, produce a lot of offspring, and grow and mature quickly. Their fast growth is usually balanced by short life spans. Furthermore, although these species often dominate immediately following a disturbance, they are unable to compete with shade-tolerant species later on and are replaced by these species through succession. However these shifts may not reflect the progressive entry to the community of the taller long-lived forms, but instead, the gradual emergence and dominance of species that may have been present, but inconspicuous directly after the disturbance.[1] Disturbances have also been shown to be important facilitators of non-native plant invasions.[2]

While plants must deal directly with disturbances because of their lack of mobility, many animals are mobile and thus are not as immediately affected by disturbance. For example, some animals could successfully evade the initial destruction of a forest fire, but can later return to the burned area and thrive on new growth on the forest floor. Disturbed communities (such as a forest after a fire) often support a wider variety of plants compared to pre-disturbance vegetation. The plants in turn support a variety of wildlife, temporarily increasing biological diversity in the forest.[3]

18.2.1: Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis (IDH) suggests that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent. At low levels of disturbance, more competitive organisms will push subordinate species to extinction and dominate the ecosystem.[4] At high levels of disturbance, due to frequent forest fires or human impacts like deforestation, all species are at risk of going extinct. According to intermediate disturbance hypothesis theory, at intermediate levels of disturbance, diversity is thus maximized because species that thrive at both early and late successional stages can coexist. Intermediate disturbance hypothesisis a nonequilibrium model used to describe the relationship between disturbance and species diversity.

The intermediate disturbance hypothesis is based on the following premises:

1. ecological disturbances have major effects on species richness within the area of disturbance,
2. interspecific competition results from one species driving a competitor to extinction and becoming dominant in the ecosystem, and
3. moderate ecological scale disturbances prevent interspecific competition.[5,6,7]

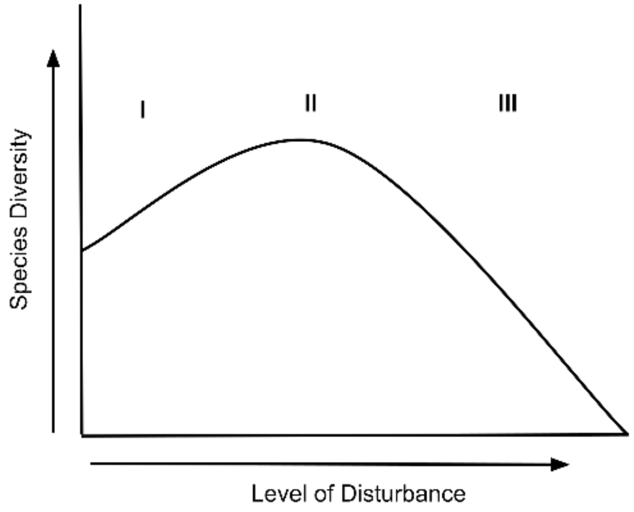


Figure 18.2.1: I describes how, at low levels of ecological disturbance species richness decreases as competitive exclusion increases; II shows that at intermediate levels of disturbance, diversity is maximized because species that thrive at both early and late successional stages can coexist; III shows that at high levels of disturbance species richness is decreased due to an increase in species movement. "Intermediate Disturbance Hypothesis Graph" by Sciencerelatedusername is licensed under CC BY-SA 4.0.

Disturbances act to disrupt stable ecosystems and clear species' habitat. As a result, disturbances lead to species movement into the newly cleared area (secondary succession).[5] Once an area is cleared there is a progressive increase in species richness and competition between species takes place. Once the conditions that create a disturbance are gone, and competition between species in the formerly disturbed area increases, species richness decreases as competitive exclusion increases.[8]

"Gause's Law", also known as competitive exclusion, explains how species that compete for the same resources cannot coexist in the same niche.[6] Each species handles change from a disturbance differently; therefore, intermediate disturbance hypothesis can be described as both "broad in description and rich in detail".[5] The broad intermediate disturbance hypothesis model can be broken down into smaller divisions which include spatial within-patch scales, spatial between-patch scales, and purely temporal models. Each subdivision within this theory generates similar explanations for the coexistence of species with habitat disturbance. Joseph H. Connell[9] proposed that relatively low disturbance leads to decreased diversity and high disturbance causes an increase in species movement. These proposed relationships lead to the hypothesis that intermediate disturbance levels would be the optimal amount of disorder within an ecosystem.

Another way of thinking about the intermediate disturbance hypothesis requires that we consider the types of organisms that could specialize in areas with different levels of disturbance. K-selected species generally demonstrate more competitive traits. Their primary investment of resources is directed towards growth, causing them to dominate stable ecosystems over a long period of time. In contrast, r-selected species colonize open areas quickly and can dominate landscapes that have been recently cleared by disturbance.[7] These characteristics attribute to the species that thrive in habitats with higher and lower amounts of disturbance. Based on the contradictory characteristics of both of these examples, areas of occasional disturbance allow both r and K species to flourish in the same area. If K-selected and r-selected species can live in the same region, species richness can reach its maximum.

Several alternative hypotheses to the intermediate disturbance hypothesis have been proposed[10]. One alternative hypothesis states that the species diversity in a disturbance-mediated coexistence between species is maximized by the presence of a disturbance regime resembling the historic processes. This is because species generally adapt to the level of disturbance in their ecosystem through evolution (whether disturbance is of high, intermediate or low level). In addition, many species (e.g. ruderal plants and fire-adapted species) even depend on a specific disturbance in ecosystems where it often occurs.

18.2.2: References

1. Nobel, I. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances.
2. Lembrechts, J.J., Pauchard, A., Lenoir, J., Nuñez, M.A., Geron, C., Ven, A., Bravo-Monasterio, P., Teneb, E., Nijs, I., & Milbau, A. (2016). Disturbance is the key to plant invasions in cold environments. *Proceedings of the National Academy of Sciences, 113*(49), pp. 14061–14066. doi:10.1073/pnas.1608980113. ISSN 0027-8424. PMC 5150417. PMID 27872292.
3. Pringle, L. (1979). Natural fire: Its ecology in forests. *William Morrow and Company, New York*, pp. 27-29.
4. Dial, R., & Roughgarden, J. (1988). Theory of marine communities: The intermediate disturbance hypothesis. *Ecology, 79*(4), pp. 1412–1424. doi:10.1890/0012-9658(1998)079[1412:TOMCTI]2.0.CO;2
5. Wilkinson, D.M. (1999). The disturbing history of intermediate disturbance. *Oikos, 84*(1), pp. 145–7.
6. Kricher, J.C. (2011). Tropical Ecology. *New Jersey, Princeton: Princeton University Press*.
7. Catford, J.A., Daehler, C.C., Murphy, H.T., Sheppard, A.W., Hardesty, B.D., Westcott, D.A., Rejmánek, M., Bellingham, P.J., et al. (2012). The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics, 14*(3), pp. 231–41. doi:10.1016/j.ppees.2011.12.002
8. Vandermeer, J., Boucher, D., Perfecto, I., & de la Cerda, I.G. (1996). A theory of disturbance and species diversity: Evidence from Nicaragua after Hurricane Joan. *Biotropica, 28*(4), pp. 600–13. doi:10.2307/2389100. JSTOR 2389100
9. Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science, 199*(4335), pp. 1302–10. Bibcode:1978Sci...199.1302C
10. Hall, A.R., Miller, A.D., Leggett, H.C., Roxburgh, S.H., Buckling, A., & Shea, K. (2012). Diversity-disturbance relationships: Frequency and intensity interact. *Biology Letters, 8*(5), pp. 768–71. doi:10.1098/rsbl.2012.0282

18.2.3: Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) and Kyle Whittinghill (University of Vermont) from the following sources:

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- https://en.wikipedia.org/wiki/Interm...nce_hypothesis
- https://en.wikipedia.org/wiki/Disturbance_(ecology)

18.3: Patterns of Diversity Following Disturbance

In general, communities in early succession will be dominated by fast-growing, well-dispersed species (opportunist, fugitive, or r-selected life-histories). As succession proceeds, these species will tend to be replaced by more competitive (K-selected) species (See Life History Strategies). Trends in ecosystem and community properties in succession have been suggested, but few appear to be general. For example, species diversity almost necessarily increases during early succession as new species arrive, but may decline in later succession as competition eliminates opportunistic species and leads to dominance by locally superior competitors.

Ecological succession was formerly seen as having a stable end-stage called the climax, sometimes referred to as the 'potential vegetation' of a site, and shaped primarily by the local climate. This idea has been largely abandoned by modern ecologists in favor of non-equilibrium ideas of ecosystems dynamics (See Intermediate Disturbance Hypothesis). Most natural ecosystems experience disturbance at a rate that makes a "climax" community unattainable. Climate change often occurs at a rate and frequency sufficient to prevent arrival at a climax state. Additions to available species pools through range expansions and introductions can also continually reshape communities.

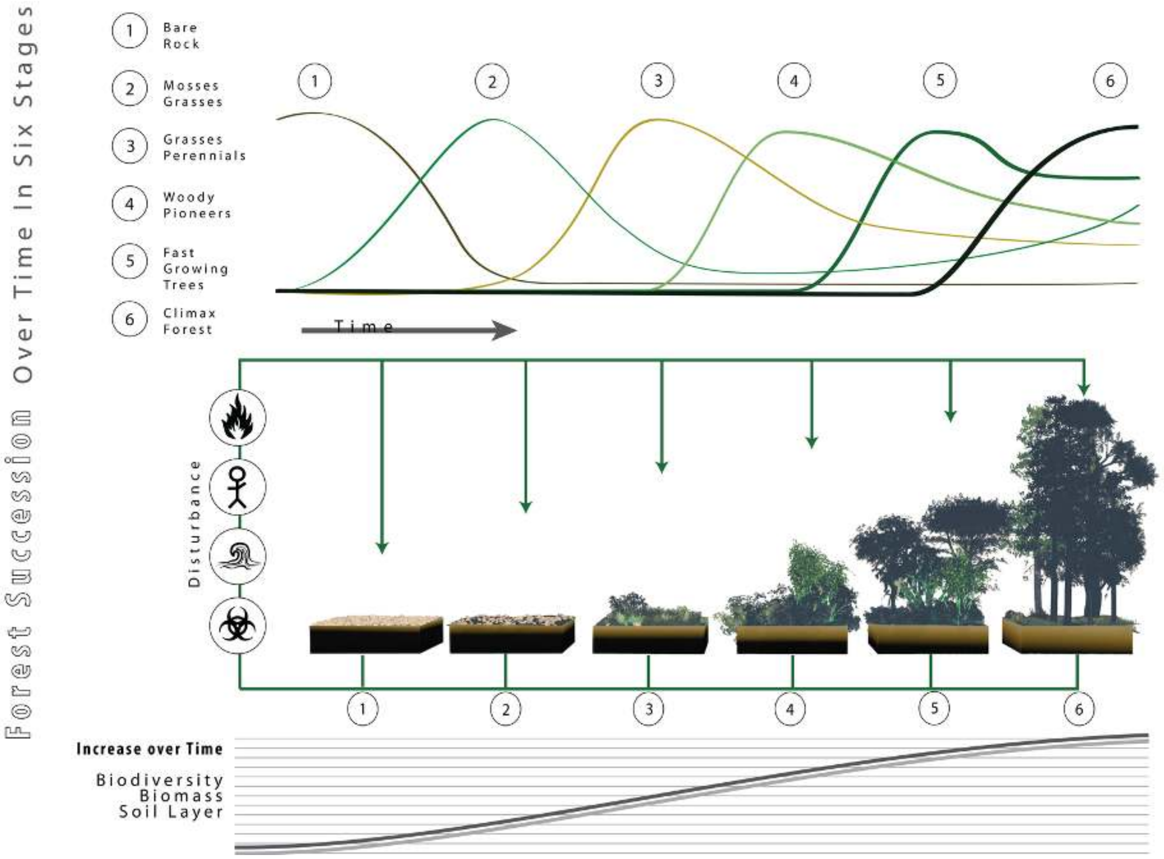


Figure 18.3.1 : Trajectory of forest secondary succession following an intense disturbance, resulting in nearly no original biomass, to a mature forest state. Biodiversity, biomass, and soil depth all increase with time, and community composition changes. Image by Lucas Martin Frey is licensed under CC BY 3.0.

18.3.1: Patterns of Diversity in Primary vs. Secondary Succession

Primary succession begins on rock formations, such as volcanoes or mountains, or in a place with no organisms or soil (eg, an abandoned parking lot or railroad). In primary succession pioneer species like lichen, algae and fungi as well as abiotic factors like wind and water start to develop soil and initiate other important mechanisms for greater diversity to flourish. These pioneer species are then replaced by plants better adapted to less harsh conditions, these plants include vascular plants like grasses and some shrubs that are able to live in thin soils that are often mineral-based. Water and nutrient levels increase with the amount of succession exhibited.[1]

The early stages of primary succession are dominated by species with small propagules (seed and spores) which can be dispersed long distances. The early colonizers—often algae, fungi, and lichens—stabilize the substrate. Nitrogen supplies are limited in new soils, and nitrogen-fixing species tend to play an important role early in primary succession.[2]

Successional dynamics following severe disturbance or removal of a pre-existing community are called **secondary succession**. Dynamics in secondary succession are strongly influenced by pre-disturbance conditions, including soil development, seed banks, remaining organic matter, and residual living organisms. Because of residual fertility and pre-existing organisms, community change in early stages of secondary succession can be relatively rapid. Secondary succession is much more commonly observed and studied than primary succession. Particularly common types of secondary succession include responses to natural disturbances such as fire, flood, and severe winds, and to human-caused disturbances such as logging and agriculture.

Unlike in primary succession, the species that dominate secondary succession, are usually present from the start of the process, often in the soil seed bank. In some systems the successional pathways are fairly consistent, and thus, are easy to predict. In others, there are many possible pathways, potentially leading to *alternative stable states*. For example, nitrogen-fixing legumes alter successional trajectories.[3]

18.3.2: Patterns of Diversity at Different Scales

While we will discuss ways to measure biodiversity more in a later chapter (see section 22.2 on Diversity Indices), it's helpful to have some vocabulary to describe patterns of biodiversity when talking about succession and disturbance.

✓ How is biodiversity measured? Part 1, Alpha, Beta, and Gamma Diversity 18.3.1

Alpha diversity (**α-diversity**) is the mean species diversity in a site at a local scale. At it's simplest, it is the number of species in a given location. More complex metrics of diversity take into account not only how many species there are, but how even their abundances are. Examples of places with extremely high alpha diversity include tropical rainforests.

Beta diversity (**β-diversity**) is the ratio between regional and local species diversity and connects alpha and gamma diversity. It describes the rate at which species composition changes across a region. For example, if every wetland in a region was inhabited by a similar suite of plant species, then the region would have low beta diversity; in contrast, if several wetlands in a region had plants communities that were distinct and had little overlap with one another, the region would have high beta diversity. Beta diversity is calculated as gamma diversity divided by alpha diversity. Beta diversity as a measure of species turnover overemphasizes the role of rare species. The difference in species composition between two sites or communities likely reflects the presence and absence of some rare species in the assemblages. Examples of places with high beta-diversity include matrices of recently disturbed and undisturbed land.

Gamma diversity (**γ-diversity**) is the total species diversity in a landscape. Here, questions of scale become very important to appropriately distinguish between alpha and gamma diversity.

These terms were introduced by R. H. Whittaker[4,5]. Whittaker's idea was that the total species diversity in a landscape (gamma diversity) is determined by two different things, the mean species diversity in sites at a more local scale (alpha diversity) and the differentiation among those sites (beta diversity). This idea can be mathematically notated in this way: $\boldsymbol{\beta=\gamma/\alpha}$. The simplest calculations of alpha and beta diversity involve reworking this equation algebraically, with the result being that alpha, beta, and gamma diversity scale together.

Disturbance and following successional change can increase biodiversity at the alpha, beta, and gamma scales, although the patterns of diversity increase are scale dependent. For instance, a recently disturbed area might have higher alpha diversity than an undisturbed area but this is a result of different patches within the area where existing biomass either was or was not removed, allowing for colonization by novel species. Thus, it is not always clear whether the increase in diversity should be attributed to alpha or gamma diversity. However, the presence of patches in different successional stages also increases beta diversity (and gamma diversity) by supporting cohorts of species with different life history traits and characteristics in the same landscape, whether or not the straightforward number of species present in any given patch is higher than any other patch. Simply comparing alpha diversity in each patch might not demonstrate the impact disturbance has on patterns of biodiversity, whereas calculating beta and gamma diversity provide a more accurate picture.

Exercise 18.3.1: Calculating Alpha, Beta, and Gamma diversity

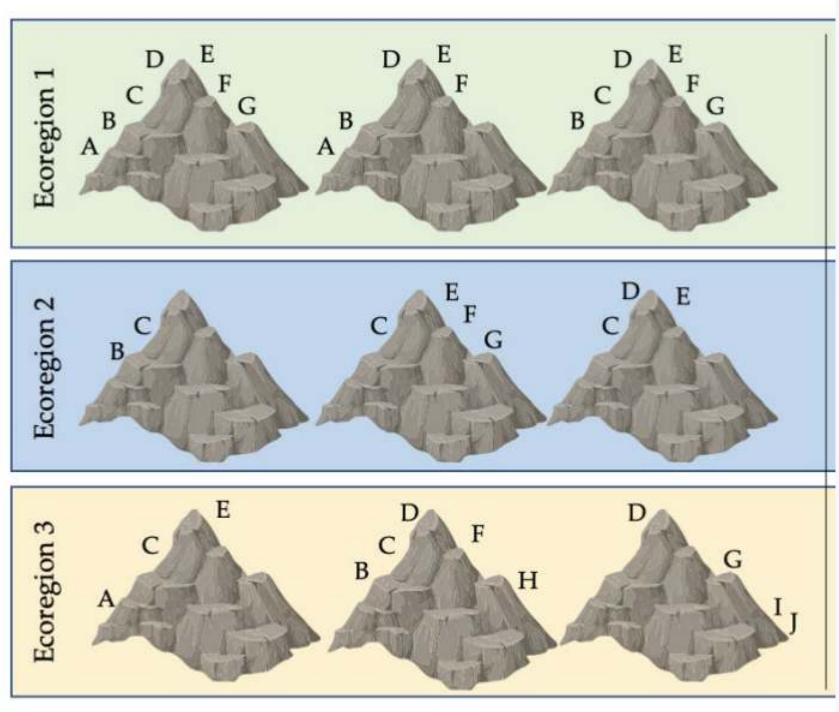
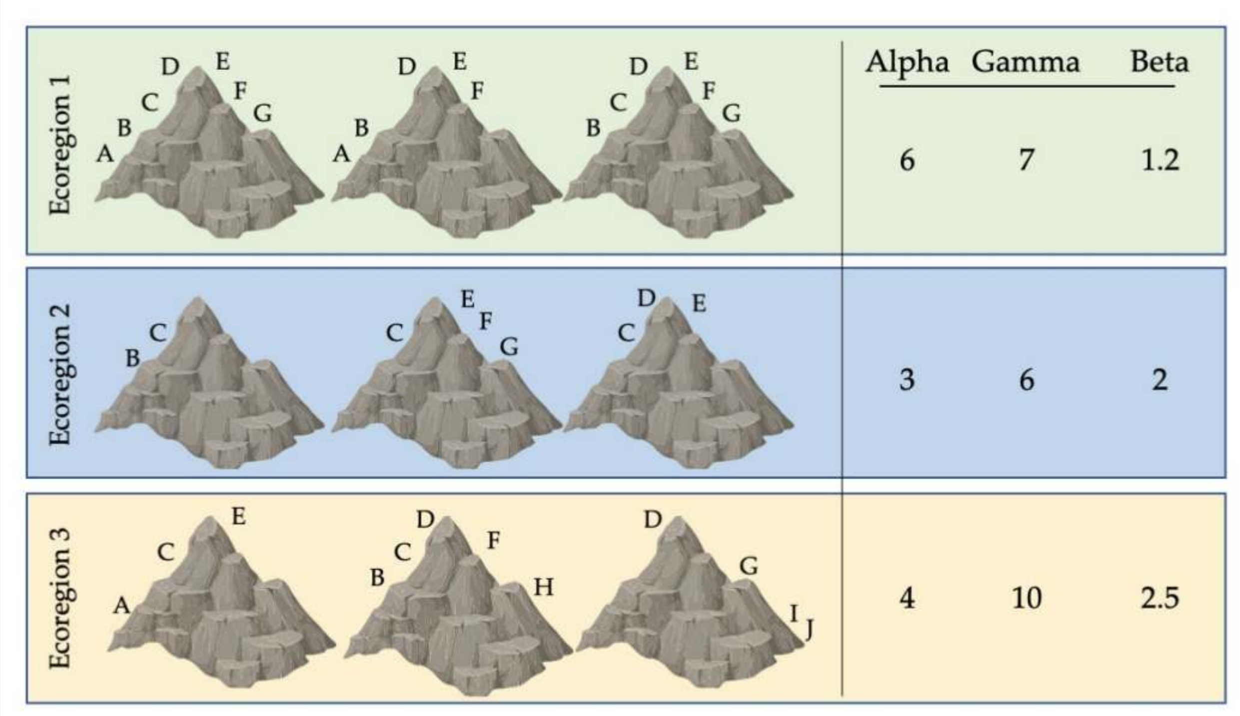


Figure 18.3.2a: This figure shows biodiversity for nine mountain peaks across three Ecoregions. Each symbol represents a different species; some species have populations on only one peak, while others are found on two or more peaks.

1. Calculate alpha, beta, and gamma diversity for each mountain/Ecoregion.

2. Does the "most diverse" mountain or Ecoregion change depending on which metrics we use?

Answer



	Alpha	Gamma	Beta
Ecoregion 1	6	7	1.2
Ecoregion 2	3	6	2
Ecoregion 3	4	10	2.5

Figure $18.3.2b$ Calculations for each alpha, beta, and gamma measurements of the three ecoregions are shown.

Ecoregion 1 has the highest highest average species richness (alpha diversity) across its three peaks. If we were only to look at average alpha diversity, we might consider it the most diverse region. However, Ecoregion 3 has much higher turnover (beta diversity) and higher species diversity at the landscape scale. Furthermore, all of the species represented in Ecoregions 1 and 2 are also represented in Ecoregion 3.

18.3.3: References

1. Fujiyoshi, M., et al. (2005). Effects of arbuscular mycorrhizal fungi and soil developmental stages on herbaceous plants growing in the early stage of primary succession on Mount Fuji. *Ecological Research*, *21*(2), pp. 278-284.
2. Korablev, A.P., & Neshataeva, V.Y. (2016). Primary plant successions of forest belt vegetation on the Tolbachinskii Dol Volcanic Plateau (Kamchatka). *Izv Akad Nauk Ser. Biol*., 4, pp. 366-376.
3. Chapin, F.S., Matson, P.A., & Mooney, H.A. (2002). Principles of terrestrial ecosystem ecology. *New York: Springer,* pp. 281–304. ISBN 0-387-95443-0.
4. Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs, 30*, pp. 279–338. doi:10.2307/1943563
5. Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon, 21*, pp. 213-251. doi:10.2307/1218190

18.3.4: Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) and Kyle Whittinghill (University of Vermont) from the following sources:

- https://en.wikipedia.org/wiki/Ecological_succession
- https://en.wikipedia.org/wiki/Primary_succession
- https://en.wikipedia.org/wiki/Gamma_diversity
- https://en.wikipedia.org/wiki/Beta_diversity
- https://en.wikipedia.org/wiki/Alpha_diversity
- Some original text written by Castilleja Olmsted
- Exercise 18.3.1 modified from Wilson and Primack's "Conservation Biology in Sub-Saharan Africa". https://books.openbookpublishers.com/10.11647/obp.0177.pdf

18.4: What causes successional change?

The trajectory of successional change can be influenced by site conditions, by the type of events initiating succession, by the interactions of the species present, and by more stochastic factors such as availability of propagules or weather conditions at the time of disturbance. Some of these factors contribute to predictability of succession dynamics; others add more probabilistic elements.

Autogenic succession can be brought by changes in the soil caused by the organisms there. These changes include accumulation of organic matter in litter or humic layer, alteration of soil nutrients, or change in the pH of soil due to the plants growing there. The structure of the plants themselves can also alter the community. For example, when larger species like trees mature, they produce shade on to the developing forest floor that tends to exclude light-requiring species. Shade-tolerant species will invade the area.

Allogenic succession is caused by external environmental influences and not by the vegetation. For example, soil changes due to erosion, leaching or the deposition of silt and clays can alter the nutrient content and water relationships in the ecosystems. Animals also play an important role in allogenic changes as they are pollinators, seed dispersers and herbivores. They can also increase nutrient content of the soil in certain areas, or shift soil about (as termites, ants, and moles do) creating patches in the habitat. This may create regeneration sites that favor certain species.

Climatic factors may be very important, but on a much longer time-scale than any other. Changes in temperature and rainfall patterns will promote changes in communities. As the climate warmed at the end of each ice age, great successional changes took place. The tundra vegetation and bare glacial till deposits underwent succession to mixed deciduous forest. The greenhouse effect resulting in increase in temperature is likely to bring profound Allogenic changes in the next century. Geological and climatic catastrophes such as volcanic eruptions, earthquakes, avalanches, meteors, floods, fires, and high wind also bring allogenic changes.

18.4.1: Models of Successional Change

Joseph Connell and Ralph Slatyer further developed the understanding of successional mechanisms in their 1977 paper and proposed that there were 3 main modes of successional development. These sequences could be understood in the context of the specific life-history theories of the individual species within an ecological community.

Facilitation model

The facilitation model is based on the assumption that only particular species with qualities ideal for "early succession" can colonize the newly exposed landforms after an ecological disturbance.

- These "colonizing" qualities include: highly effective methods of dispersal, the ability to remain dormant for long periods of time, and a rapid growth rate. However, the pioneer species are often subsequently less successful once an area has been heavily populated by surrounding species due to increased shade, litter or concentrated roots in the soil, etc.[1]
- Thus, the presence of early successional species often changes the environment so that the habitat is less hospitable for the original species’ own ecological demands and facilitates the invasion of later-successional species.

The facilitation model suggests that the presence of an initial species aids and increases the probability of the growth of a second species. For example, the presence of alder plants aids the growth of willow and poplar seedlings in an Alaskan floodplain.[2] Alder roots contain nitrogen-fixing bacteria, which greatly increase the amount of inorganic nitrogen present in soils. This increased availability of nitrogen aids the growth of both willow and poplar seedlings in areas without other competition. Eventually, however, willow and poplar grow more rapidly than alder, leading to a reduction in the abundance of the pioneer species, and eventually, spruce becomes a later-succession species, due to its increased ability (over alder) to grow in shaded areas.

Another case of facilitation comes from the colonization of lakeshore sand dunes.[1,3] Adjacent pioneer plants colonize the otherwise moving sands and alter the environmental constraints of the sandy environment to better suit other plant species, which can then allow for soil binding to take place.[4] The giant saguaro cactus, in this respect, can only survive in the shade of other plants (or in some cases rocks) – pioneer species facilitate their existence by providing shade. (The argument has also been made that this type of interaction is exemplary of the tolerance model; see below).[1]

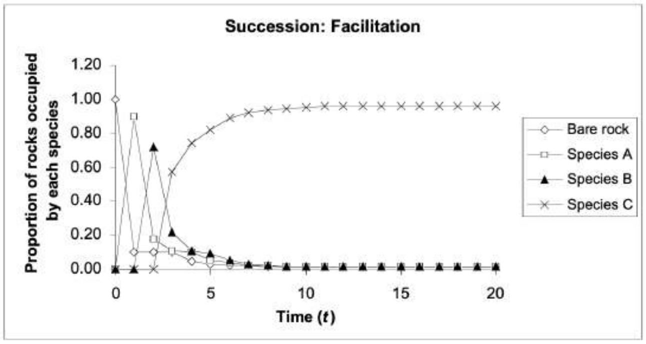


Figure 18.4.1:
Bare rock is frequently replaced by species A, species A by species B, and species B by species C. All these species are equally likely to be replaced by bare rock. Species C is unique in that it is almost always replaced by itself, only rarely by bare rock, and never by other species.
Source: Donovan and Welden.

Tolerance model

In this case, new pioneer species neither inhibit nor facilitate the growth and success of other species. The sequences of succession are thus entirely dependent on life-history characteristics such as the specific amount of energy a species allocates to growth.[1]

- The climax community is composed of the most "tolerant" species that can co-exist with other species in a more densely populated area. Eventually, dominant species replace or reduce pioneer species abundance through competition.

The tolerance model is completely dependent upon life history characteristics. Each species has an equally likely chance to establish itself in the early stages of succession and their establishment results in no environmental changes or impacts on other species.[5] Eventually, early species, typically dominated by r-selected species, which prioritize fast rates of reproduction, are out-competed by K-selected species (species that become more dominant when there is competition for limited resources).

For example, we can examine succession in the Loess Plateau in China, where there is initial dominance of the *Artemisia scoparia* (virgate wormwood), the pioneer species. Over time, however, the *Bothriochloa ischaemum* (yellow bluestem) becomes the dominant species and the abundance of *A. scoparia* greatly declines. This is due to the rapid rate of reproduction of the *A. scoparia*, resulting in the species' early abundance, and the dominant competition from the K-selected *B. ischaemum*, resulting in that species' later abundance.[6]

A characteristic that is often associated with the tolerance model and well documented in forest succession is survival in conditions of shade. As an uninhabited area becomes populated by different plant species, shade increases – which makes less light available for the next generation. Species that are better adapted to shady conditions will then become dominant.

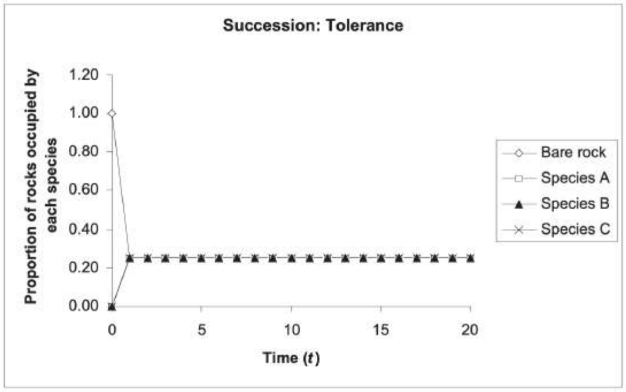


Figure 18.4.2: Any species is equally likely to replace any other, and equally susceptible to disturbance. *Source:* Donovan and Welden.

Inhibition model

Earlier successional species actually inhibit growth of later successional species and reduce growth of colonizing species already present.[1]

- Example: Pioneer species might modify the environment through rapid growth and make the area increasingly shady (essentially increasing competition for light).
- The environment is thus less hospitable to other potential colonizing species.
- The only possibility for new growth/colonization in this successional sequence arises when a disturbance leads to dominating species being destroyed, damaged, or removed. This frees up resources and allows for the invasion of other species that were not previously present

In this model, one species inhibits the presence of another, either through direct means, such as predation (by eating the other species or attacking them), or indirect means, such as competition for resources.

Sometimes in inhibition models, the time of establishment of a species determines which species becomes dominant. This phenomenon is referred to as the priority effect and suggests that the species that became established earlier are more likely to become the dominant species. One example of the inhibition model, and the priority effect, occurs in South Australia. In areas where bryozoans are established first, tunicates and sponges cannot grow.

The inhibition model has also been observed at work in forest ecosystems; in these systems the early arrivers hold a monopoly on the land, keeping other species out. Closed shrub canopies have been known to prevent tree growth and access to land for periods of up to 45 years – in an experimental study on inhibition it was found that areas occupied by large areas of Lantana (*Lantana camara)* sprawling shrubs excluded and inhibited the growth of tree species.[1,7]

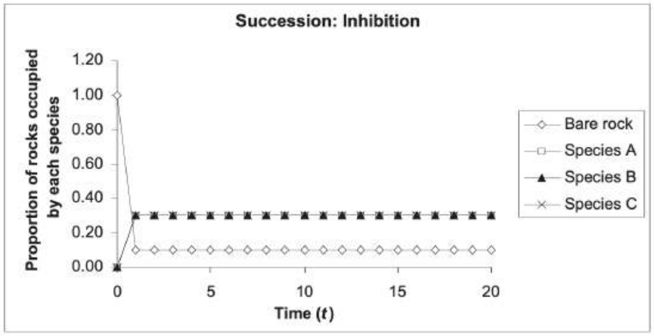


Figure 18.4.3: Each species is equally likely to colonize bare rock, and all species are equally susceptible to disturbance. Each species holds its site and inhibits occupancy by all others, so replacement occurs only by disturbance. *Source:* Donovan and Welden.

References

1. Connell, J.H., & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist, 111*(982), pp. 1119-1144.
2. Walker, L.R., & Chapin, F.S. III. (1986). Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology, 67*(6), pp. 1508-1523.
3. Walker, L.R., et al. (1986). The role of life history processes in primary succession on an Alaskan Floodplain. *Ecology, 67*(5), pp. 1243-1253.
4. "Sand Dunes." National Biological Information Infrastructure- Home. Accessed 29 Apr. 2011. <https://web.archive.org/web/20110727031615/http://www.nbii.gov/portal/server.pt/community/sand_dunes/1311>.
5. Moorcroft, P. (2011). Terrestrial succession. *Organismic and Evolutionary Biology, 55*. Maxwell Dworkin, Cambridge.
6. Wang, G.H. (2002). Plant traits and soil chemical variables during a secondary vegetation succession in abandoned fields on the loess plateau. *Acta Botanica Sinica, 44*(8), pp. 990-998.
7. Ricklefs, R.E. (2008). The economy of nature. *New York, NY: W.H. Freeman and Co.*

Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) and Kyle Whittinghill (University of Vermont) from the following sources:

- https://en.wikipedia.org/wiki/Ecological_succession
- https://en.wikipedia.org/wiki/Connell%E2%80%93Slatyer_model_of_ecological_succession
- Donovan and Welden https://blog.uvm.edu/tdonovan-vtcfwru/files/2020/06/28-Donovan-pages-115-EE.pdf

---

18.5: The Role of Consumers and Alternative Stable States

18.5.1: Succession in Consumers

Animal communities also undergo change throughout successional time. In the lichen stage fauna is sparse. It comprises a few mites, ants and spiders living in cracks and crevices. The fauna undergoes a qualitative increase during the herb grass stage. The animals found during this stage include nematodes, insects larvae, ants, spiders, mites, etc. The animal population increases and diversifies with the development of the forest climax community. The fauna consists of invertebrates like slugs, snails, worms, millipedes, centipedes, ants, bugs; and vertebrates such as squirrels, foxes, mice, moles, snakes, various birds, salamanders and frogs. The pioneering fauna will colonize an area only after flora and fungi have inhabited the area. Soil fauna, ranging from microscopic protists to larger invertebrates, have a role in soil formation and nutrient cycling. Bacteria and fungi are the most important groups in the breakdown of organic detritus left by primary producing plants such as skeletal soil, moss and algae. Soil invertebrates enhance fungal activity by breaking down detritus. As soil develops, earthworms and ants alter soil characteristics. Worm burrows aerate soil and ant hills alter sediment particle size dispersal, altering soil character profoundly.

Though vertebrates in general would not be considered pioneer species, there are exceptions. Natterjack toads are specialists in open, sparsely vegetated habitats which may be at an early seral stage.[1] Wide-ranging generalists visit early succession stage habitats, but are not obligate species of those habitats because they use a mosaic of different habitats. Vertebrates can effect early seral stages. Herbivores may alter plant growth. Fossorial mammals could alter soil and plant community development. In a profound example, a seabird colony transfers considerable nitrogen into infertile soils, thereby altering plant growth. A keystone species may facilitate the introduction of pioneer species by creating new niches. For example, beavers may flood an area, allowing new species to immigrate.[2]

Succession of micro-organisms including fungi and bacteria occurring within a microhabitat is known as microsuccession or serule. Like in plants, microbial succession can occur in newly available habitats (primary succession) such as surfaces of plant leaves, recently exposed rock surfaces (i.e., glacial till) or animal infant guts,[3] and also on disturbed communities (secondary succession) like those growing in recently dead trees, decaying fruits,[4] or animal droppings.

18.5.2: Alternative Stable States

One of the main ways consumers can affect succession is through the redirection of successional trajectories. By preferentially consuming some species, consumers can change the direction of succession, resulting in a different community type than would typically be predicted. Expected successional trajectories are predicted based on the observation of community changes through time, or through space-for-time substitutions where stands of different ages are compared, with the expectation that the youngest stands will grow to look like the oldest as time passes. However, given substantial perturbations, communities may end up going down an entirely different path than we would predict. Sometimes, they will even get "stuck" in this state, and never return to look as we would expect. This becomes especially problematic when they place they get "stuck" is low-diversity or dominated by invasive species, and makes it very hard to restore healthy ecosystems.

We can visualize a community about to undergo succession as a ball about to roll down a hill. The trajectory of succession is predictable, and gravity will pull the ball to the bottom of the hill. Disturbance can provide energy to push the ball back up the hill, but it should consistently return to the same stable end point. However, the ball may exist in a landscape with many low points, where the ball would have to roll far up a hill to change positions. Thus, there may be several **alternative stable states** where the community will be resistant to change. Catalysts, such as invasive species or ecosystem engineering animals can push the ball over a peak and into a different valley, resulting in a different endpoint to our successional trajectory. At this point, even a disturbance may not provide enough energy to push the ball all the way back up the hill and over a peak into the original successional trajectory. The new endpoint is stable, and hard to restore from.

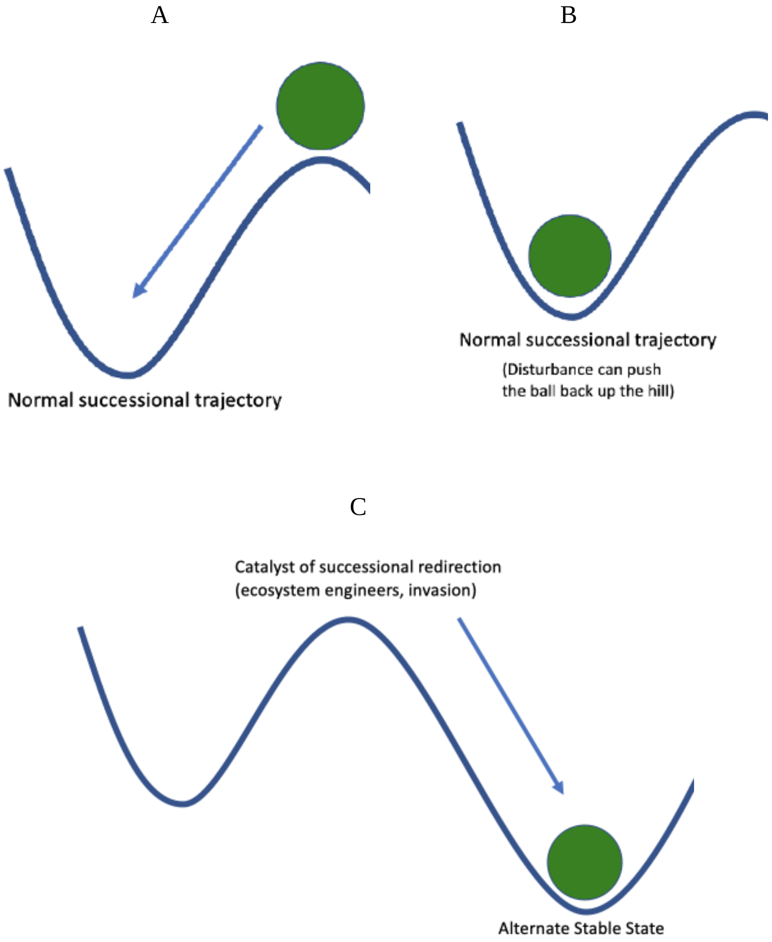


Figure 18.5.1: a) the starting point of early succession, which should proceed "downhill" along a predictable trajectory. b) the stable climax community at the end of a successional trajectory. c) some catalyst has pushed our community out of its original state and into an alternative stable community state.

✓ Box18.5.1: Moose range expansions and implications for succession

As the cover of forested land increases and the climate warms, moose (*Alces alces americana*) are expanding their range on the northern and southern edges, even as far south as Connecticut[5]. Moose often spend time in early-successional forests because of the high-availability of young tree and shrub growth to browse on. Moose not only browse the tips of trees, reducing their ability to grow vertically, but they can actually break trees in half as they try to reach the palatable tips of branches and leaves. As a result, moose may be redirecting the trajectory of early-successional forests, especially in the southernmost edges of their range, in Connecticut, by preferentially browsing certain species of trees while avoiding others[6].

A typical successional trajectory for a mixed-hardwood forest in Connecticut would look something like this:

Figure $18.5.2A$: Typical successional trajectory.

However, when moose browsing is added to the equation, we would expect one of two possible outcomes.

1. If moose browse all species equally and they are sufficiently abundant, they may actually delay succession, keeping the forest in a more-open, shorter state (the ball takes longer to roll down the hill).

Figure $18.5.2B$: Possible outcome of typical successional trajectory when moose are added to the scenario, where the moose delay the succession development rate.

2. If moose browse preferentially, avoiding species they dislike (such as Spruce), they may redirect the trajectory of the forest. The mature forest which eventually takes hold will be dominated by these browse-resistant tree species, and the community composition will look very different than the trajectory in the absence of moose.

Figure $18.5.2C$: Alternate possible outcome of typical successional trajectory when moose are added to the scenario, where the moose redirect the species diversity.

Both of these outcomes occur where moose are present, but which outcome we see is contingent on the abundances of preferred and non-preferred tree species. In the first case, if moose are controlled or removed in the third time point, the closed forest should eventually look like the original successional trajectory. However, in the second case, even if moose are no longer present in the third time point (this is likely, because moose frequent open, younger forests), the forest will still be dominated by browse-tolerant unpalatable tree species. It will no longer resemble the expected successional trajectory, and it will be unlikely to revert without major disturbance. The ability of moose to redirect succession in this way makes them an example of an ecosystem engineer. In the second case, by keeping forests open and in an early successional stage for longer, moose provide habitat and maintain food resources for many species of bird and other small animals.

References

1. Faucher, L., Hénocq, L., Vanappelghem, C., Roundel, S., Tocqueville, R., Galina, S., Godé, C., Jaquiéry, J., & Arnaud, J.F. (2017). When new human-modified habitats favor the expansion of an amphibian pioneer species: Evolutionary history of the natterjack toad (Bubo calamity) in a coal basin. *Molecular Ecology*, *26*(17), pp. 4434–4451. doi:10.1111/mec.14229. ISSN 1365-294X. PMID 28667796. S2CID 25656968.[permanent dead link]
2. Wallwork, J.A. (1970). Ecology of soil animals. *McGowan-Hill*. ISBN 978-0070941250.
3. Ortiz-Álvarez, R., Fierer, N., de los Ríos, A., Casamayor, E.O., Barberán, A. (2018). Consistent changes in the taxonomic structure and functional attributes of bacterial communities during primary succession. *The ISME Journal*, *12*(7), pp. 1658–1667. doi:10.1038/s41396-018-0076-2. ISSN 1751-7370. PMC 6018800. PMID 29463893.

4. Martin, P.L., King, W., Bell, T.H., & Peter, K. (2021). The decay and fungal succession of apples with bitter rot across a vegetation diversity gradient. *Phytobiomes Journal: PBIOMES*–06–21-0039-R. doi:10.1094/PBIOMES-06-21-0039-R. ISSN 2471-2906.
5. http://wildlifeofct.com/moose.html
6. Olmsted, C.F., Betras, T.L., Pasquini, S.C., DeStephano, S., Faison, E.K., & Carson, W.P. (2021). Characteristics of stem-breaking by moose (Alces alces, Cervidae): A case-study and worldwide review. *The Journal of the Torrey Botanical Society, 147*(4), pp. 304-315.

Contributors and Attributions

Modified by Castilleja Olmsted (University of Pittsburgh) and Kyle Whittinghill (University of Vermont) from the following sources:

- Original text for Alternative Stable States and Box 1, ball diagrams, by Castilleja Olmsted.
- Forest illustrations for Box 1 by Tiffany Betras, reproduced and modified here with permission.
- https://en.wikipedia.org/wiki/Ecological_succession
- https://en.wikipedia.org/wiki/Pioneer_species

CHAPTER OVERVIEW

19: Food Webs

Learning Objectives

- Differentiate among the components of food webs, the sources of energy to food webs, and the types of food webs
- Use quantifiable characteristics to describe and compare food webs
- Appreciate the key ecosystem role that apex predators play through trophic cascades

Summary

The food webs of all ecosystems have autotrophs at the base; these producers may fix carbon using energy from the sun (photoautotrophs) or from specific chemical compounds (chemoautotrophs). The energy produced at the base of the food web moves through several levels of heterotrophs, including detritivores, herbivores, omnivores, and carnivores, but some of this energy is lost during each transfer up the food web. When the apex predator or keystone predator of an ecosystem is removed, this can result in a trophic cascade that impacts the entire food web. Food webs are extremely complex, and cannot be easily depicted on paper, so the food webs we see are simplifications of reality; the simplest form is a food chain, which involved a linear sequence of interactions from primary producer to apex predator. Scientists quantify food webs by calculating transfer efficiency, food web length, and food web connectance.

19.1: Introduction to and Components of Food Webs

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of adenosine triphosphate, ATP), especially those responsible for building large molecules from smaller compounds, and life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

Food Chains and Food Webs

In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain.

Food chains do not accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A food web is a graphic representation of a holistic, nonlinear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics (Figure 19.1.1).

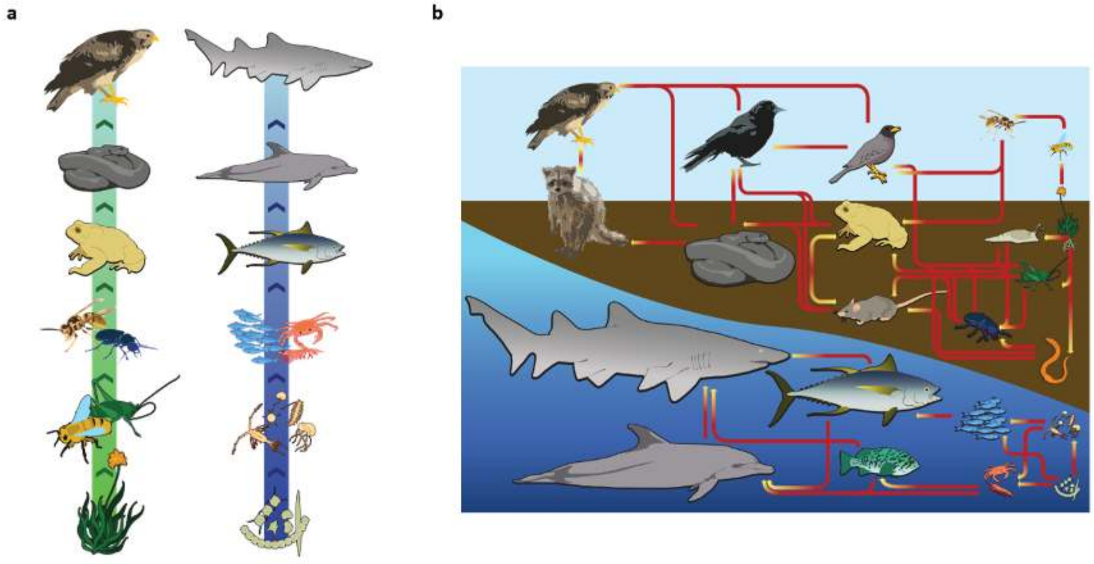


Figure 19.1.1: Example of simplified food chains (a) and food webs (b) of terrestrial and marine ecosystems. Developed by LadyofHats and licensed under CC0.

Though more complex than a food chain, a food web remains a simplified illustration of the direct and indirect trophic interactions among species in an ecosystem. Food webs often aggregate many species into trophic groups, which are functional groups of species that have the same predators and prey in a food web. Software can be used to model more complex interactions (Figure 19.1.2), but no food web model can capture all of the complexity found within a natural ecosystem.

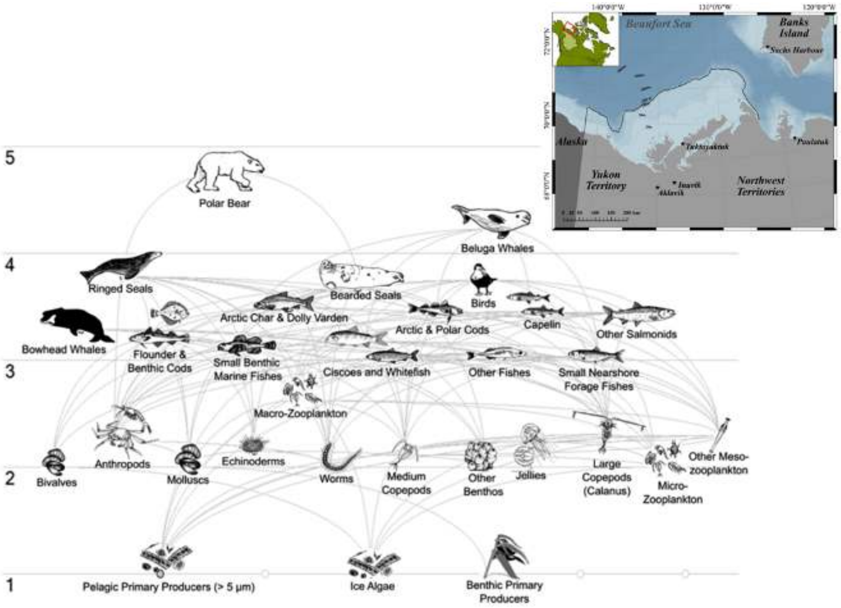


Figure 19.1.2: An example of a more complex food web developed by Hoover et al. (2021) using a program called Ecopath. This food web depicts trophic relationships among species in the Canadian Beaufort Sea. Horizontal lines represent trophic level. Image licensed under CC-BY 4.0.

Components of a Food Web

The three basic ways in which organisms get food are as producers, consumers, and decomposers.

- Producers (autotrophs) are typically plants or algae. Plants and algae do not usually eat other organisms, but pull nutrients from the soil or the ocean and manufacture their own food using photosynthesis. For this reason, they are called primary producers. In this way, it is energy from the sun that usually powers the base of the food chain (Cengage Learning, 2002). An exception occurs in deep-sea hydrothermal ecosystems, where there is no sunlight. Here primary producers manufacture food through a process called chemosynthesis (van Dover, 2000).
- Consumers (heterotrophs) are species that cannot manufacture their own food and need to consume other organisms. Animals that eat primary producers (like plants) are called herbivores. Animals that eat other animals are called carnivores, and animals that eat both plants and other animals are called omnivores.
- Decomposers (detritivores) break down dead plant and animal material and wastes and release it again as energy and nutrients into the ecosystem for recycling. Decomposers, such as bacteria and fungi (mushrooms), feed on waste and dead matter, converting it into inorganic chemicals that can be recycled as mineral nutrients for plants to use again.

Autotrophs

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as **autotrophs**: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (**photoautotrophs**) use sunlight as an energy source, whereas chemosynthetic autotrophs (**chemoautotrophs**) use inorganic molecules as an energy source. Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (Figure 19.1.3). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

Figure 19.1.3: Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

✓ Not Your Average Food Web: Deep Sea 19.1.1

Food webs in the deep sea vary depending on proximity to seamount, hydrothermal vents, and trenches. In areas near hydrothermal vents, chemosynthetic bacteria are the major primary producers. These chemoautotrophs are what provides energy for the rest of the trophic levels in this system.

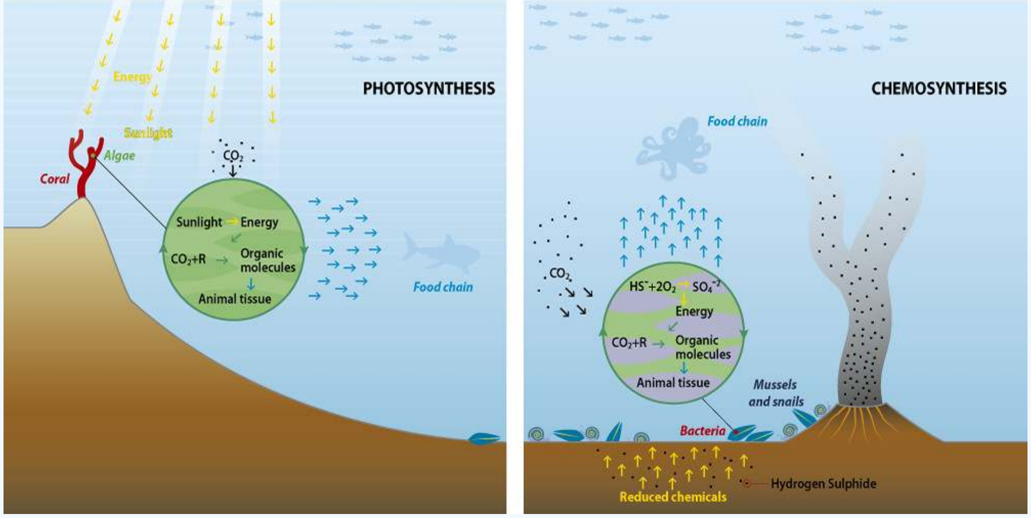


Figure 19.1.4: A comparison of photosynthetic (left) vs. chemosynthetic (right) food webs. Diagram developed by GRID-Arendal and licensed under CC-SA-NC.

Species in deep-sea ecosystems have adapted to interact with each other in many ways. One key interaction is the symbiosis between many species and chemosynthetic bacteria in hydrothermal vent systems. These bacteria live within the body of species like tubeworms, which are dependent on the bacteria to survive, similar to the relationship between zooxanthellae and coral. Another important type of deep sea community develops when a dead whale (or other large marine organism) carcass sinks to the ocean floor and provides an influx of nutrients. The communities support scavengers like hagfish, opportunists like bristle worms, and eventually enter a sulfophilic stage that appears similar to a hydrothermal vent community.

Figure 19.1.5: Whale falls serve as an extremely important influx of nutrients to the sun-starved deep ocean. This photo shows a Whale skeleton submerged in Monterey Bay National Marine Sanctuary, covered in octopuses and several other species. Photo by National Marine Sanctuaries is licensed under CC 2.0.

Heterotrophs

Unlike autotrophs, **heterotrophs** consume rather than produce biomass energy as they metabolize, grow, and add to levels of secondary production. A food web depicts a collection of polyphagous heterotrophic consumers that network and cycle the flow of energy and nutrients from a productive base of self-feeding autotrophs (Pimm et al., 1991; Odum & Barrett, 2005; Benke, 2010). Autotrophs and heterotrophs come in all sizes, from microscopic to many tonnes - from cyanobacteria to giant redwoods, and from viruses to blue whales.

A gradient exists between trophic levels running from complete autotrophs that obtain their sole source of carbon from the atmosphere, to mixotrophs (such as carnivorous plants) that are autotrophic organisms that partially obtain organic matter from sources other than the atmosphere, and complete heterotrophs that must feed to obtain organic matter.

There are different kinds of feeding relations that can be roughly divided into herbivory, carnivory, scavenging and parasitism. Some of the organic matter eaten by heterotrophs, such as sugars, provides energy. An often overlooked but key component of food webs are the decomposers.

✓ Not Your Average Food Web: Wasp-Waist Ecosystems 19.1.2

Food webs can be controlled by top-down mechanisms (predator abundance determines the abundance of lower trophic levels), bottom-up mechanisms (primary producer abundance determines the abundance of higher trophic levels), or a combination of both. In wasp-waist food webs, population dynamics are controlled by planktivorous lower trophic level species such as sardine, anchovy, and small squids rather than the bottom or the top (Cury et al., 2011). These lower trophic level species often have high abundance but low diversity. The term “wasp-waist” describes the shape of these food webs, with many species existing at lower trophic levels (i.e., the plankton) and at higher trophic level (i.e., the predators), but very few lower trophic level species linking the plankton and the predators. These lower trophic level species exert top-down control on zooplankton and bottom-up control on top predators, with environmental factors largely affecting their abundance (Cury et al., 2000; Cury et al., 2003). Wasp-waist ecosystems are highly vulnerable to collapse when forage fish decline due to the critical energetic links that they provide between highly available zooplankton and larger predators (Shannon, 2000).

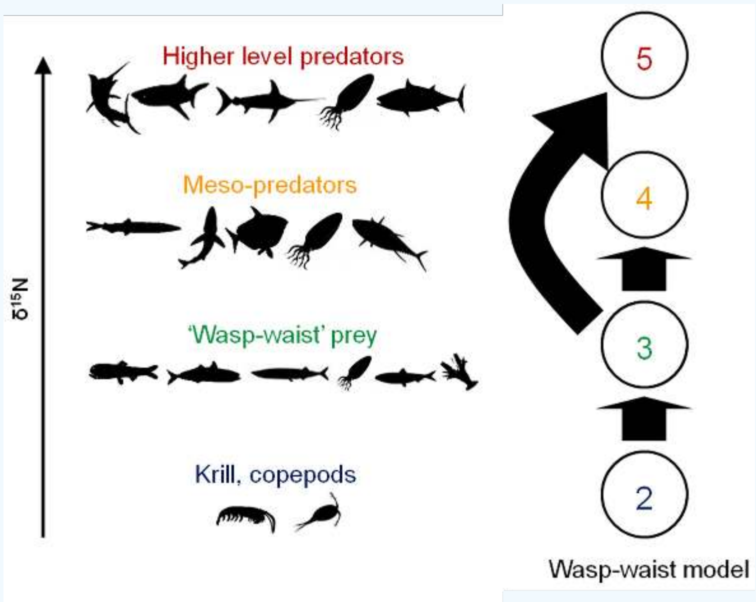


Figure 19.1.6: A diagram showing the structure of a wasp-waist model for the California Current Large Marine Ecosystem. Arrows indicate inputs of a trophic group to another (credit: modified from Madigan et al., 2012).

Scavengers are animals that consume dead organisms that have died from causes other than predation or have been killed by other predators (Tan & Corlett, 2011). While scavenging generally refers to carnivores feeding on carrion, it is also a herbivorous feeding behavior (Getz, 2011). Scavengers play a fundamental role in the environment through the removal of decaying organisms, serving as a natural sanitation service (Ogada et al., 2011). While microscopic and invertebrate decomposers break down dead organisms into simple organic matter which are used by nearby autotrophs, scavengers help conserve energy and nutrients obtained from carrion within the upper trophic levels, and are able to disperse the energy and nutrients farther away from the site of the carrion than decomposers (Olson et al., 2016). Decomposers and detritivores complete this process, by consuming the remains left by scavengers. Scavengers are not typically thought to be detritivores, as they generally eat large quantities of organic matter.

Decomposers are often left off food webs, but if included, they mark the end of a food chain (Hutchinson, 2013). Thus food chains start with primary producers and end with decay and decomposers. Since decomposers recycle nutrients, leaving them so they can be reused by primary producers, they are sometimes regarded as occupying their own trophic level (Kane et al., 2016; Pahl & Ruedas, 2021).

Detritivores (also known as **detrivores**, **detritophages**, **detritus feeders**, or **detritus eaters**) are heterotrophs that obtain nutrients by consuming detritus (decomposing plant and animal parts as well as feces) (Wetzel, 2001). By doing so, detritivores contribute to decomposition and to nutrient cycles. Plant tissues are made up of resilient molecules (cellulose, chitin, lignin and xylan) that decay at a much lower rate than other organic molecules. The activity of detritivores is the reason why we do not see an accumulation of plant litter in nature (Keddy, 2017; Sagi et al., 2019). **Coprophagy** is a specific case of detritivory used to describe animals that eat feces (their own, from another individual of their species, or from another species).

Detritivores are an important aspect of many ecosystems. They can live on any type of soil with an organic component, including marine ecosystems, where they are termed interchangeably with bottom feeders. Typical detritivorous animals include millipedes, springtails, woodlice, dung flies, slugs, many terrestrial worms, sea stars, sea cucumbers, fiddler crabs, and some sedentary polychaete worms.

Decomposers are organisms that break down dead or decaying organisms; they carry out decomposition, a process possible by only certain kingdoms, such as fungi (NOAA, 2014). Like herbivores and predators, decomposers are heterotrophic, meaning that they use organic substrates to get their energy, carbon and nutrients for growth and development. While the terms decomposer and detritivore are often interchangeably used, detritivores *ingest* and digest dead matter internally, while decomposers *directly absorb* nutrients through external chemical and biological processes (Keddy, 2017). Thus, invertebrates such as earthworms, woodlice, and sea cucumbers are technically detritivores, not decomposers, since they must ingest nutrients - they are unable to absorb them externally (Sagi et al., 2019).

Figure 19.1.7: Fungi are the primary decomposers in most environments, illustrated here *Mycena interrupta*. Only fungi produce the enzymes necessary to decompose lignin, a chemically complex substance found in wood.

✓ Not Your Average Food Web: Detrital Web 19.1.3

Detritus is dead particulate organic material, as distinguished from dissolved organic material. Detritus typically includes the bodies or fragments of bodies of dead organisms, and fecal material. Detritus typically hosts communities of microorganisms that colonize and decompose (i.e. remineralize) it. In terrestrial ecosystems it is present as leaf litter and other organic matter that is intermixed with soil, which is denominated "soil organic matter". The detritus of aquatic ecosystems is organic material that is suspended in the water and accumulates in depositions on the floor of the body of water; when this floor is a seabed, such a deposition is denominated "marine snow".

Figure 19.1.8: Earthworms are soil-dwelling detritivores.

Figure 19.1.9: Two Adonis blue butterflies lap at a small lump of feces lying on a rock.

In a detrital web, plant and animal matter is broken down by decomposers, e.g., bacteria and fungi, and moves to detritivores and then carnivores (Gönenç et al., 2007). There are often relationships between the detrital web and the grazing web. Mushrooms produced by decomposers in the detrital web become a food source for deer, squirrels, and mice in the grazing web. Earthworms are detritivores that consume decaying leaves and are then consumed by a variety of wildlife, especially birds.

Trophic Level

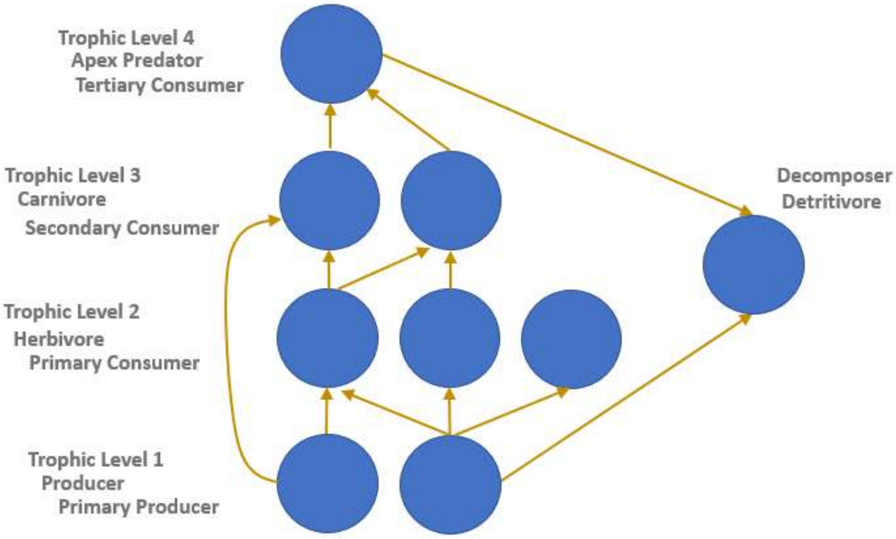
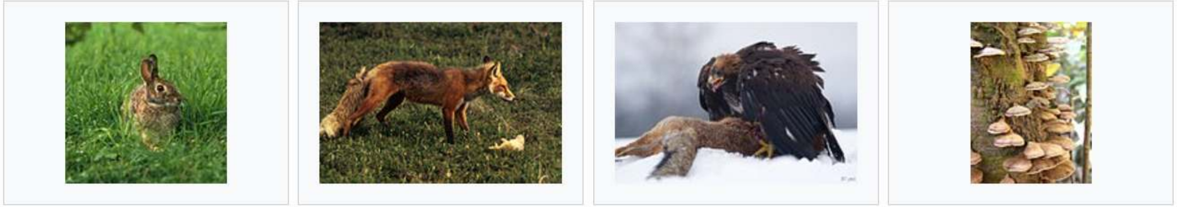


Figure 19.1.10: Food web diagram showing the various ways in which organism roles can be differentiated. Developed by N. Gownaris.

The **trophic level** of an organism is the position it occupies in a food web. The trophic level of an organism is the number of steps it is from the start of a food chain. A food web starts at trophic level 1 with primary producers, followed by herbivores at level 2, carnivores at level 3 or higher, and apex predators at level 4 or 5. The path along the chain can form either a one-way flow or a food "web". Ecological communities with higher biodiversity form more complex trophic paths. The word trophic derives from the Greek τροφή (trophē) referring to food or nourishment (merriam-webster.com, 2017).

- Level 1: Plants and algae make their own food and are called producers.
- Level 2: Herbivores eat plants and are called primary consumers.
- Level 3: Carnivores that eat herbivores are called secondary consumers.
- Level 4: Carnivores that eat other carnivores are called tertiary consumers.
- Apex predators by definition have no predators and are at the top of their food web.



Second trophic level
Rabbits eat plants at the first trophic level, so they are primary consumers.

Third trophic level
Foxes eat rabbits at the second trophic level, so they are secondary consumers.

Fourth trophic level
Golden eagles eat foxes at the third trophic level, so they are tertiary consumers.

Decomposers
The fungi on this tree feed on dead matter, converting it back to nutrients that primary producers can use.

Figure 19.1.11: Examples of species found at each trophic level of a terrestrial ecosystem.

The trophic level concept was introduced in a historical landmark paper on trophic dynamics in 1942 by Raymond L. Lindeman. The basis of trophic dynamics is the transfer of energy from one part of the ecosystem to another (Odum & Heald, 1975; Cortés, 1999). The trophic dynamic concept has served as a useful quantitative heuristic, but it has several major limitations including the precision by which an organism can be allocated to a specific trophic level. Omnivores, for example, are not restricted to any single level. Nonetheless, recent research has found that discrete trophic levels do exist, but "above the herbivore trophic level, food webs are better characterized as a tangled web of omnivores.” (Pauly et al., 1998).

Figure 19.1.12: Killer whales (orca) are apex predators but they are divided into separate populations that hunt specific prey, such as tuna, small sharks, and seals.

The fisheries scientist Daniel Pauly sets the values of trophic levels to one in plants and detritus, two in herbivores and detritivores (primary consumers), three in secondary consumers, and so on. The definition of the trophic level, TL, for any consumer species is (Pauly & Palomares, 2005)

$$TL_i = 1 + \sum_j (TL_j \cdot DC_{ij}) \tag{19.1.1}$$

where

$$TL_j \tag{19.1.2}$$

is the fractional trophic level of the prey j, and

$$DC_{ij} \tag{19.1.3}$$

represents the fraction of j in the diet of i. That is, the consumer trophic level is one plus the weighted average of how much different trophic levels contribute to its food.

In the case of marine ecosystems, the trophic level of most fish and other marine consumers takes a value between 2.0 and 5.0. The upper value, 5.0, is unusual, even for large fish (Cortés, 1999), though it occurs in apex predators of marine mammals, such as polar bears and orcas (Pauly et al., 1998).

✓ Not Your Average Food Web: Microbial Loop 19.1.4

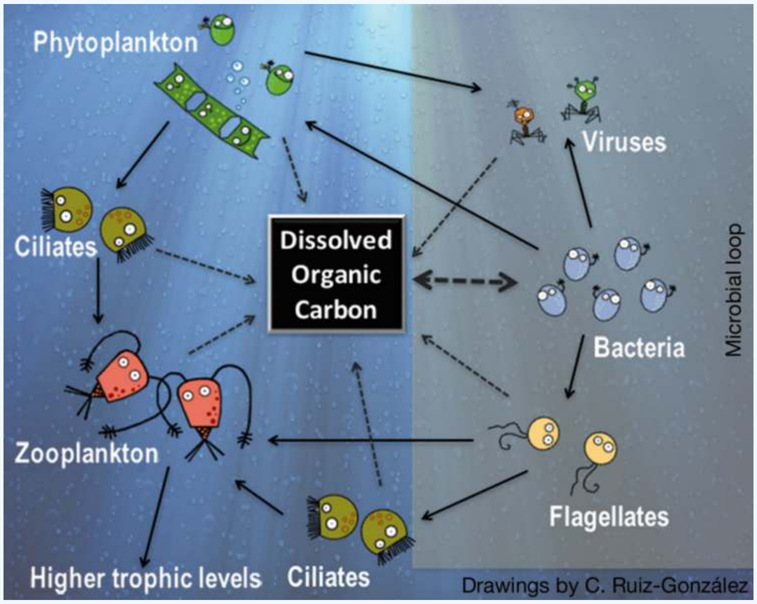


Figure 19.1.13: Simplified microbial food web in the sunlit ocean by Anders et al. is licensed under CC-BY-SA 4.0. Left side: classic description of the carbon flow from photosynthetic algae to grazers and higher trophic levels in the food chain. Right side: microbial loop, with bacteria using dissolved organic carbon to gain biomass, which then re-enters the classic carbon flow through protists. Based on DeLong & Karl (2005).

The microbial food web refers to the combined trophic interactions among microbes in aquatic environments. These microbes include viruses, bacteria, algae, heterotrophic protists (such as ciliates and flagellates) (Mostajir et al., 2015). Scientists have relatively recently begun to appreciate the importance of this microscopic food web to the functioning of higher trophic levels.

In aquatic environments, microbes constitute the base of the food web. Single celled photosynthetic organisms such as diatoms and cyanobacteria are generally the most important primary producers in the open ocean. Many of these cells, especially cyanobacteria, are too small to be captured and consumed by small crustaceans and planktonic larvae. Instead, these cells are consumed by phagotrophic protists which are readily consumed by larger organisms. Viruses can infect and break open bacterial cells and (to a lesser extent), planktonic algae (a.k.a. phytoplankton). Therefore, viruses in the microbial food web act to reduce the population of bacteria and, by lysing bacterial cells, release particulate and dissolved organic carbon (DOC). DOC may also be released into the environment by algal cells. The microbial loop describes a pathway in the microbial food web where DOC is returned to higher trophic levels via the incorporation into bacterial biomass.

Ecological pyramids

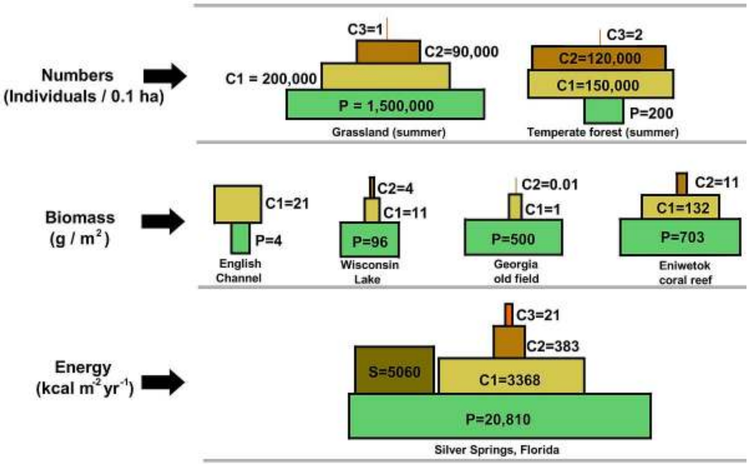


Figure 19.1.14: Illustration of a range of ecological pyramids, including **top** pyramid of numbers, **middle** pyramid of biomass, and **bottom** pyramid of energy. The terrestrial forest (summer) and the English Channel ecosystems exhibit inverted pyramids.*Note:* trophic levels are not drawn to scale and the pyramid of numbers excludes microorganisms and soil animals. *Abbreviations:* P=Producers, C1=Primary consumers, C2=Secondary consumers, C3=Tertiary consumers, S=Saprotrophs (Odum & Barrett, 2005).

Ecological trophic pyramids are typically one of three kinds: 1) pyramid of numbers, 2) pyramid of biomass, or 3) pyramid of energy (Odum & Barrett, 2005). In a pyramid of numbers, the number of consumers at each level decreases significantly, so that a single top consumer, (e.g., a polar bear or a human), will be supported by a much larger number of separate producers. There is usually a maximum of four or five links in a food chain, although food chains in aquatic ecosystems are more often longer than those on land. Eventually, all the energy in a food chain is dispersed as heat (Odum & Barrett, 2005).

Pyramid structure can vary across ecosystems and across time. In some instances biomass pyramids can be inverted. This pattern is often identified in aquatic and coral reef ecosystems. The pattern of biomass inversion is attributed to different sizes of producers. Aquatic communities are often dominated by producers that are smaller than the consumers that have high growth rates. Aquatic producers, such as planktonic algae or aquatic plants, lack the large accumulation of secondary growth as exists in the woody trees of terrestrial ecosystems. However, they are able to reproduce quickly enough to support a larger biomass of grazers. This inverts the pyramid. Primary consumers have longer lifespans and slower growth rates that accumulate more biomass than the producers they consume. Phytoplankton live just a few days, whereas the zooplankton eating the phytoplankton live for several weeks and the fish eating the zooplankton live for several consecutive years (Spellman, 2008). Aquatic predators also tend to have a lower death rate than the smaller consumers, which contributes to the inverted pyramidal pattern. Population structure, migration rates, and environmental refuge for prey are other possible causes for pyramids with biomass inverted. Energy pyramids, however, will always have an upright pyramid shape if all sources of food energy are included and this is dictated by the second law of thermodynamics (Odum & Barrett, 2005; Wang et al., 2009).

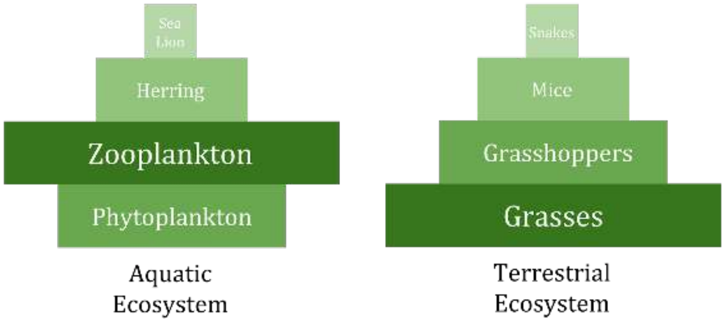


Figure 19.1.15: A pyramid of biomass shows the total biomass of the organisms involved at each trophic level of an ecosystem. These pyramids are not necessarily upright. There can be lower amounts of biomass at the bottom of the pyramid if the rate of primary production per unit biomass is high.

19.2: Quantifying Food Webs

Ecologists collect data on trophic levels and food webs to statistically model and mathematically calculate parameters, such as those used in other kinds of network analysis (e.g., graph theory), to study emergent patterns and properties shared among ecosystems. There are different ecological dimensions that can be mapped to create more complicated food webs, including: species composition (type of species), richness (number of species), biomass (the dry weight of plants and animals), productivity (rates of conversion of energy and nutrients into growth), and stability (food webs over time). A food web diagram illustrating species composition shows how change in a single species can directly and indirectly influence many others. The sections below describe three metrics that ecologists use to describe and quantify food webs (Transfer Efficiency, Food Chain Length, Connectance).

Transfer Efficiency

The biomass of each trophic level decreases from the base of the chain to the top. This is because energy is lost to the environment with each transfer as entropy increases. About eighty to ninety percent of the energy is expended for the organism's life processes or is lost as heat or waste. Only about ten to twenty percent of the organism's energy is generally passed to the next organism (Spellman, 2008). The amount can be less than one percent in animals consuming less digestible plants, and it can be as high as forty percent in zooplankton consuming phytoplankton (Kent, 2000). Graphic representations of the biomass or productivity at each trophic level are called ecological pyramids or trophic pyramids. The proportion of energy that is transferred from one trophic level to the next is known as the **transfer efficiency** of a food web.

The **ten percent law** of transfer of energy from one trophic level to the next can be attributed to Raymond Lindeman (1942) (Odum & Barrett, 2005). However, Lindeman did not call it a "law" and cited transfer efficiencies ranging from 0.1% to 37.5%. According to this law, during the transfer of organic food energy from one trophic level to the next higher level, only about ten percent of the transferred energy is stored as flesh. The remaining is lost during transfer, broken down in respiration, or lost to incomplete digestion by higher trophic level.

When organisms are consumed, approximately 10% of the energy in the food is fixed into their flesh and is available for the next trophic level (carnivores or omnivores). When a carnivore or an omnivore in turn consumes that animal, only about 10% of energy is fixed in its flesh for the higher level. Again, it is important to remember that the 10% value represents an estimate and that, in reality, transfer efficiency varies highly among ecosystems, time periods, and trophic levels.

Example: The Sun releases 10,000 J of energy, then plants take only 100 J of energy from sunlight (this is an exception to the 10% rule, since only 1% of energy is taken up by plants from sun); thereafter, a deer would take 10 J (10% of energy) from the plant. A wolf eating the deer would only take 1 J (10% of energy from deer). A human eating the wolf would take 0.1J (10% of energy from wolf), etc.

The ten percent law provides a basic understanding on the cycling of food chains. Furthermore, the ten percent law shows the inefficiency of energy capture at each successive trophic level. The rational conclusion is that energy efficiency is best preserved by sourcing food as close to the initial energy source as possible.

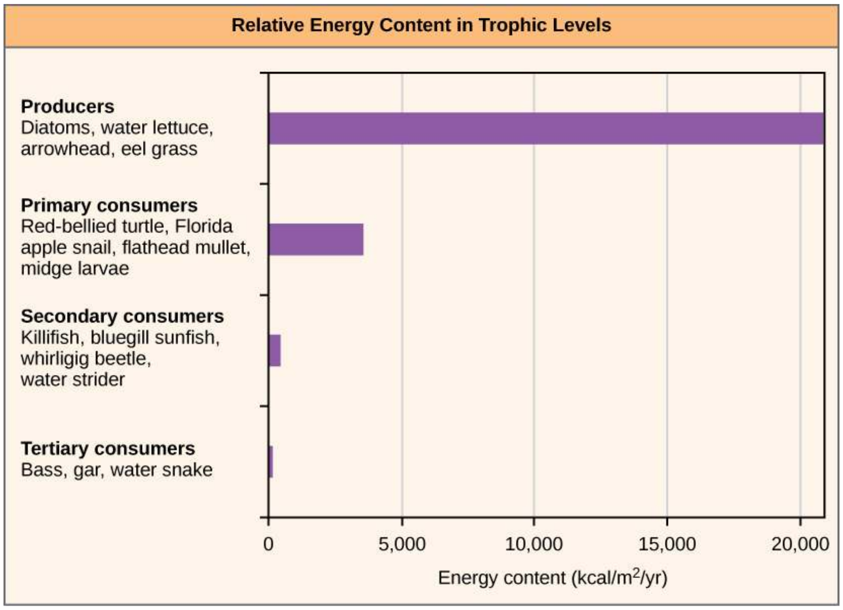


Figure 19.2.1: The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available, and usually, but not always, supports a smaller mass of organisms at the next level.

Food Chain Length

A common metric used to quantify food web trophic structure is food chain length. Food chain length is another way of describing food webs as a measure of the number of species encountered as energy or nutrients move from the plants to top predators (Post, 1993). In its simplest form, the length of a chain is the number of links between a trophic consumer and the base of the web or the maximum trophic level of a species in that food web. The mean chain length of an entire web is the arithmetic average of the lengths of all chains in a food web (Pimm, 1979; Odum & Barrett, 2005). In a simple predator-prey example, a deer is one step removed from the plants it eats (chain length = 1) and a wolf that eats the deer is two steps removed from the plants (chain length = 2). Because energy is lost at each transfer from one trophic level to the next (see Transfer Efficiency), the maximum number of trophic levels is generally constrained to only four or five levels. The number of trophic levels is ultimately determined by the productivity at the base of the food web and by how efficiently this energy is transferred up the food chain. Greater productivity and higher efficiency can support a greater number of trophic levels.

Connectance

Food webs are extremely complex. Complexity is a measure of an increasing number of permutations and it is also a metaphorical term that conveys the mental intractability or limits concerning unlimited algorithmic possibilities. In food web terminology, complexity is a product of the number of species and connectance (Neutel et al., 2002; Leveque, 2003; Proctor et al., 2005). Connectance is "the fraction of all possible links that are realized in a network" (Dunne et al., 2002). These concepts were derived and stimulated through the suggestion that complexity leads to stability in food webs, such as increasing the number of trophic levels in more species rich ecosystems. This hypothesis was challenged through mathematical models suggesting otherwise, but subsequent studies have shown that the premise holds in real systems (Neutel et al., 2002; Banasek-Richter et al., 2009).

While the complexity of real food webs connections are difficult to decipher, ecologists have found mathematical models on networks an invaluable tool for gaining insight into the structure, stability, and laws of food web behaviors relative to observable outcomes. Quantitative formulas simplify the complexity of food web structure. The number of trophic links (tL), for example, is converted into a connectance value:

$$\mathbf{C=L/[S(S-1)/2]} \tag{19.2.1}$$

where, S(S-1)/2 is the maximum number of binary connections among S species (Paine 1988). "Connectance (C) is the fraction of all possible links that are realized (L/S2) and represents a standard measure of food web complexity..." (Williams et al., 2002).

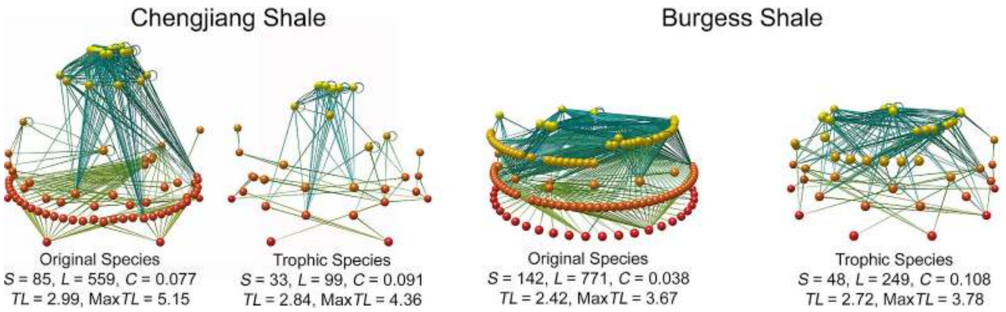


Figure 19.2.2: Food web and trophic level of the Chengjiang and Burgess Shale. S: number of species (nodes). L: number of trophic links. C: connectance; L/S2. MaxTL: maximum trophic level of a species in the web. Paleoecological studies can reconstruct fossil food-webs and trophic levels. Primary producers form the base (red spheres), predators at top (yellow spheres), the lines represent feeding links. Original food-webs (left) are simplified (right) by aggregating groups feeding on common prey into coarser grained trophic species (Dunne et al., 2008). Figure developed by Dunne et al. 2008 is licensed under CC-BY 4.0.

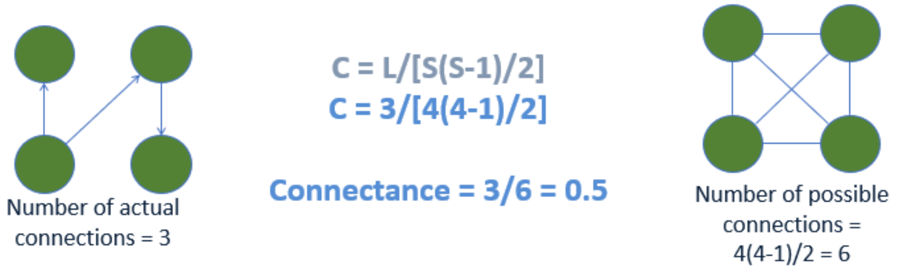


Figure 19.2.3: Worked example of calculating connectance for a food web. Diagram by N. Gownaris and A. Wilson.

✓ Techniques for Studying Food Webs 19.2.1

Food web linkages, or the feeding relationships between species inhabiting a shared ecosystem, are an ecological lens through which ecosystem structure and function can be assessed, and thus are fundamental to informing sustainable resource management. Empirical feeding datasets have traditionally been painstakingly generated from stomach content analysis, direct observations and from biochemical trophic markers (stable isotopes, fatty acids, molecular tools). Each approach carries inherent biases and limitations, as well as advantages.

Traditional Approaches to Studying Food Webs

Traditional approaches to food web analysis include gut and scat content analysis. In these analyses, the diet of species is determined based on the remains of prey found in their stomachs or in their feces. These approaches are limited because they only allow researchers to examine the hard parts or otherwise undigested components of prey (e.g., otoliths, or ear bones, of fish and teeth of mice). Over the past two decades, stable isotope analysis has become an increasingly common approach to studying food webs. Even more recently, two new methods to studying food webs have emerged: the use of remotely operated vehicles and the use of DNA in feces and gut contents. Below, we provide an example of a recent study using remotely operated vehicles to study food webs and diet in the deep sea.

Figure 19.2.4: Traditional food web analysis has often entailed gut content analysis or fecal content analysis. Scientists use the bits of prey that remain to calculate estimates of variables like percent occurrence for each prey type. The top photo (taken by N. Gownaris, licenced CC-BY) shows a tilapia in the stomach of a Nile perch; very rarely is gut content analysis this straightforward! The bottom photo (inside the owl pellet by Art Siegel and licensed under CC-BY-NC 2.0) shows prey remains removed from an owl pellet, including teeth, claws, and bones of owl prey.

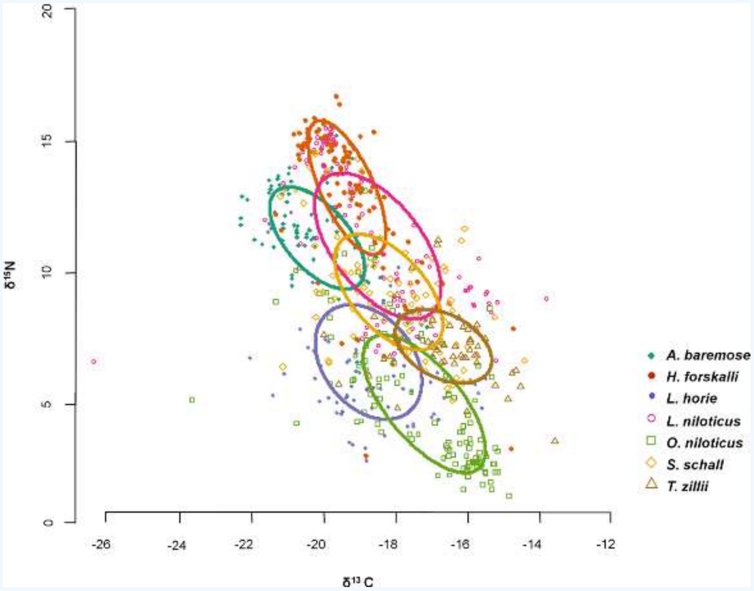


Figure 19.2.5: An example of a food web study using stable isotopes of seven key fish species in Lake Turkana, Kenya. In stable isotope studies, δ13C provides information on the foraging habitat of each species, while δ15N provides information on the trophic level. Species foraging more offshore or more pelagically have a lower δ13C signature and species feeding at

lower trophic levels have a lower δ15N signature. In this example, *H. forskalii* is a pelagic fish (i.e., it feeds in the lake's open waters) and has the highest trophic level among the species studied. Figure from Gownaris et al., 2015.

The Use of Remotely Operated Vehicles to Understand Understudied Food Webs

Within the deep sea, Earth's largest ecosystem, the challenge of gathering empirical feeding data for food webs is particularly formidable due to logistical access and sampling constraints (Robison, 2004). Analyzing the contents of a consumer's stomach (gut or stomach content analysis) is the common and most directly quantitative way of inferring diet, and is an irreplaceable approach for determining the taxonomic identity of food web components. However, for deeper-dwelling fishes with internal gas spaces, stomach eversion can confound this approach (Drazen & Sutton, 2017). These analyses may also fail to quantify gelatinous prey that are readily digested and become quickly unrecognizable (Hyslop, 1980; Choy, 2013).

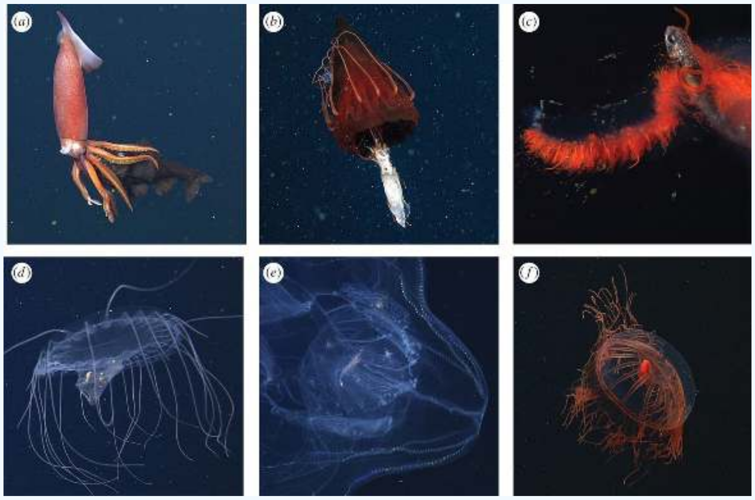


Figure 19.2.6: A suite of six illustrative ROV frame grabs of pelagic predators and their prey included in Choy et al. (2017). No scale bars for size are available from these sequences. From left to right, top to bottom: (a) *Gonatus sp.* (squid) feeding on a bathylagid fish (Bathylagidae); (b) *Periphylla periphylla*, the helmet jellyfish, feeding on a gonatid squid (Gonatidae), with a small narcomedusa (*Aegina sp.*) also captured; (c) an undescribed physonect siphonophore known as 'the galaxy siphonophore' feeding on a lanternfish of the family Myctophidae; (d) a narcomedusa, *Solmissus*, ingesting a salp chain (Salpida); (e) the ctenophore *Thalassocalyce inconstans*, with a euphausiid (Euphausiacea) in its gut; and (f) the trachymedusa, *Halitrephes maasi*, with a large, red mysid (Mysidae) in its gut. Figure from Choy et al., 2017.

Choy et al. (2017) used 27 years (1991–2016) of *in situ* feeding observations collected by remotely operated vehicles (ROVs) to quantitatively characterize the deep pelagic food web of central California within the California Current, complementing existing studies of diet and trophic interactions with a unique perspective. Seven hundred and forty-three independent feeding events were observed with ROVs from near-surface waters down to depths approaching 4000 m, involving an assemblage of 84 different predators and 82 different prey types, for a total of 242 unique feeding relationships. The greatest diversity of prey was consumed by narcomedusae, followed by physonect siphonophores, ctenophores and cephalopods. This study highlighted key interactions within the poorly understood 'jelly web', showing the importance of medusae, ctenophores and siphonophores as key predators, whose ecological significance is comparable to large fish and squid species within the central California deep pelagic food web.

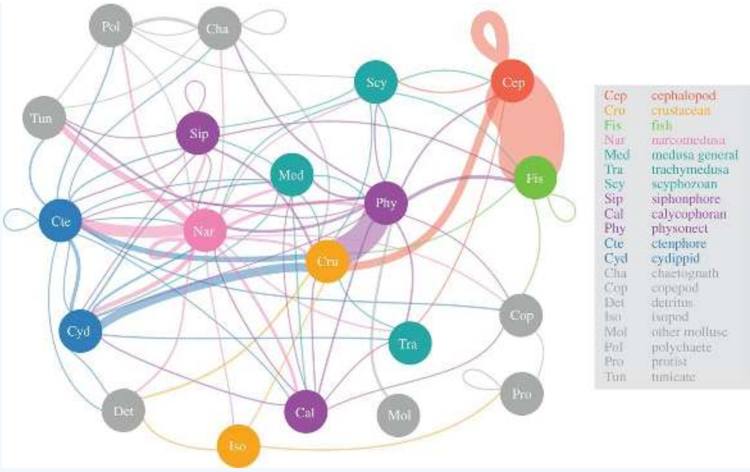


Figure 19.2.7: An *in situ* perspective of the food web derived from ROV-based observations of feeding, as represented by 20 broad taxonomic groupings. The linkages between predator to prey are coloured according to predator group origin, and loops indicate within-group feeding. The thickness of the lines or edges connecting food web components is scaled to the log of the number of unique ROV feeding observations across the years 1991–2016 between the two groups of animals. The different groups have eight colour-coded types according to main animal types as indicated by the legend and defined here: red, cephalopods; orange, crustaceans; light green, fish; dark green, medusa; purple, siphonophores; blue, ctenophores and grey, all other animals. In this plot, the vertical axis does not correspond to trophic level, because this metric is not readily estimated for all members. Note that for the Sip and Med groups, there are overlapping sub-groups (calycophoran and physonect siphonophores, and trachymedusa and scyphozoan medusa, respectively), which is attributed to varying levels of taxonomic discrimination possible from *in situ* video observations. Figure from Choy et al., 2017.

19.3: Trophic Cascades

Trophic cascades are powerful indirect interactions that can control entire ecosystems, occurring when a trophic level in a food web is suppressed. For example, a top-down cascade will occur if predators are effective enough in predation to reduce the abundance, or alter the behavior of their prey, thereby releasing the next lower trophic level from predation (or herbivory if the intermediate trophic level is a herbivore).

The trophic cascade is an ecological concept which has stimulated new research in many areas of ecology. For example, it can be important for understanding the knock-on effects of removing top predators from food webs, as humans have done in many places through hunting and fishing.

A **top-down cascade** is a trophic cascade where the top consumer/predator controls the primary consumer population. In turn, the primary producer population thrives. The removal of the top predator can alter the food web dynamics. In this case, the primary consumers would overpopulate and exploit the primary producers. Eventually there would not be enough primary producers to sustain the consumer population. Top-down food web stability depends on competition and predation in the higher trophic levels. Invasive species can also alter this cascade by removing or becoming a top predator. This interaction may not always be negative. Studies have shown that certain invasive species have begun to shift cascades; and as a consequence, ecosystem degradation has been repaired (Kotta et al., 2018; Megrey & Werner).

These trophic interactions shape patterns of biodiversity globally. Humans and climate change have affected these cascades drastically. One example can be seen with sea otters (*Enhydra lutris*) on the Pacific coast of the United States of America. Over time, human interactions caused a removal of sea otters. One of their main prey, the pacific purple sea urchin (*Strongylocentrotus purpuratus*) eventually began to overpopulate. The overpopulation caused increased predation of giant kelp (*Macrocystis pyrifera*). As a result, there was extreme deterioration of the kelp forests along the California coast (Estes & Palmisano, 1974; Szpak et al., 2013). This is why it is important for countries to regulate marine and terrestrial ecosystems (Zhang et al., 2018).

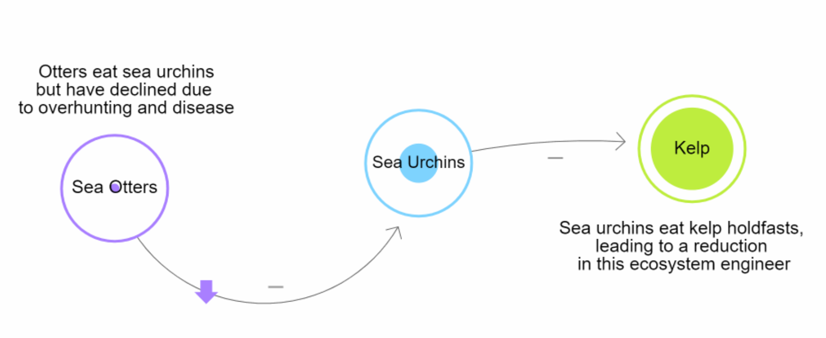


Figure 19.3.1 : Diagram representing the trophic cascade that occurs when sea otters are removed from coastal marine ecosystems in California, ultimately driving a reduction in habitat due to the loss of Kelp. Developed by N. Gownaris using loopy. Create your own using LOOPY: a tool for thinking in systems (ncase.me)

Predator-induced interactions could heavily influence the flux of atmospheric carbon if managed on a global scale. For example, a study was conducted to determine the cost of potential stored carbon in living kelp biomass in sea otter (*Enhydra lutris*) enhanced ecosystems. The study valued the potential storage between $205 million and $408 million dollars (US) on the European Carbon Exchange (2012) (Wilmers et al., 2012).

One criticism of trophic cascades is that, in nature, communities rarely act as food chains with discrete trophic levels. Most communities, however, have complex food webs. In real food webs, consumers often feed at multiple trophic levels (omnivory), organisms often change their diet as they grow larger, cannibalism occurs, and consumers are subsidized by inputs of resources from outside the local community, all of which blur the distinctions between trophic levels (Polis & Strong, 1996).

Classic Examples of Trophic Cascades

The earliest empirical demonstrations of trophic cascades came from marine and, especially, aquatic ecosystems. In addition to the sea otter example discussed above, two famous examples include:

- In North American lakes, piscivorous fish can dramatically reduce populations of zooplanktivorous fish; zooplanktivorous fish can dramatically alter freshwater zooplankton communities, and zooplankton grazing can in turn have large impacts on phytoplankton communities. Removal of piscivorous fish can change lake water from clear to green by allowing phytoplankton to flourish (Carpenter et al., 1985).
- In the Eel River, in Northern California, fish (steelhead and roach) consume fish larvae and predatory insects. These smaller predators prey on midge larvae, which feed on algae. Removal of the larger fish increases the abundance of algae (Power, 1990).

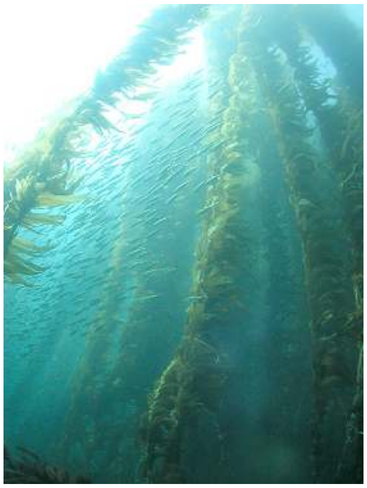


Figure 19.3.2: Healthy Pacific kelp forests, like this one at San Clemente Island of California's Channel Islands, have been shown to flourish when sea otters are present. When otters are absent, sea urchin populations can irrupt and severely degrade the kelp forest ecosystem. This image by Aquaimages is licensed under CC BY-SA 2.5.

More recent examples of trophic cascades in marine ecosystems have been identified:

- An example of a cascade in a complex, open-ocean ecosystem occurred in the northwest Atlantic during the 1980s and 1990s. The removal of Atlantic cod (*Gadus morhua*) and other ground fishes by sustained overfishing resulted in increases in the abundance of the prey species for these ground fishes, particularly smaller forage fishes and invertebrates such as the northern snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*). The increased abundance of these prey species altered the community of zooplankton that serve as food for smaller fishes and invertebrates as an indirect effect (Frank et al., 2005).
- A similar cascade, also involving the Atlantic cod, occurred in the Baltic Sea at the end of the 1980s. After a decline in Atlantic cod, the abundance of its main prey, the sprat (*Sprattus sprattus*), increased (Alheit et al. 2005) and the Baltic Sea ecosystem shifted from being dominated by cod into being dominated by sprat. The next level of trophic cascade was a decrease in the abundance of *Pseudocalanus acuspes* (Mollmann et al., 2008), a copepod which the sprat prey on.
- On Caribbean coral reefs, several species of angelfishes and parrotfishes eat species of sponges that lack chemical defenses. Removal of these sponge-eating fish species from reefs by fish-trapping and netting has resulted in a shift in the sponge community toward fast-growing sponge species that lack chemical defenses (Loh & Pawlik, 2014). These fast-growing sponge species are superior competitors for space, and overgrow and smother reef-building corals to a greater extent on overfished reefs (Loh et al., 2015).

The fact that the earliest documented trophic cascades all occurred in lakes and streams led a scientist to speculate that fundamental differences between aquatic and terrestrial food webs made trophic cascades primarily an aquatic phenomenon. Trophic cascades were restricted to communities with relatively low species diversity, in which a small number of species could have overwhelming influence and the food web could operate as a linear food chain. Additionally, well documented trophic cascades at that point in time all occurred in food chains with algae as the primary producer. Trophic cascades, Strong argued, may only occur in communities with fast-growing producers which lack defenses against herbivory.

Subsequent research has documented trophic cascades in terrestrial ecosystems, including:

- A classic example of a terrestrial trophic cascade is the reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park, which reduced the number, and changed the behavior, of elk (*Cervus canadensis*). This in turn released several plant species from grazing pressure and subsequently led to the transformation of riparian ecosystems. This example of a trophic cascade is vividly shown and explained in the viral video "How Wolves Change Rivers" (Sustainable Human, 2014).
- In the coastal prairie of Northern California, yellow bush lupines are fed upon by a particularly destructive herbivore, the root-boring caterpillar of the ghost moth. Entomopathogenic nematodes kill the caterpillars, and can increase the survival and seed production of lupines (Strong et al., 1999; Preisser, 2003).
- In Costa Rican rain forest, a clerid beetle specializes in eating ants. The ant *Pheidole bicornis* has a mutualistic association with *Piper* plants: the ant lives on the *Piper* and removes caterpillars and other insect herbivores. The clerid beetle, by reducing the abundance of ants, increases the leaf area removed from *Piper* plants by insect herbivores (Letourneau & Dyer, 1998).

Critics pointed out that published terrestrial trophic cascades generally involved smaller subsets of the food web (often only a single plant species). This was quite different from aquatic trophic cascades, in which the biomass of producers as a whole were reduced when predators were removed. Additionally, most terrestrial trophic cascades did not demonstrate reduced plant biomass when predators were removed, but only increased plant damage from herbivores (Polis et al., 2000). It was unclear if such damage would actually result in reduced plant biomass or abundance.

In 2002 a meta-analysis found trophic cascades to be generally *weaker* in terrestrial ecosystems, meaning that changes in predator biomass resulted in smaller changes in plant biomass (Shurin et al., 2002). In contrast, a study published in 2009 demonstrated that multiple species of trees with highly varying autecologies are in fact heavily impacted by the loss of an apex predator (Beschta & Ripple, 2009). Another study, published in 2011, demonstrated that the loss of large terrestrial predators also significantly degrades the integrity of river and stream systems, impacting their morphology, hydrology, and associated biological communities (Beschta & Ripple, 2011).

An Ecosystem-Wide Trophic Cascade: The Wolves of Yellowstone National Park

The critics' model is challenged by studies accumulating since the reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park. The gray wolf, after being extirpated in the 1920s and absent for 70 years, was reintroduced to the park in 1995 and 1996. Since then a three-tiered trophic cascade has been reestablished involving wolves, elk (*Cervus elaphus*), and woody browse species such as aspen (*Populus tremuloides*), cottonwoods (*Populus* spp.), and willows (*Salix* spp.). Mechanisms likely include actual wolf predation of elk, which reduces their numbers, and the threat of predation, which alters elk behavior and feeding habits, resulting in these plant species being released from intensive browsing pressure. Subsequently, their survival and recruitment rates have significantly increased in some places within Yellowstone's northern range. This effect is particularly noted among the range's riparian plant communities, with upland communities only recently beginning to show similar signs of recovery (Ripple & Beschta, 2012).

Examples of this phenomenon include:

- A 2–3 fold increase in deciduous woody vegetation cover, mostly of willow, in the Soda Butte Creek area between 1995 and 1999 (Groshong, 2004).
- Heights of the tallest willows in the Gallatin River valley increasing from 75 cm to 200 cm between 1998 and 2002 (Ripple & Beschta, 2004).

- Heights of the tallest willows in the Blacktail Creek area increased from less than 50 cm to more than 250 cm between 1997 and 2003. Additionally, canopy cover over streams increased significantly, from only 5% to a range of 14–73% (Beschta & Ripple, 2007).
- In the northern range, tall deciduous woody vegetation cover increased by 170% between 1991 and 2006 (Baril, 2009).
- In the Lamar and Soda Butte Valleys the number of young cottonwood trees that had been successfully recruited went from 0 to 156 between 2001 and 2010 (Ripple & Beschta, 2012).

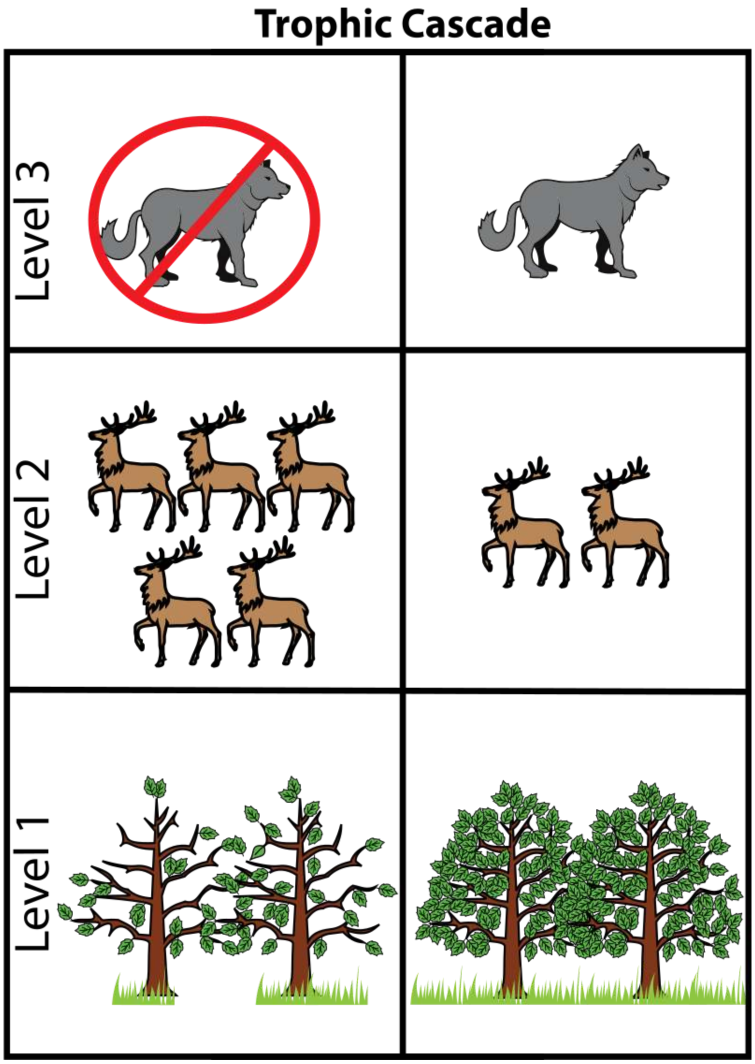


Figure 19.3.3 : This diagram illustrates trophic cascade caused by removal of the top predator. When the top predator is removed the population of deer is able to grow unchecked and this causes over-consumption of the primary producers. This image by Zirguezi is licensed under CC BY 3.0.

Trophic cascades also impact the biodiversity of ecosystems, and when examined from that perspective wolves appear to be having multiple, positive cascading impacts on the biodiversity of Yellowstone National Park. These impacts include:

- Scavengers, such as ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and even grizzly bears (*Ursus arctos horribilis*), are likely subsidized by the carcasses of wolf kills (Wilmers et al., 2003).
- In the northern range, the relative abundance of six out of seven native songbirds which utilize willow was found to be greater in areas of willow recovery as opposed to those where willows remained suppressed (Baril, 2009).

- Bison (*Bison bison*) numbers in the northern range have been steadily increasing as elk numbers have declined, presumably due to a decrease in interspecific competition between the two species (Painter & Ripple, 2012).
- Importantly, the number of beaver (*Castor canadensis*) colonies in the park has increased from one in 1996 to twelve in 2009. The recovery is likely due to the increase in willow availability, as they have been feeding almost exclusively on it. As keystone species, the resurgence of beaver is a critical event for the region. The presence of beavers has been shown to positively impact streambank erosion, sediment retention, water tables, nutrient cycling, and both the diversity and abundance of plant and animal life among riparian communities (Ripple & Beschta, 2012).

There are a number of other examples of trophic cascades involving large terrestrial mammals, including:

- In both Zion National Park and Yosemite National Park, the increase in human visitation during the first half of the 20th century was found to correspond to the decline of native cougar (*Puma concolor*) populations in at least part of their range. Soon after, native populations of mule deer (*Odocoileus hemionus*) erupted, subjecting resident communities of cottonwoods (*Populus fremontii*) in Zion and California black oak (*Quercus kelloggii*) in Yosemite to intensified browsing. This halted successful recruitment of these species except in refugia inaccessible to the deer. In Zion the suppression of cottonwoods increased stream erosion and decreased the diversity and abundance of amphibians, reptiles, butterflies, and wildflowers. In parts of the park where cougars were still common these negative impacts were not expressed and riparian communities were significantly healthier (Ripple & Beschta, 2006; Ripple & Beschta, 2008).
- In sub-Saharan Africa, the decline of lion (*Panthera leo*) and leopard (*Panthera pardus*) populations has led to a rising population of olive baboon (*Papio anubis*). This case of mesopredator release negatively impacted already declining ungulate populations and is one of the reasons for increased conflict between baboons and humans, as the primates raid crops and spread intestinal parasites (Prugh et al., 2009; Estes et al., 2011).
- In the Australian states of New South Wales and South Australia, the presence or absence of dingoes (*Canis lupus dingo*) was found to be inversely related to the abundance of invasive red foxes (*Vulpes vulpes*). In other words, the foxes were most common where the dingoes were least common. Subsequently, populations of an endangered prey species, the dusky hopping mouse (*Notomys fuscus*) were also less abundant where dingoes were absent due to the foxes, which consume the mice, no longer being held in check by the top predator (Letnic & Dworjanyn, 2011).

19.4: Sources and Attributions

Contributors and Attributions

This chapter was compiled and written by N. Gownaris with text taken from the following CC-BY resources:

- **Trophic Cascade by Wikipedia, the free encyclopedia**
- **Trophic Level by Wikipedia, the free encyclopedia**
- **Food Web by Wikipedia, the free encyclopedia**
- **Ecological Pyramid by Wikipedia, the free encyclopedia**
- **Decomposer by Wikipedia, the free encyclopedia**
- **Detritivore by Wikipedia, the free encyclopedia**
- **Detritus by Wikipedia, the free encyclopedia**
- **Scavenger by Wikipedia, the free encyclopedia**
- **Microbial Food Web by Wikipedia, the free encyclopedia**
- **Ecological Efficiency by Wikipedia, the free encyclopedia**
- **Ecology of Ecosystems (Chapter 46.1) from OpenStaxx Biology 2e**
- **Energy Flow through Ecosystems (Chapter 46.2) from OpenStaxx Biology 2e**
- **Madigan, D. J., Carlisle, A. B., Dewar, H., Snodgrass, O. E., Litvin, S. Y., Micheli, F., & Block, B. A. (2012). Stable isotope analysis challenges wasp-waist food web assumptions in an upwelling pelagic ecosystem. *Scientific reports*, *2*(1), 1-10.**
- **Choy, C. A., Haddock, S. H., & Robison, B. H. (2017). Deep pelagic food web structure as revealed by in situ feeding observations. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868), 20172116.**
- **Hoover, C., Giraldo, C., Ehrman, A., Suchy, K. D., MacPhee, S. A., Brewster, J., ... & Loseto, L. (2021). The Canadian Beaufort Shelf trophic structure: evaluating an ecosystem modelling approach by comparison with observed stable isotopic structure. *Arctic Science*, 1-21.**

Sources

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., & Wasmund, N. (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, *62*(7), pp. 1205–1215. doi:10.1016/j.icesjms.2005.04.024.

Banasek-Richter, C., Bersier, L.L., Cattin, M., Baltensperger, R., Gabriel, J., Merz, Y., et al. (2009). Complexity in quantitative food webs. *Ecology, 90*(6), pp. 1470–1477. doi:10.1890/08-2207.1. hdl:1969.1/178777. PMID 19569361.

Barbosa, P., & Castellanos, I. (Eds.). (2005). Ecology of predator-prey interactions, pp. 306, Oxford University Press.ISBN 9780199883677.

Baril, L.M. (2009). Change in deciduous woody vegetation, implications of increased willow (Salix spp.) growth for bird species diversity and willow species composition in and around Yellowstone National Park's northern range (MS). *Bozeman, USA: Montana State University*.

Benke, A.C. (2010). Secondary production. *Nature Education Knowledge, 1*(8), pp. 5.

Beschta, R.L., & Ripple, W.J. (2011). The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology*, 157–158, 88–98. doi:10.1016/j.geomorph.2011.04.042.

Beschta, R.L., & W.J. Ripple. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western. *United States Biological Conservation, 142*, pp. 2401–2414.

Beschta, R.L., & Ripple, W.J. (2007). Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. *Western North American Naturalist, 67*(4), pp. 613–617. doi:10.3398/1527-0904(2007)67[613:iwhany]2.0.co;2.

Carpenter, S.R., Kitchell, J.F., & Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. *BioScience, 35*(10), pp. 634–639. doi:10.2307/1309989. JSTOR 1309989.

Choy, C.A., Portner, E., Iwane, M., & Drazen, J.C. (2013). Diets of five important predatory mesopelagic fishes of the central North Pacific. *Mar. Ecol. Prog. Ser., 492*, pp. 169–184. (doi:10.3354/meps10518)

Choy, C.A., Haddock, S.H., & Robison, B.H. (2017). Deep pelagic food web structure as revealed by in situ feeding observations. *Proceedings of the Royal Society B: Biological Sciences, 284*(1868), 20172116.

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci., 56*(5), pp. 707–717. doi:10.1006/jmsc.1999.0489.

Cury, P., et al. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci., 57*, pp. 603–618 (2000).

Cury, P.M., et al. (2011). Global seabird response to forage fish depletion - one-third for the birds. *Science, 334*, pp. 1703–1706.

Cury, P., Shannon, L., & Shin, Y.-J. (2003). In Sinclair, M., & Valdimarsson, G. (Eds.), *Responsible fisheries in the marine ecosystem*, (pp. 103–123). AO, Rome, & CABI Publishing, Wallingford, UK.

Definition of Trophic. www.merriam-webster.com. Retrieved 16 April 2017.

Drazen, J.C., & Sutton, T.T. (2017). Dining in the deep: The feeding ecology of deep-sea fishes. *Annu. Rev. Mar. Sci., 9*, pp. 337–366. (doi:10.1146/annurev-marine-010816-060543)

Dunne, J.A., Williams, R.J., Martinez, N.D., Wood, R.A., & Erwin, D.H. (2008). Compilation and Network Analyses of Cambrian Food Webs. *PLoS Biol., 6*(4): e102. doi:10.1371/journal.pbio.0060102

Dunne, J.A., Williams, R.J., & Martinez, N.D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences, 99*(20), pp. 12917–12922. Bibcode:2002PNAS...9912917D. doi:10.1073/pnas.192407699. PMC 130560. PMID 12235364.

Dunne, J.A., Williams, R.J., Martinez, N.D., Wood, R.A., Erwin, D.H., & Dobson, Andrew P. (2008). Compilation and network analyses of cambrian food webs. *PLOS Biology, 6*(4): e102. doi:10.1371/journal.pbio.0060102. PMC 2689700. PMID 18447582.

Eisenberg, C. (2011). The wolf's tooth: Keystone predators, trophic cascades, and biodiversity. pp. 15. Island Press. ISBN 978-1-59726-398-6.

Estes, J.A., & Palmisano, J.F. (1974). Sea otters: Their role in structuring nearshore communities. *Science, 185*(4156), pp. 1058–1060. doi:10.1126/science.185.4156.1058. PMID 17738247. S2CID 35892592.

Estes, J.A., et al. (2011). Trophic Downgrading of Planet Earth. *Science*, *333*(6040), pp. 301–306. CiteSeerX 10.1.1.701.8043. doi:10.1126/science.1205106. PMID 21764740. S2CID 7752940.

Frank, K.T.; Petrie, B., Choi, J.S., & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science, 308*(5728), pp. 1621–1623. doi:10.1126/science.1113075. ISSN 0036-8075. PMID 15947186. S2CID 45088691.

Getz, W. (2011). Biomass transformation webs provide a unified approach to consumer–resource modelling. *Ecology Letters, 14*(2), pp. 113–124. doi:10.1111/j.1461-0248.2010.01566.x. PMC 3032891. PMID 21199247.

Santos, G.N., Danac, A.C., & Ocampo, J.P. (2003). E-biology ii. *Rex Book Store*. p. 58. ISBN 978-971-23-3563-1.

Gönenç, I.E., Koutitonsky, V.G., & Rashleigh, B. (2007). Assessment of the fate and effects of toxic agents on water resources. *Springer*. p. 279. ISBN 978-1-4020-5527-0.

Gownaris, N.J., Pikitch, E.K., Ojwang, W.O., Michener, R., & Kaufman, L. (2015). Predicting species’ vulnerability in a massively perturbed system: The fishes of Lake Turkana, Kenya. *PloS one, 10*(5), e0127027.

Groombridge, B., & Jenkins, M. (2002). World atlas of biodiversity: Earth's living resources in the 21st century. *World Conservation Monitoring Centre, United Nations Environment Programme*. ISBN 978-0-520-23668-4.

Groshong, L.C. (2004). Mapping riparian vegetation change in Yellowstone's Northern Range using high spatial resolution imagery (MA Thesis). *Eugene, Oregon, USA: University of Oregon*.

Hutchinson, J. (2013). Tyrannosaurus rex: Predator or media hype? *What's in John's Freezer?* Retrieved August 26, 2013.

Hyslop E.J. (1980). Stomach contents analysis: A review of methods and their application. *J. Fish Biol., 17*, pp. 411–429. (doi:10.1111/j.1095-8649.1980.tb02775.x)

Kane; et al. (2016). Body size as a driver of scavenging in theropod dinosaurs. *The American Naturalist, 187*(6), pp. 706–16. doi:10.1086/686094. hdl:10023/10617. PMID 27172591. S2CID 3840870.

Keddy, P. (2017). Plant ecology, origins, processes, consequences (2nd Ed.). *New York: Cambridge University Press*. pp. 92–93. ISBN 978-1-107-11423-4.

Kent, M. (2000). Advanced biology. *Oxford University Press US*. p. 511. ISBN 978-0-19-914195-1.

Kotta, J., Wernberg, T., Jänes, H., Kotta, I., Nurkse, K., Pärnoja, M., & Orav-Kotta, H. (2018). Novel crab predator causes marine ecosystem regime shift. *Scientific Reports, 8*(1), pp. 4956. doi:10.1038/s41598-018-23282-w. PMC 5897427. PMID 29651152.

Letnic, M .,& Dworjanyn, S.A. (2011). Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography, 34*(5), pp. 827–835. doi:10.1111/j.1600-0587.2010.06516.x.

Letourneau, D.K., & Dyer, L.A. (1998). Experimental test in lowland tropical forest shows top-down effects through four trophic levels. *Ecology, 79*(5), pp. 1678–1687. doi:10.2307/176787. JSTOR 176787.

Leveque, C., ed. (2003). Ecology: From ecosystem to biosphere. Science Publishers. p. 490. ISBN 978-1-57808-294-0.

Loh, T.L., et al. (2015). Indirect effects of overfishing on Caribbean reefs: Sponges overgrow reef-building corals. PeerJ. 3: e901. doi:10.7717/peerj.901. PMC 4419544. PMID 25945305.

Loh, T.L., & Pawlik, J.R. (2014). Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proceedings of the National Academy of Sciences, 111*(11), pp. 4151–4156. doi:10.1073/pnas.1321626111. ISSN 0027-8424. PMC 3964098. PMID 24567392.

Madigan, D.J., Carlisle, A.B., Dewar, H., Snodgrass, O.E., Litvin, S.Y., Micheli, F., & Block, B.A. (2012). Stable isotope analysis challenges wasp-waist food web assumptions in an upwelling pelagic ecosystem. *Scientific reports, 2*(1), pp. 1-10.

Megrey, B., & Werner, F. Evaluating the role of topdown vs. bottom-up ecosystem regulation from a modeling perspective.

Mollmann, C., Muller-Karulis, B., Kornilovs, G., & St. John, M.A. (2008). Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: Regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES Journal of Marine Science, 65*(3), pp. 302–310. doi:10.1093/icesjms/fsm197.

Mostajir, B., Amblard, C., Buffan-Dubau, E., De Wit, R., Lensi, R., & Sime-Ngando, T. (2015). Microbial food webs in aquatic and terrestrial ecosystems. In Bertrand, J.C., Caumette, P., Lebaron, P., Matheron, R., Normand, P., & Sime-Ngando, T. (Eds.), *Environmental Microbiology: Fundamentals and Applications,* (pp. 485-510). Microbial Ecology, Springer. ISBN 9789401791182.

Murdoch, W.M. (1966). Community structure, population control, and competition – a critique. *The American Naturalist, 100*(912), pp. 219–226. doi:10.1086/282415. S2CID 84354616.

Neutel, A., Heesterbeek, J.A.P., & de Ruiter, P.D. (2002). Stability in real food webs: Weak link in long loops. *Science, 295*(550), pp. 1120–1123. Bibcode:2002Sci...296.1120N. doi:10.1126/science.1068326. hdl:1874/8123. PMID 12004131. S2CID 34331654. Archived from the original (PDF) on 2011-09-28.

NOAA. ACE Basin National Estuarine Research Reserve: Decomposers. Archived from the original on 2014-10-09. Retrieved 2012-09-17.

Odum, E.P., & Barrett, G.W. (2005). Fundamentals of ecology (5th ed.). Brooks/Cole, a part of Cengage Learning. ISBN 978-0-534-42066-6. Archived from the original on 2011-08-20.

Odum, W.E., & Heald, E.J. (1975). The detritus-based food web of an estuarine mangrove community. Pages 265–286 In Cronin, L.E. (Eds.), *Estuarine research* (pp. 265-286). Academic Press, New York.

Ogada, D.L., Keesing, F., & Virani, M.Z. (2011). Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences, 1249*(1), pp. 57–71. Bibcode:2012NYASA1249...57O. doi:10.1111/j.1749-6632.2011.06293.x. ISSN 0077-8923. PMID 22175274. S2CID 23734331.

Olson, Z.H., Beasley, J.C., & Rhodes, O.E. (2016). Carcass type affects local scavenger guilds more than habitat connectivity. *PLOS ONE, 11*(2): e0147798. Bibcode:2016PLoSO..1147798O. doi:10.1371/journal.pone.0147798. ISSN 1932-6203. PMC 4757541. PMID 26886299.

Pahl and Ruedas (2021). Carnosaurs as apex scavengers: Agent-based simulations reveal possible vulture analogues in late Jurassic Dinosaurs. *Ecological Modelling*, 458. doi:10.1016/j.ecolmodel.2021.109706e.

Paine, R.T. (1988). Road maps of interactions or grist for theoretical development? *Ecology, 69*(6), pp. 1648–1654. doi:10.2307/1941141. JSTOR 1941141. Archived from the original (PDF) on 2011-07-28.

Painter, L.E., & Ripple, W.J. (2012). Effects of bison on willow and cottonwood in northern Yellowstone National Park. *Forest Ecology and Management, 264*, pp. 150–158. doi:10.1016/j.foreco.2011.10.010.

Pauly, D., & Palomares, M.L. (2005). Fishing down marine food webs: It is far more pervasive than we thought. *Bulletin of Marine Science, 76*(2), pp. 197–211. Archived from the original (PDF) on 14 May 2013.

Pauly, D., Trites, A., Capuli, E., & Christensen, V. (1998). Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci., 55*(3), pp. 467–481. doi:10.1006/jmsc.1997.0280.

Pimm, S.L. (1979). The structure of food webs. *Theoretical Population Biology, 16*(2), pp. 144–158. doi:10.1016/0040-5809(79)90010-8. PMID 538731. Archived from the original (PDF) on 2011-09-27.

Pimm, S.L., Lawton, J.H., & Cohen, J.E. (1991). Food web patterns and their consequences. *Nature, 350*(6320), pp. 669–674. Bibcode:1991Natur.350..669P. doi:10.1038/350669a0. S2CID 4267587. Archived from the original (PDF) on 2010-06-10.

Polis, G.A., Sears, A.L, W., Huxel, G.R., et al. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution, 15*(11), pp. 473–475. doi:10.1016/s0169-5347(00)01971-6. PMID 11050351.

Polis, G.A., & Strong, D.R. (1996). Food web complexity and community dynamics. *The American Naturalist, 147*(5), pp. 813–846. doi:10.1086/285880. S2CID 85155900.

Post, D.M. (1993). The long and short of food-chain length. *Trends in Ecology and Evolution, 17*(6), pp. 269–277. doi:10.1016/S0169-5347(02)02455-2.

Power, M.E. (1990). Effects of fish in river food webs. *Science, 250*(4982), pp. 811–814. doi:10.1126/science.250.4982.811. PMID 17759974. S2CID 24780727.

Preisser, E.L. (2003). Field evidence for a rapidly cascading underground food web. *Ecology, 84*(4). pp. 869–874. doi:10.1890/0012-9658(2003)084[0869:fefarc]2.0.co;2.

Proctor, J.D., & Larson, B.M.H. (2005). Ecology, complexity, and metaphor. *BioScience, 55*(12), pp. 1065–1068. doi:10.1641/0006-3568(2005)055[1065:ECAM]2.0.CO;2.

Proulx, S.R., Promislow, D.E.L., & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends in Ecology and Evolution, 20*(6), 345–353. doi:10.1016/j.tree.2005.04.004. PMID 16701391. Archived from the original (PDF) on 2011-08-15.

Prugh, L.R., et al. (2009). The Rise of the Mesopredator. *BioScience, 59*(9), pp. 779–791. doi:10.1525/bio.2009.59.9.9. S2CID 40484905.

Raffaelli, D. (2002). From Elton to mathematics and back again. *Science, 296*(5570), pp. 1035–1037. doi:10.1126/science.1072080. PMID 12004106. S2CID 177263265.

Rickleffs, R.E. (1996). The economy of nature. *University of Chicago Press*. p. 678. ISBN 978-0-7167-3847-3.

Ripple, W.J., & Beschta, R.L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation, 145*, pp. 205–213. doi:10.1016/j.biocon.2011.11.005.

Ripple, W.J., & Beschta, R.L. (2004). Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management, 200*(1–3), pp. 161–181. doi:10.1016/j.foreco.2004.06.017.

Ripple, W.J., & Beschta, R.L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation, 133*(4), pp. 397–408. doi:10.1016/j.biocon.2006.07.002.

Ripple, W.J., & Beschta, R.L. (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation, 141*(5), pp. 1249–1256. doi:10.1016/j.biocon.2008.02.028.

Robison, B.H. (2004). Deep pelagic biology. *J. Exp. Mar. Biol. Ecol. 300*, pp. 253–272. (doi:10.1016/j.jembe.2004.01.012)

Sagi, N., Grünzweig, J.M.,& Hawlena, D. (2019). Burrowing detritivores regulate nutrient cycling in a desert ecosystem. *Proceedings Biological Sciences, 286*(1914): 20191647. doi:10.1098/rspb.2019.1647. PMC 6842856. PMID 31662076.

Science of Earth Systems. Cengage Learning. 2002. p. 537. ISBN 978-0-7668-3391-3.

Shannon, L.J., Cury, P.M. & Jarre, A. (2000). Modelling effects of fishing in the Southern Benguela ecosystem. *ICES J. Mar. Sci.*, pp. 720–72221934 .

Shurin, J.B., Borer, E.T., Seabloom, E.W. Anderson, K., Blanchette, C.A., Broitman, B, Cooper, S.D., & Halpern, B.S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, *5*(6), pp. 785–791. doi:10.1046/j.1461-0248.2002.00381.x.

Spellman, F.R. (2008). The science of water: Concepts and applications. *CRC Press*. p. 165. ISBN 978-1-4200-5544-3.

Strong, D.R., Whipple, A.V., Child, A.L., & Dennis, B. (1999). Model selection for a subterranean trophic cascade: Root-feeding caterpillars and entomopathogenic nematodes. *Ecology, 80*(8), pp. 2750–2761. doi:10.2307/177255. JSTOR 177255.

Sustainable Humans. 2014. "How Wolves Change Rivers"

Szpak, P., Orchard, T.J., Salomon, A.K., & Gröcke, D.R. (2013). Regional ecological variability and impact of the maritime fur trade on nearshore ecosystems in southern Haida Gwaii (British Columbia, Canada): Evidence from stable isotope analysis of rockfish (Sebastes spp.) bone collagen. *Archaeological and Anthropological Sciences.* doi:10.1007/s12520-013-0122-y. S2CID 84866250.

Tan, C.K.W., & Corlett, R.T. (2011). Scavenging of dead invertebrates along an urbanisation gradient in Singapore. *Insect Conservation and Diversity, 5*(2), pp. 138–145. doi:10.1111/j.1752-4598.2011.00143.x. ISSN 1752-458X. S2CID 86467187.

van Dover, C. (2000). The ecology of deep-sea hydrothermal vents. *Princeton University Press*. p. 399. ISBN 978-0-691-04929-8.

Wang, H., Morrison, W., Singh, A., & Weiss, H. (2009). Modeling inverted biomass pyramids and refuges in ecosystems. *Ecological Modelling, 220*(11), pp. 1376–1382. doi:10.1016/j.ecolmodel.2009.03.005. Archived from the original (PDF) on 2011-10-07.

Wetzel, R.G. (2001). Limnology: Lake and river ecosystems (3rd. ed.). *Academic Press*. p. 700. ISBN 978-0-12-744760-5.

Whitman, W.B., Coleman, D.C., & Wieb, W.J. (1998). Prokaryotes: The unseen majority. *Proc. Natl. Acad. Sci. USA.*, *95*(12), pp. 6578–83. Bibcode:1998PNAS...95.6578W. doi:10.1073/pnas.95.12.6578. PMC 33863. PMID 9618454.

Williams, R.J., Berlow, E.L., Dunne, J.A., Barabási, A., & Martinez, N.D. (2002). Two degrees of separation in complex food webs. *Proceedings of the National Academy of Sciences, 99*(20), pp. 12913–12916. Bibcode:2002PNAS...9912913W. doi:10.1073/pnas.192448799. PMC 130559. PMID 12235367.

Wilmers, C.C., Estes, J.A., Edwards, M., Laidre, K.L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment, 10*(8), pp. 409–415. doi:10.1890/110176. ISSN 1540-9309. S2CID 51684842.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., & Getz, W.M. (2003). Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology, 72*(6), pp. 909–916. doi:10.1046/j.1365-2656.2003.00766.x.

Zhang, J., Qian, H., Girardello, M., Pellissier, V., Nielsen, S.E., & Svenning, J.C. (2018). Trophic interactions among vertebrate guilds and plants shape global patterns in species diversity. *Proceedings of the Royal Society B: Biological Sciences, 285*(1883): 20180949. doi:10.1098/rspb.2018.0949. PMC 6083253. PMID 30051871.

CHAPTER OVERVIEW

20: Biogeochemical Cycles

Learning Objectives

- Summarize the concept of biogeochemical cycles
- Explain the hydrologic cycle and its importance for Ecology
- Distinguish between the biological and biogeochemical cycles of carbon
- Describe the nitrogen cycle and its various pools and fluxes
- Illustrate the phosphorus cycle and the effects of phosphorus on the environment
- Define eutrophication and dead zones and their importance for Ecology
- Explain the sulfur cycle

Topic hierarchy

Summary

This chapter discusses earths major biological and biogeochemical cycles including cycling of water, carbon, nitrogen, phosphorus, sulfur. After a brief introduction to biogeochemical cycles and a review of the hydrologic cycle, the pools and fluxes of the major elemental cycles are introduced. Effects of the changes in the carbon, nitrogen, and phosphorus cycles caused by humans are also discussed including the concepts of eutrophication and dead zones in aquatic and marine systems.

20.1: Biogeochemical Cycles

Key Points

- Carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur are conserved and recycled in the atmosphere, on land, in water, or beneath the earth's surface.
- Materials are recycled via erosion, weathering, water drainage, and the movement of tectonic plates.
- Water is essential to all living processes, while carbon is found in all organic (carbon-based) macromolecules.
- Nitrogen and phosphorus are major components of nucleic acids and play major roles in agriculture.
- Sulfur plays a role in the three-dimensional folding of proteins and is released into the atmosphere by the burning of fossil fuels.

Biogeochemical Cycles: Introduction

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic (carbon-based) molecules (carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur) take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the earth's surface. The cycling of these elements is interconnected. Geologic processes, such as weathering, erosion, water drainage, and the movement of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**. It is important to remember that while matter and energy are processed in cycles, they aren't necessarily moving in a simple circle and don't really have a beginning or an end. Today, **anthropogenic** (human) activities are altering all major ecosystems and the biogeochemical cycles they drive.

The components of organic molecules are constantly being stored and recycled as part of their biogeochemical cycle. Water, which contains hydrogen and oxygen, is essential to all living processes. The hydrosphere is the area of the earth where water movement and storage occurs. Water can be liquid on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers) or exist as water vapor in the atmosphere. Carbon, found in all organic macromolecules, is an important constituent of fossil fuels. Nitrogen, a major component of our nucleic acids and proteins, is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

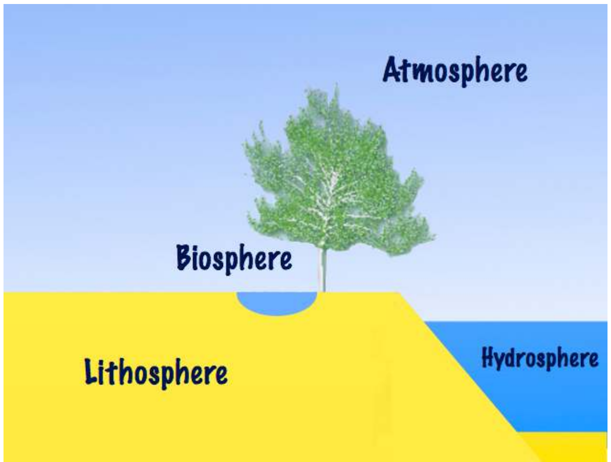


Figure 20.1.1:

Earth has a hydrosphere, where water movement and storage occurs. The cycle is important for leaching certain components of organic matter into rivers, lakes, and oceans, and is a reservoir for carbon.

The cycling of all of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

What pops into your mind when you hear the word *reservoir*? Probably a body of water, small or large, that is impounded behind a dam. In Earth systems science, the term ***reservoir*** is used for *a distinctive kind of place where a certain kind of material is stored, or resides, for some period of time*. This part of a cycle that holds an element or water for a short period of time is sometimes also called an **exchange pool,** or **pool**. For example, the atmosphere is an exchange pool for water. It usually holds water (in the form of water vapor) for just a few days. Some other examples of reservoirs or pools for water you will encounter in the course include glaciers; the soil layer; the aggregate of bodies of fresh water on the continents (rivers and lakes). Material moves into and out of reservoirs. *The rate at which a given material moves between reservoirs* is called a ***flux***. If the flux of material into and out of a given reservoir is the same for some period of time, that reservoir is said to be in a ***steady state***. Commonly, however, the flux in and the flux out are not equal.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) from the following sources

- Section 10.1 from *The Environment of the Earth's Surface* by John Southard Professor Emeritus (Earth, Atmospheric and Planetary Sciences) at Massachusetts Institute of Technology Sourced from MIT OpenCourseware
- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY
- **6.6: Water Cycle** by CK-12: Biology Concepts, is licensed CC BY-NC
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

- **12.1: Introduction - Systems, Cycles, Reservoirs, and Fluxes** by John Southard is licensed CC BY-NC-SA 4.0. Original source: https://ocw.mit.edu/courses/12-090-the-environment-of-the-earths-surface-spring-2007/.

20.2: The Water (Hydrologic) Cycle

Key Points

- Water cycling affects the climate, transports minerals, purifies water, and replenishes the land with fresh water.
- Water with a longer residence time, such as water in oceans and glaciers, is not available for short-term cycling, which occurs via evaporation.
- Surface water evaporates (water to water vapor) or sublimates (ice to water vapor), which deposits large amounts of water vapor into the atmosphere.
- Water vapor in the atmosphere condenses into clouds and is eventually followed by precipitation, which returns water to the earth's surface.
- Rain percolates into the ground, where it may evaporate or enter bodies of water.
- Surface runoff enters oceans directly or via streams and lakes.

The Water (Hydrologic) Cycle

Water is essential for all living processes. The human body is more than one-half water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on earth, 97.5 percent of it is non-potable salt water (Figure $20.2.1-2$). Of the remaining water, 99 percent is locked underground as water or as ice but this water is inconveniently located, mostly in Antarctica and Greenland. Shallow groundwater is the largest reservoir of usable fresh water. Less than one percent of fresh water is present in lakes and rivers, the most heavily used water resources. If all of world's water was shrunk to the size of 1 gallon, then the total amount of fresh water would be about 1/3 cup, and the amount of readily usable fresh water would be 2 tablespoons.

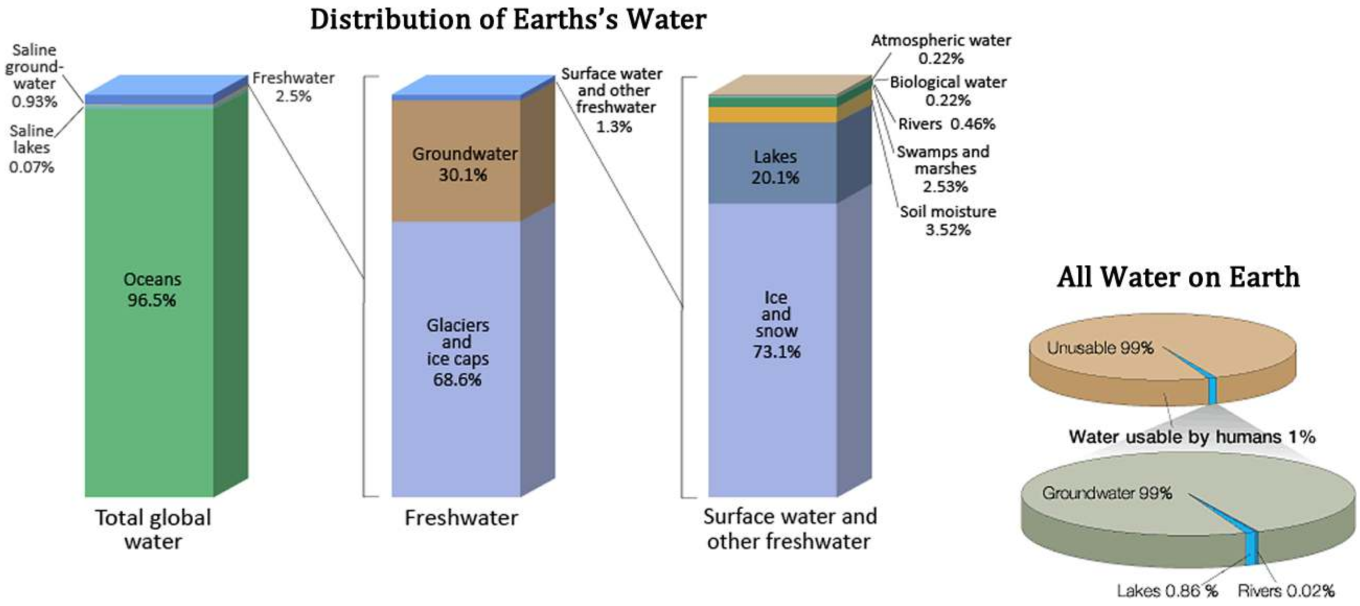


Figure $20.2.1$: Bar charts of the Distribution of Earth's Water including total global water, fresh water, and surface water and other fresh water and pie charts of water usable by humans and sources of usable water reveal that only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things. *Source: United States Geographical Survey Igor Skiklomanov's chapter "World fresh water resources" in Peter H. Gleick (editor), 1993, Water in Crisis: A Guide to the World's Fresh Water Resources.*

Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

Water is the only common substance that occurs naturally on Earth in three forms: solid, liquid and gas. The **hydrosphere** is the area of Earth where water movement and water storage occurs. **Water reservoirs** are the locations where water is stored. (Note that this term can also refer to artificial lakes created by dams.) Water is found as a liquid on the surface (rivers, lakes, oceans) and beneath the surface (groundwater), as ice (polar ice caps and glaciers), and as water vapor in the atmosphere. Figure 20.2.2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir.

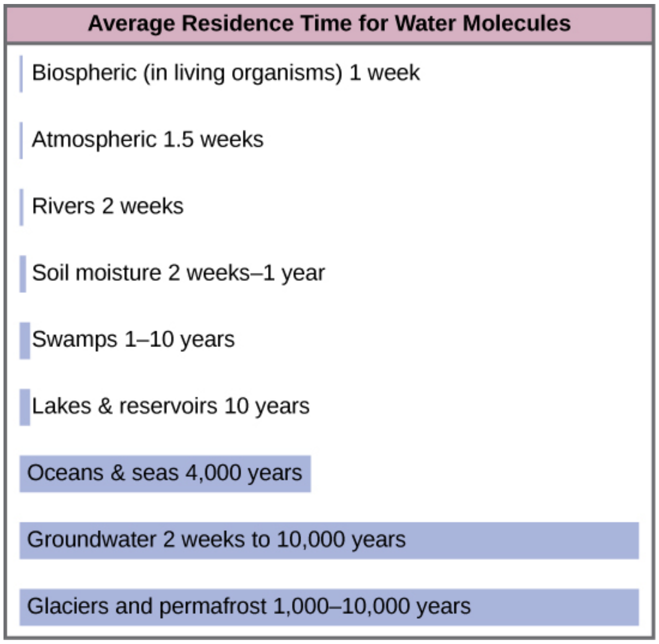


Figure 20.2.2: Average residence time that water remains in each reservoir. Water remains in organisms for about one week, in the atmosphere for 1.5 weeks, in rivers for two weeks, as soil moisture from two weeks to a year, in swamps for 1-10 years, in lakes for 10 years, in oceans and seas for 4,000 years, as groundwater for 2 weeks to 10,000 years, and in glaciers or as permafrost for 1,000-10,000 years. Image from OpenStax (CC-BY).

Water cycling is extremely important to ecosystem dynamics as it has a major influence on climate and, thus, on the environments of ecosystems. For example, when water evaporates, it takes up energy from its surroundings, cooling the environment. When it condenses, it releases energy, warming the environment. The evaporation phase of the cycle purifies water, which then replenishes the land with fresh water. The flow of liquid water and ice transports minerals across the globe. It is also involved in reshaping the geological features of the earth through processes including erosion and sedimentation.

The various processes that occur during the cycling of water are illustrated in Figure 20.2.4

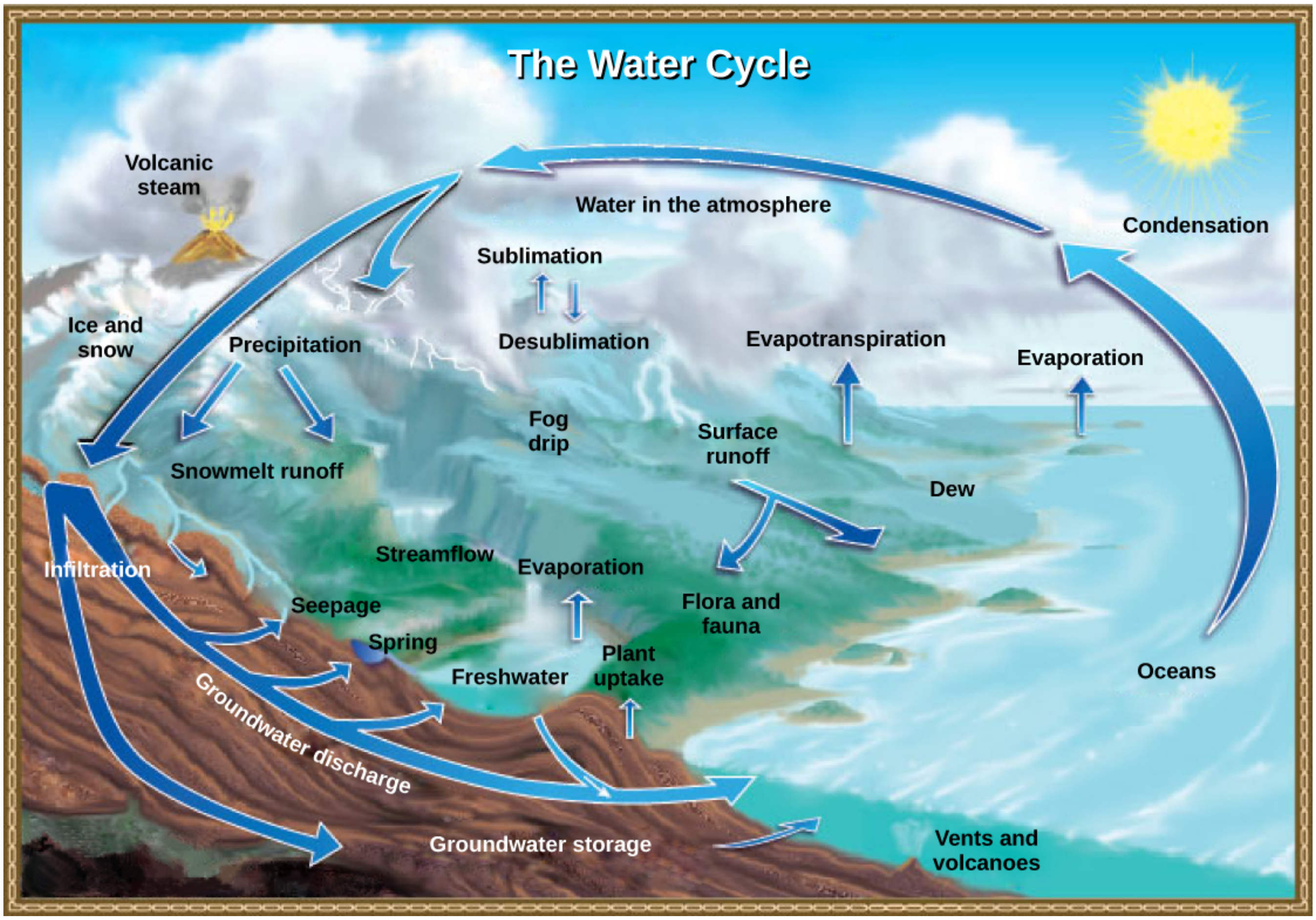


Figure 20.2.4: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean (credit: modification of work by John M. Evans and Howard Perlman, USGS).

The water cycle is driven by the Sun’s energy as it warms the oceans and other surface waters. This leads to evaporation (water to water vapor) of liquid surface water and sublimation (ice to water vapor) of frozen water, thus moving large amounts of water into the atmosphere as water vapor. As the water vapor rises in the atmosphere, it cools and condenses. **Condensation** is the process in which water vapor changes to tiny droplets of liquid water. Over time, this water vapor condenses into clouds as liquid or frozen droplets and eventually leads to precipitation (rain or snow), which returns water to Earth’s surface. Most precipitation falls into the ocean. Some frozen precipitation becomes part of ice caps and glaciers. These masses of ice can store frozen water for hundreds of years or longer. Rain reaching Earth’s surface may evaporate again, flow over the surface, or percolate into the ground. Most easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

In most natural terrestrial environments rain encounters vegetation before it reaches the soil surface. A significant percentage of water evaporates immediately from the surfaces of plants. What is left reaches the soil and begins to move down. Surface runoff will occur only if the soil becomes saturated with water in a heavy rainfall. **Infiltration** is the process through which water sinks into the ground and is determined by the soil or rock type through which water moves. Most water in the soil will be taken up by plant roots. The plant will use some of this water for its own metabolism, and some of that will find its way into animals that eat the plants, but much of it will be lost back to the atmosphere through a process known as **evapotranspiration**. Water enters the vascular system of the plant through the roots and evaporates, or transpires, through the stomata of the leaves. Water in the soil that is not taken up by a plant and that does not evaporate is able to percolate into the subsoil and bedrock. Here it forms groundwater.

Groundwater is a significant reservoir of fresh water. It exists in the pores between particles in sand and gravel, or in the fissures in rocks. Shallow groundwater flows slowly through these pores and fissures and eventually finds its way to a stream or lake where it becomes a part of the surface water again. Streams do not flow because they are replenished from rainwater directly; they flow because there is a constant inflow from groundwater below. Some groundwater is found very deep in the bedrock and can persist there for millennia. Most groundwater reservoirs, or **aquifers**, are the source of drinking or irrigation water drawn up through wells. In many cases these aquifers are being depleted faster than they are being replenished by water percolating down from above.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. More precipitation falls near the equator, and landmasses there are characterized by a tropical rainforest climate (Figure $20.2.5$). Less precipitation tends to fall near 20–30° north and south latitude, where the world's largest deserts are located. These rainfall and climate patterns are related to global wind circulation cells. The intense sunlight at the equator heats air, causing it to rise and cool, which decreases the ability of the air mass to hold water vapor and results in frequent rainstorms. Around 30° north and south latitude, descending air conditions produce warmer air, which increases its ability to hold water vapor and results in dry conditions. Both the dry air conditions and the warm temperatures of these latitude belts favor evaporation. Global precipitation and climate patterns are also affected by the size of continents, major ocean currents, and mountains.

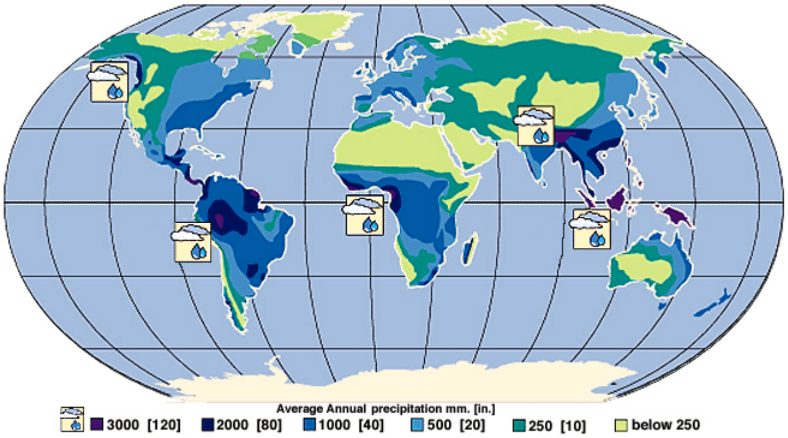
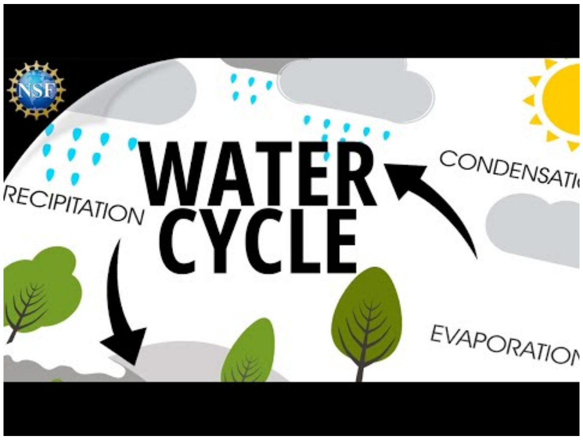


Figure $20.2.5$: The false-color map above shows the amount of rain that falls around the world. Areas of high rainfall include Central and South America, western Africa, and Southeast Asia. Since these areas receive so much rainfall, they are where most of the world's rainforests grow. Areas with very little rainfall usually turn into deserts. The desert areas include North Africa, the Middle East, western North America, and Central Asia. *Source: United States Geological Survey Earth Forum, Houston Museum Natural Science.*

An important part of the water cycle is how water varies in salinity, which is the abundance of dissolved ions in water. The saltwater in the oceans is highly saline, with about 35,000 mg of dissolved ions per liter of seawater. Evaporation is a distillation process that produces nearly pure water with almost no dissolved ions. As water vaporizes, it leaves the dissolved ions in the original liquid phase. Eventually, condensation forms clouds and sometimes precipitation. After rainwater falls onto land, it dissolves minerals in rock and soil, which increases its salinity. Rain and surface runoff are major ways in which minerals, including phosphorus and sulfur, are cycled from land to water. Freshwater (such as lakes, rivers, and near-surface groundwater) has a relatively low salinity.

The steps of the water cycle are also explained in the video below.



Human Interactions with The Water Cycle

Humans alter the water cycle by extracting large amounts of freshwater from surface waters as well as groundwater. Freshwater supply is one of the most important provisioning ecosystem services on which human well-being depends. By 2000, the rate of our water extraction from rivers and aquifers had risen to almost 4000 cubic kilometers per year. The greatest use of this water is for irrigation in agriculture, but significant quantities of water are also extracted for public and municipal use, as well as industrial applications and power generation (Figure 20.2.6.

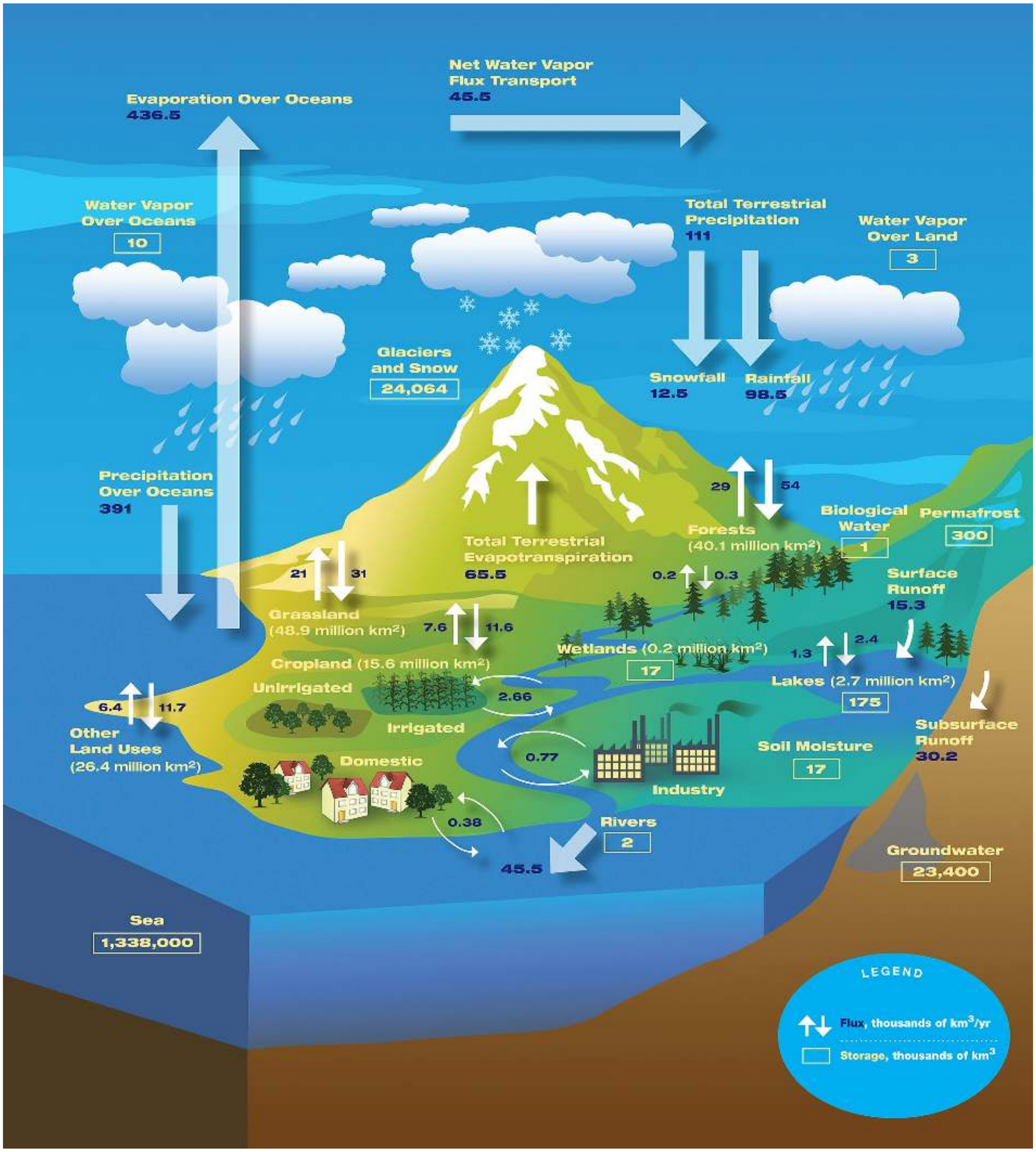


Figure 20.2.6: The water cycle including human use of water. "The Water Cycle" by Atmospheric Infrared Sounder is available in the public domain.

Other major human interventions in the water cycle involve changes in land cover and infrastructure development of river networks. As we have deforested areas for wood supply and agricultural development we have reduced the amount of vegetation, which naturally acts to trap precipitation as it falls and slow the rate of infiltration into the ground. As a consequence, surface runoff has increased. This, in turn, means flood peaks are greater and erosion is increased. Erosion lowers soil quality and deposits sediment in river channels, where it can block navigation and harm aquatic plants and animals. Where agricultural land is also drained these effects can be magnified. Urbanization also accelerates streamflow by preventing precipitation from filtering into the soil and shunting it into drainage systems.

Additional physical infrastructure has been added to river networks with the aim of altering the volume, timing, and direction of water flows for human benefit. This is achieved with reservoirs, weirs, aqueducts and diversion channels (Figure 20.2.7). For example, so much water is removed or redirected from the Colorado River in the western United States that, despite its considerable size, in some years it is dry before reaching the sea in Mexico. In an extreme example, the Aral Sea in Central Asia has decreased to only 10% of its initial size after water was diverted for agriculture (see this case study for more details).

Figure 20.2.7: The California Aqueduct carries water needed for agriculture from Northern California to Southern California. Image by USGS (public domain).

We also exploit waterways through their use for navigation, recreation, hydroelectricity generation and waste disposal. These activities, especially waste disposal, do not necessarily involve removal of water, but do have impacts on water quality and water flow that have negative consequences for the physical and biological properties of aquatic ecosystems.

The water cycle is key to the ecosystem service of climate regulation as well as being an essential supporting service that impacts the function of all ecosystems. Consider the widespread impacts on diverse natural and human systems when major droughts or floods occur. Consequently, human disruptions of the natural water cycle have many undesirable effects and challenge sustainable development. There are two major concerns. First, the need to balance rising human demand with the need to make our water use sustainable by reversing ecosystem damage from excess removal and pollution of water. Traditionally, considerable emphasis has been on finding and accessing more supply, but the negative environmental impacts of this approach are now appreciated, and improving the efficiency of water use is now a major goal. Second, there is a need for a safe water supply in many parts of the world, which depends on reducing water pollution and improving water treatment facilities.

Although **glaciers** represent the largest reservoir of fresh water, they generally are not used as a water source because they are located too far from most people (Figure 20.2.8). Melting glaciers do provide a natural source of river water and groundwater. During the last Ice Age there was as much as 50% more water in glaciers than there is today, which caused sea level to be about 100 m lower. Over the past century, sea level has been rising in part due to melting glaciers. If Earth's climate continues to warm, the melting glaciers will cause an additional rise in sea level.

Figure 20.2.8: Mountain Glacier in Argentina Glaciers are the largest reservoir of fresh water but they are not used much as a water resource directly by society because of their distance from most people. *Source: Luca Galuzzi – www.galuzzi.it.*

Further "Reading"

For more information on the water cycle you might want to watch this water cycle video from USGS.

Contributors and Attributions

Modified by Kyle Whittinghill and Melissa Ha from the following sources

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY from *Biology 2e* by OpenStax (CC-BY). Access for free at openstax.org.
- **6.6: Water Cycle** by CK-12: Biology Concepts, is licensed CC BY-NC
- Biogeochemical Cycles and the Flow of Energy in the Earth System and Water Cycle and Fresh Water Supply from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Water Cycle and Fresh Water Supply, Water Supply Problems and Solutions, and Biogeochemical Cycles from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- The Water Cycle, Water Use and Distribution, and Groundwater from *An Introduction to Geology* by Chris Johnson et al. (licensed under CC-BY-NC-SA)
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

20.3: The Carbon Cycle

Key Points

- Carbon is present in all organic molecules; carbon compounds contain large amounts of energy, which humans use as fuel.
- The biological carbon cycle is the rapid exchange of carbon among living things; autotrophs use carbon dioxide produced by heterotrophs to produce glucose and oxygen, which are then utilized by heterotrophs.
- The biogeochemical cycle occurs at a much slower rate than the biological cycle since carbon is stored in carbon reservoirs for long periods of time.
- Carbon dioxide from the atmosphere dissolves in water, combining with water molecules to form carbonic acid, which then ionizes to carbonate and bicarbonate ions.
- Most of the carbon in the ocean is in the form of bicarbonate ions, which can combine with seawater calcium to form calcium carbonate (CaCO3), a major component of marine organism shells.
- Carbon can enter the soil as a result of the decomposition of living organisms, the weathering of rocks, the eruption of volcanoes, and other geothermal systems.

The Carbon Cycle

Carbon, the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain energy, and many of these compounds from plants and algae have remained stored as fossilized carbon, which humans use as fuel. Since the 1800s, the use of fossil fuels has accelerated. As global demand for Earth’s limited fossil fuel supplies has risen since the beginning of the Industrial Revolution, the amount of carbon dioxide in our atmosphere has increased as the fuels are burned. This increase in carbon dioxide has been associated with climate change and is a major environmental concern worldwide.

The carbon cycle is most easily studied as two interconnected subcycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in Figure $20.3.1$. The overall effect is that carbon is constantly recycled in the dynamic processes taking place in the atmosphere, at the surface and in the crust of the earth. The vast majority of carbon resides as inorganic minerals in crustal rocks. Other **reservoirs** of carbon, places where carbon accumulates, include the oceans and atmosphere. Some of the carbon atoms in your body today may long ago have resided in a dinosaur's body, or perhaps were once buried deep in the Earth's crust as carbonate rock minerals.

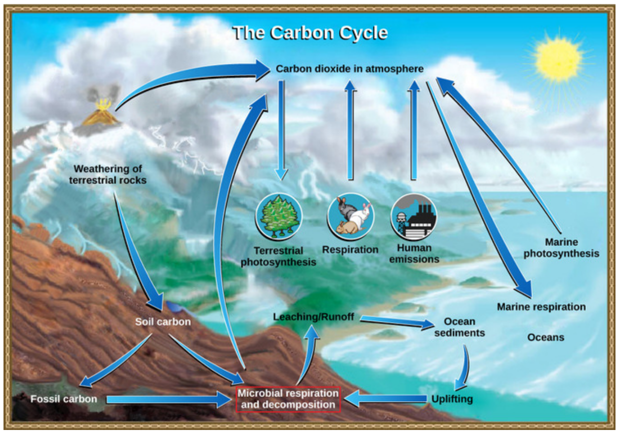


Figure $20.3.1$: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, while respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and human emissions bring this stored carbon back into the carbon cycle.

Carbon Cycles Quickly between Organisms and the Atmosphere

Cells run on the chemical energy found mainly in carbohydrate molecules, and the majority of these molecules are produced by one process: **photosynthesis.** Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build other organic molecules like complex carbohydrates (such as starch), proteins and lipids. The energy stored in the bonds to hold these molecules together is released when an organism breaks down food. Cells then use this energy to perform work, such as movement. The energy that is harnessed from photosynthesis enters the ecosystems of our planet continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on Earth. Photosynthesis also results in the release of oxygen into the atmosphere. In short, to eat and breathe humans depend almost entirely on the organisms that carry out photosynthesis.

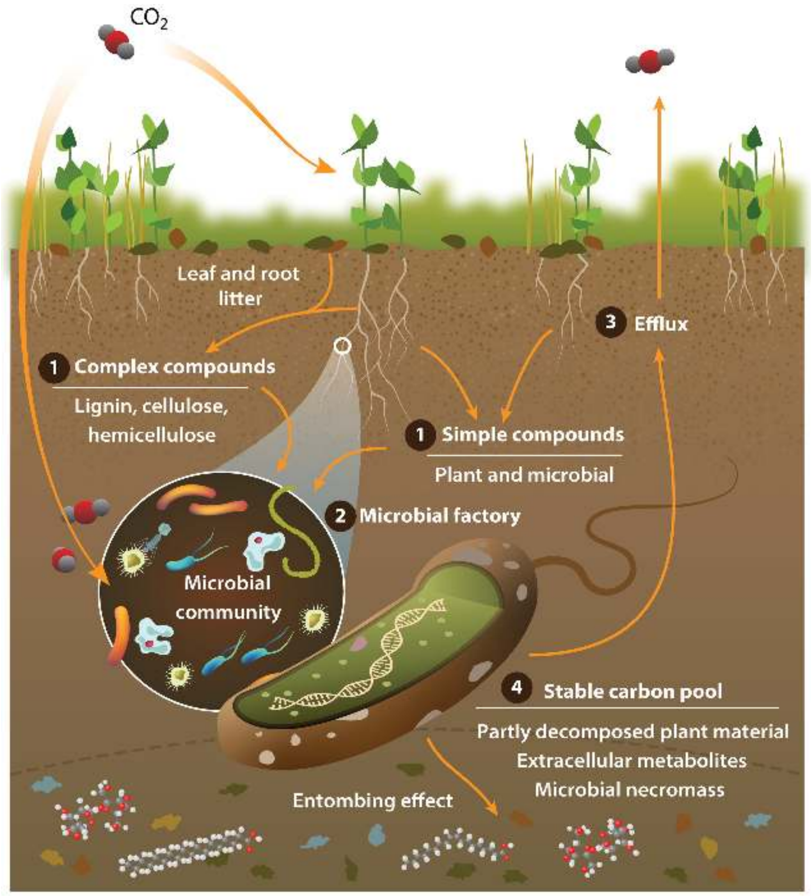
Figure 20.3.2: (a) Plants, (b) algae, and (c) certain bacteria, called cyanobacteria, are can carry out photosynthesis. Algae can grow over enormous areas in water, at times completely covering the surface (credit a: Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: “eutrophication&hypoxia”/Flickr; credit c: NASA; scale-bar data from Matt Russell).

Some organisms can carry out photosynthesis, whereas others cannot. An **autotroph** is an organism that can produce its own food. The Greek roots of the word autotroph mean “self” (auto) “feeder” (troph). Plants are the best-known autotrophs, but others exist, including certain types of bacteria and algae (Figure 20.3.2). Oceanic algae contribute enormous quantities of food and oxygen to global food chains. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high-energy compounds, such as glucose. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (bicarbonate, HCO_3^-).

Heterotrophs are organisms incapable of photosynthesis that must therefore obtain energy and carbon from food by consuming other organisms. The Greek roots of the word *heterotroph* mean “other” (*hetero*) “feeder” (*troph*), meaning that their food comes from other organisms. Even if the organism being consumed is another animal, it traces its stored energy back to autotrophs and the process of photosynthesis. Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Humans are heterotrophs, as are all animals and fungi. A deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer (Figure 20.3.3). Using this reasoning, all food eaten by humans can be traced back to autotrophs that carry out photosynthesis.

Figure 20.3.3: The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed (credit: Steve VanRiper, U.S. Fish and Wildlife Service).

Plants, animals, and other organisms break down organic molecules during the process of **aerobic cellular respiration**, which consumes oxygen and releases energy, water and carbon dioxide. Carbon dioxide is returned to the atmosphere during gaseous exchange. Another process by which organic material is recycled is the decomposition of dead organisms such as leaf and root litter. During this process, bacteria and fungi break down the complex organic compounds into simpler organic compounds (Figure 20.3.4). Decomposers may use aerobic or anaerobic respiration (decomposition with or without oxygen) thereby releasing carbon dioxide or methane (CH_4).



Naylor D, et al. 2020.
Annu. Rev. Environ. Resour. 45:29–59

Figure 20.3.4: "Soil carbon cycle through the microbial loop" by Dan Naylor, Natalie Sadler, Arunima Bhattacharjee, Emily B. Graham, Christopher R. Anderton, Ryan McClure, Mary Lipton, Kirsten S. Hofmockel and Janet K. Jansson is licensed under CC BY-SA 4.0.

Photosynthesis and respiration are actually reciprocal to one another with regard to the cycling of carbon: photosynthesis removes carbon dioxide from the atmosphere and respiration returns it (Figure 20.3.5). A significant disruption of one process can therefore affect the amount of carbon dioxide in the atmosphere.

Photosynthesis Equation			
Carbon dioxide +	Water $\xrightarrow{\text{SUNLIGHT}}$	Sugar +	Oxygen
$6CO_2$	$6H_2O$	$C_6H_{12}O_6$	$6O_2$

Figure 20.3.5: This equation means that six molecules of carbon dioxide (CO_2) combine with six molecules of water (H_2O) in the presence of sunlight. This produces one molecule of glucose ($C_6H_{12}O_6$) and six molecules of oxygen (O_2).

Within marine ecosystems (Figure 20.3.6) phytoplankton photosynthesize and then are either decomposed by bacteria or consumed by zooplankton.

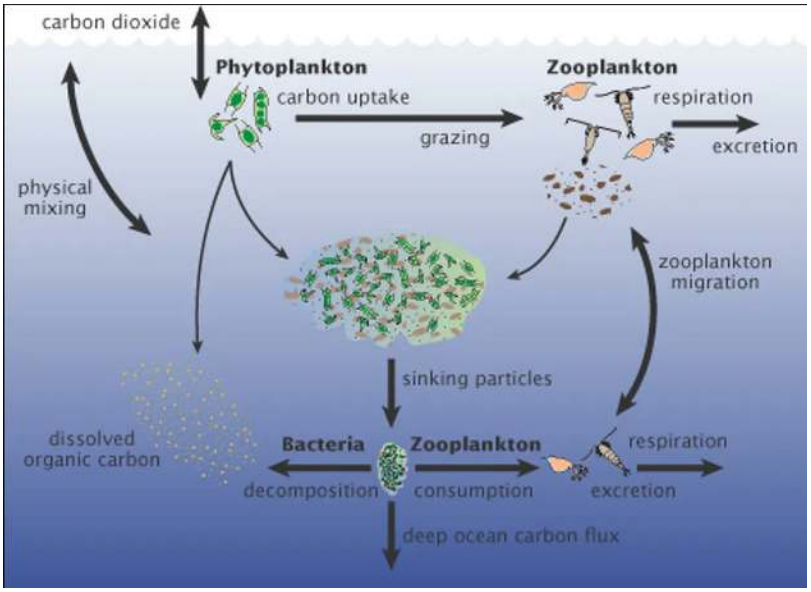


Figure 20.3.6: "Marine Carbon Cycle" by NASA is available in the public domain.

Cellular respiration is only one process that releases carbon dioxide. Physical processes, such as the eruption of volcanoes and release from **hydrothermal vents** (openings in the ocean floor) add carbon dioxide to the atmosphere. Additionally, the **combustion** of wood and fossil fuels releases carbon dioxide. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each.

Carbon Cycles Slowly between Land and the Ocean

The movement of carbon through land, water, and air is complex, and, in many cases, it occurs much more slowly geologically than the movement between living organisms (Figure 20.3.7). Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, rocks (including fossil fuels), and Earth’s interior.

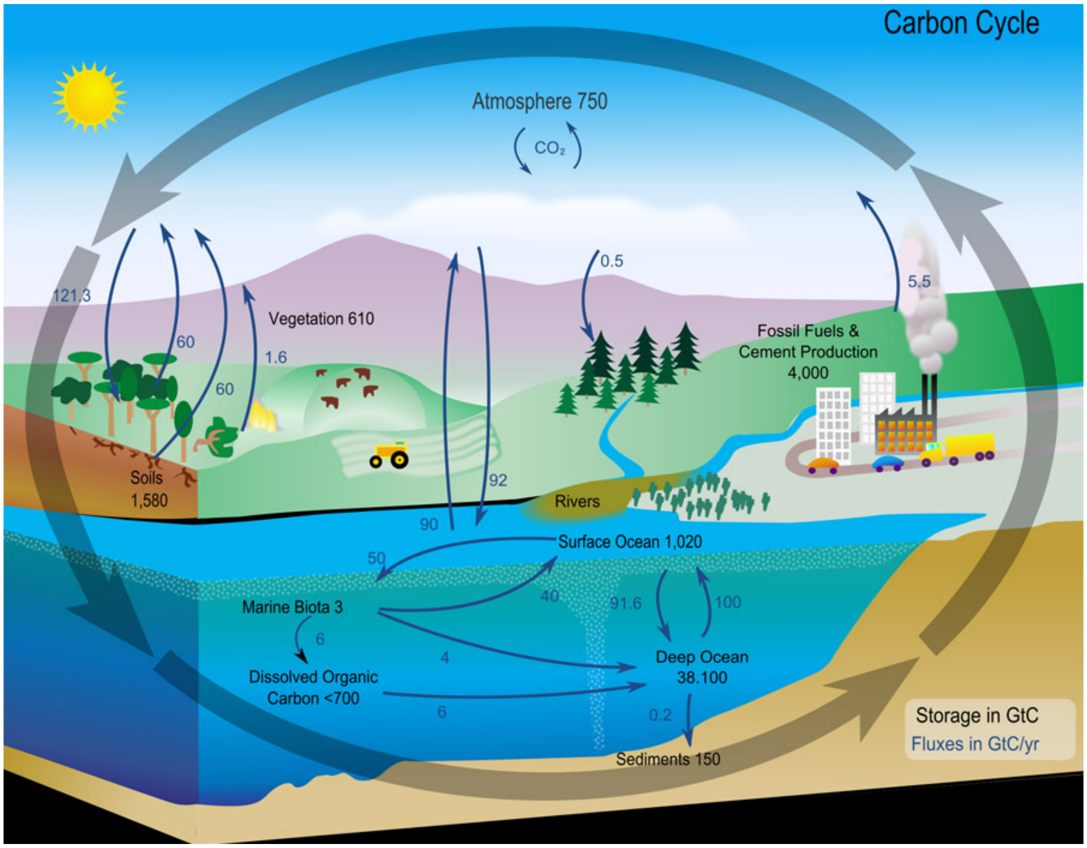
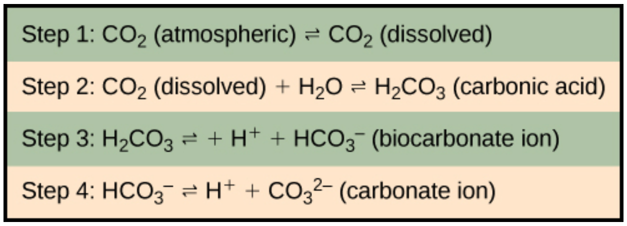


Figure 20.3.7: Global Carbon Cycle including storage and fluxes. "Carbon Cycle" by NASA is available in the public domain.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide that is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each, and each one affects the other reciprocally. Atmospheric carbon dioxide also dissolves in the ocean, reacting with water molecules to form carbonic acid and then dissociating into bicarbonate (HCO_3^-) and carbonate ions (CO_3^{2-}). More than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with calcium ions in the seawater to form calcium carbonate ($CaCO_3$), a major component of the shells of marine organisms. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.


Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)

Step 2: CO_2 (dissolved) $+$ H_2O $\rightleftharpoons$ H_2CO_3 (carbonic acid)

Step 3: H_2CO_3 $\rightleftharpoons$ $+$ H^+ $+$ HCO_3^- (biocarbonate ion)

Step 4: HCO_3^- $\rightleftharpoons$ H^+ $+$ CO_3^{2-} (carbonate ion)

Figure 20.3.8: Formation of bicarbonate---carbon dioxide reacts with water to form bicarbonate and carbonate ions.

On land, carbon is stored in soil as organic carbon as a result of the decomposition of living organisms or from **weathering** of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Partially decomposed plants and algae are sometimes buried and compressed between layers of sediments. After millions of years fossil fuels such as coal, oil, and natural gas are formed. Fossil fuels are considered a non-renewable resource because their use far exceeds their rate of formation. A non-renewable resource is either regenerated very slowly or not at all.

Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within Earth by the process of **subduction**: the movement of one tectonic plate beneath another. The ocean sediments are subducted by the actions of **plate**

tectonics, melted and then returned to the surface during volcanic activity. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.Plate tectonics can also cause **uplifting**, returning ocean sediments to land.

Importance of the Carbon Cycle

The carbon cycle is crucially important to the biosphere. If not for the recycling processes, carbon might long ago have become completely sequestered in crustal rocks and sediments, and life would no longer exist (Figure $20.3.9$). Photosynthesis not only makes energy and carbon available to higher trophic levels, but it also releases gaseous oxygen (O_2). Gaseous oxygen is necessary for cellular respiration to occur. Photosynthetic bacteria were likely the first organisms to perform photosynthesis, dating back 2-3 billion years ago. Thanks to their activity, and a diversity of present-day photosynthesizing organisms, Earth's atmosphere is currently about 21% O_2. Also, this O_2 is vital for the creation of the ozone layer, which protects life from harmful ultraviolet radiation emitted by the sun. Ozone (O_3) is created from the breakdown and reassembly of O_2.

Figure $20.3.9$: Decomposers will break down the organic compounds in this fallen tree at Cliffs of the Neuse State Park in Wayne County, North Carolina, releasing carbon dioxide into the atmosphere. Decomposition ensures that carbon dioxide will be available in the atmosphere for photosynthetic organisms, which then provide carbon for consumers. "Fallen" by Gerry Dincher is licensed under CC BY-SA 2.0.

The global carbon cycle contributes substantially to the provisioning ecosystem services upon which humans depend. We harvest approximately 25% of the total plant biomass that is produced each year on the land surface to supply food, fuel wood and fiber from croplands, pastures and forests. In addition, the global carbon cycle plays a key role in regulating ecosystem services because it significantly influences climate via its effects on atmospheric CO_2 concentrations.

Human Alteration of the Carbon Cycle

Atmospheric CO_2 concentration increased from 280 parts per million (ppm) to 413 ppm between the start of industrial revolution in the late eighteenth century and 2020. This reflected a new flux in the global carbon cycle—anthropogenic CO_2 emissions—where humans release CO_2 into the atmosphere by burning fossil fuels and changing land use. Fossil fuel burning takes carbon from coal, gas, and oil reserves, where it would be otherwise stored on very long time scales, and introduces it into the active carbon cycle. Land use change releases carbon from soil and plant biomass pools into the atmosphere, particularly through the process of deforestation for wood extraction or conversion of land to agriculture. Carbon dioxide is also added to the atmosphere by the breeding and raising of livestock. In 2018, the additional flux of carbon into the atmosphere from anthropogenic sources was estimated to be 36.6 gigatons of carbon (GtC = 1 billion tons of carbon)—a significant disturbance to the natural carbon cycle that had been in balance for several thousand years previously. High levels of carbon dioxide in the atmosphere cause warming that results in climate change.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) and Melissa Ha from the following sources:

- Biogeochemical Cycles, Energy, and Energy Enters Ecosystems Through Photosynthesis from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Carbon Cycle from *Biology* by John W. Kimball (licensed under CC-BY)
- Energy Flow through Ecosystems from *General Biology* by OpenStax (licensed under CC-BY)
- Soil and Sustainability and Biogeochemical Cycles and the Flow of Energy in the Earth System from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Cycling of Matter from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Nutrient Cycles from *Life Sciences Grade 10* by Siyavula (CC-BY)

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY
- Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0.
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

- **20.2: Biogeochemical Cycles** by OpenStax is licensed CC BY 4.0.

20.4: The Nitrogen Cycle

Key Points

- Bacteria, such as cyanobacteria, convert nitrogen into nitrogen gas via nitrogen fixation.
- Nitrogen fixation occurs in three steps: ammonification, nitrification, and denitrification.
- Human activity can release nitrogen into the environment by the combustion of fossil fuels and by the use of artificial fertilizers in agriculture.
- Atmospheric nitrogen is responsible for acid rain, the release of greenhouse gasses, and eutrophication.
- Nitrogen fixation can be performed by marine bacteria; nitrogen falls to the ocean floor as sediment and is then moved to land, becoming incorporated into terrestrial rock.

Key Terms

- **denitrification**: process of converting nitrates into nitrogen gas, especially by the action of bacteria
- **nitrification**: the conversion of ammonium into nitrites (NO2−) by nitrifying bacteria
- **ammonification**: the formation of ammonia or its compounds from nitrogenous compounds, especially as a result of bacterial decomposition

The Nitrogen Cycle

All organisms require nitrogen because it is an important component of nucleic acids, proteins, and other organic molecules. Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly-bonded, triple-covalent N_2), even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world through **nitrogen fixation (**Figure $20.4.1-2$, the process of converting nitrogen gas into ammonia (NH_3), which spontaneously becomes ammonium (NH_4^+). Ammonium is found in bodies of water and in the soil (figure $20.4.1-2$).

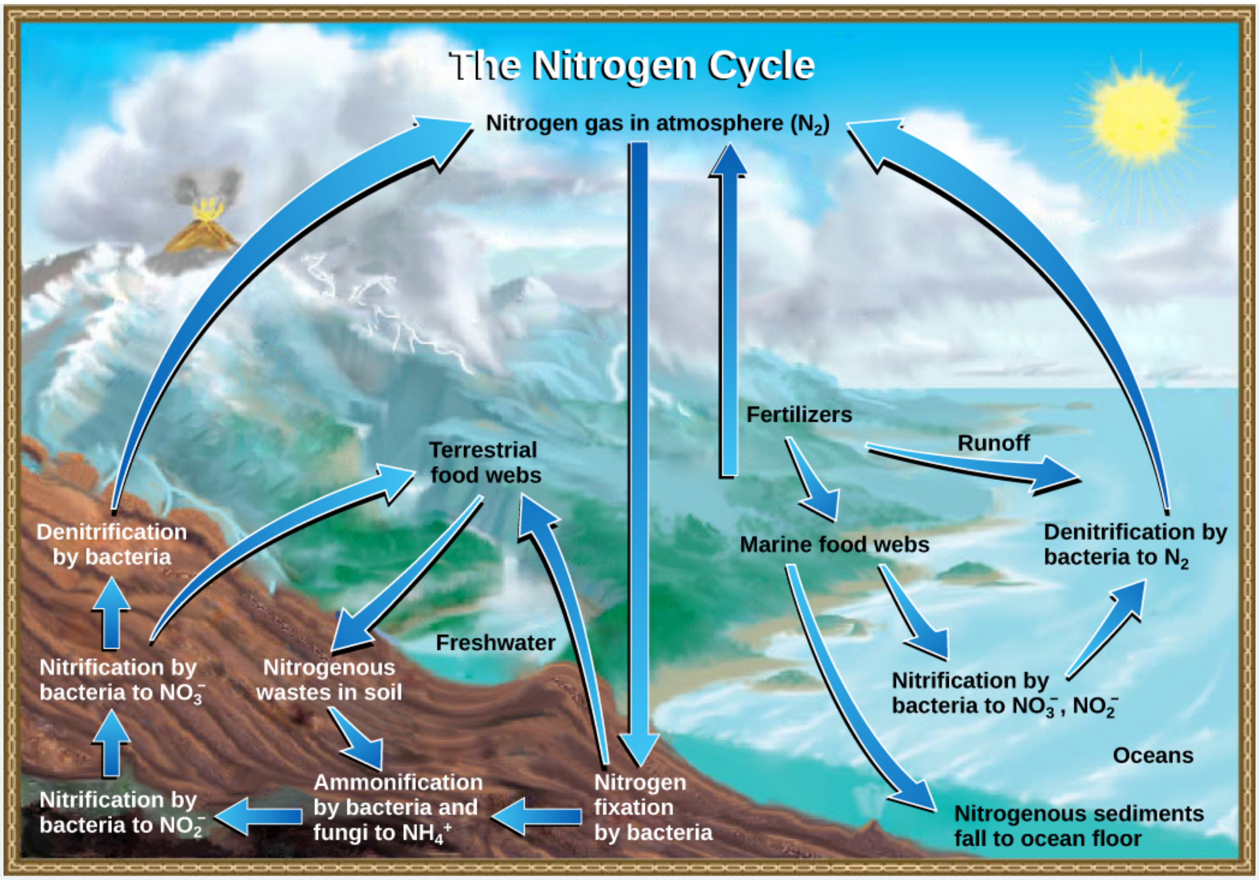


Figure 20.4.1: Nitrogen enters the living world from the atmosphere through nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need (credit: modification of work by John M. Evans and Howard Perlman, USGS).

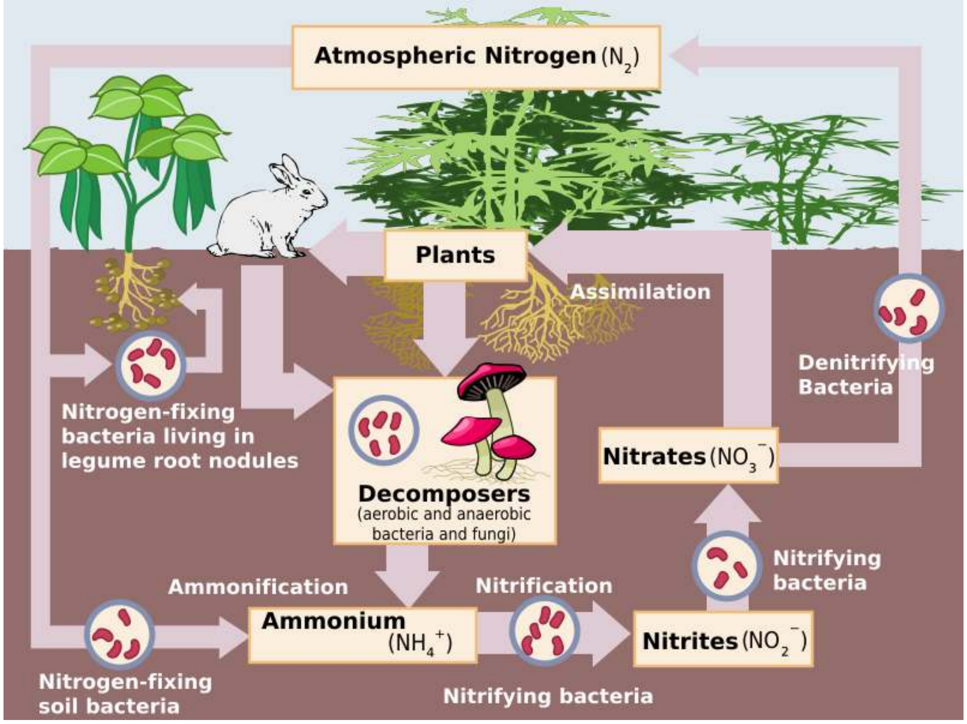


Figure 20.4.2: In the nitrogen cycle, nitrogen-fixing bacteria in the soil or legume root nodules convert nitrogen gas (N_2) from the atmosphere to ammonium (NH_4^+). Nitrification occurs when bacteria convert ammonium to nitrites (NO_2^-) and then to nitrates (NO_3^-). Nitrates re-enter the atmosphere as nitrogen gas through denitrification by bacteria. Plants assimilate ammonium and nitrates, producing organic nitrogen, which is available to consumers. Decomposers, including aerobic and anaerobic bacteria and fungi, break down organic nitrogen and release ammonium through ammonification. "Nitrogen cycle" by Johann Dréo & Raeky is licensed under CC BY-SA 3.0.

Three processes are responsible for most of the nitrogen fixation in the biosphere. The first is **atmospheric fixation** by lightning. The enormous energy of lightning breaks nitrogen molecules and enables their atoms to combine with oxygen in the air forming nitrogen oxides. These dissolve in rain, forming nitrates, that are carried to the earth. Atmospheric nitrogen fixation probably contributes some 5-8% of the total nitrogen fixed. The second process is **industrial fixation.** Under great pressure, at a temperature of 600°C (1112°F), and with the use of a **catalyst** (which facilitates chemical reactions), atmospheric nitrogen and hydrogen can be combined to form ammonia (NH_3). Ammonia can be used directly as fertilizer, but most of it is further processed to urea and ammonium nitrate (NH_4NO_3).

The third process is **biological fixation** by certain free-living or symbiotic bacteria, which incorporate nitrogen into their macromolecules. Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Nitrogen-fixing cyanobacteria are essential to maintaining the fertility of semi-aquatic environments like rice paddies. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers. Some nitrogen fixing bacteria form a symbiotic relationship with plants in the legume family, which includes beans, peas, soybeans, alfalfa, and clovers (figure 20.4.3). *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Some nitrogen-fixing bacteria even establish symbiotic relationships with animals, e.g., termites and "shipworms" (wood-eating bivalves). Although the first stable product of the process is ammonia, this is quickly incorporated into protein and other organic nitrogen compounds.

Figure 20.4.3: Nitrogen-fixing bacteria live in the spherical nodules of this soybean root. Image by United Soybean Board is licensed under CC BY 2.0.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. Plants and other producers directly use ammonium and nitrates to make organic molecules through the process of **assimilation (**Figure 20.4.2). This nitrogen is now available to consumers. Consumers excrete organic nitrogen compounds that return to the environment. Additionally dead organisms at each trophic level contain organic nitrogen.

As shown in Figure 20.4.2, the nitrogen that enters living systems by nitrogen fixation is eventually converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the **ammonification** or **nitrogen mineralization** process converts nitrogenous waste from living organisims or the remains of dead organisms into ammonium (NH_4^+) by certain bacteria and fungi. Second, this ammonium is then converted to nitrites (NO_2^-) and then nitrates (NO_3^-) by nitrifying bacteria and archaea, such as *Nitrosomonas* or *Nitrobacter*, through the process of **nitrification**. In addition, both soil and the ocean contain **archaeal** microbes, assigned to the Crenarchaeota, that convert ammonia to nitrites. They are more abundant than the nitrifying bacteria and may turn out to play an important role in the nitrogen cycle.. Like ammonium, nitrites and nitrates are found in water and the soil. Some nitrates are converted back into nitrogen gas, which is released into the atmosphere. The process, called **denitrification**, is conducted by bacteria, such as *Pseudomonas* and *Clostridium*, which use nitrate when decomposing organic matter in the absence of oxygen. In the process of denitrification several intermediates are formed and may be released to the atmosphere including nitric oxide (NO) and nitrous oxide (N_2O, a greenhouse gas). Under anaerobic conditions in marine and freshwater systems other species of bacteria are able to oxidize ammonia with nitrite forming nitrogen gas in a process called **anammox** (anaerobic ammonia oxidation).

In marine ecosystems, nitrogen compounds created by bacteria, or through decomposition, collects in ocean floor sediments. It can then be moved to land in geologic time by uplift of Earth’s crust and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[1]

Human Alteration of the Nitrogen Cycle

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers (which contain nitrogen and phosphorus compounds) in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Humans are also increasing the amount of reactive nitrogen in the environment by the cultivation of nitrogen fixing crops, such as soybeans. If the nitrogen fixation from leguminous crops (e.g. beans, alfalfa) is included, then the anthropogenic flux of nitrogen from the atmosphere to the land exceeds natural fluxes to the land. Atmospheric nitrogen (other than N_2) is associated with several effects on Earth’s ecosystems including the production of **acid deposition** (as nitric acid, HNO_3), also known as acid rain. Acid deposition damages healthy trees, destroys aquatic systems and erodes building materials such as marble and limestone. Like carbon dioxide, nitrous oxide (N_2O) is a greenhouse gas, potentially causing climate change when released during denitrification.

Humans are primarily dependent on the nitrogen cycle as a supporting ecosystem service for crop and forest productivity. Nitrogen fertilizers are added to enhance the growth of many crops and plantations (figure $20.4.4$). The enhanced use of fertilizers in agriculture was a key feature of the green revolution that boosted global crop yields in the 1970s. The industrial production of nitrogen-rich fertilizers has increased substantially over time and now matches more than half of the input to the land from biological nitrogen fixation (90 megatons = 1 million tons of nitrogen each year). If the nitrogen fixation from legume crops is included, then the anthropogenic flux of nitrogen from the atmosphere to the land exceeds natural fluxes to the land. Fertilizers are washed into lakes, streams, and rivers by surface runoff, resulting in saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the overgrowth of algae, the depletion of oxygen, and death of aquatic fauna. Excess nitrates in water supplies have also been linked to human health problems.

Figure 20.4.4: Fertilizer containing nitrogen is conventionally applied at large scales in agriculture. Image by Bob Nichols, USDA Natural Resources Conservation Service is available in the public domain.

Efforts to reduce nitrogen pollution focus on increasing the efficiency of synthetic fertilizer use, altering feeding of animals to reduce nitrogen content in their excreta, and better processing of livestock waste and sewage sludge to reduce ammonia release. At the same time, increasing demand for food production from a growing global population with a greater appetite for meat is driving greater total fertilizer use, so there is no guarantee that better practices will lead to a reduction in the overall amount of nitrogen pollution.

References

1 Morford, S.L., Houlton, B.Z., & Dahlgren, R.A. (2011). Increased forest ecosystem carbon and nitrogen storage from nitrogen rich bedrock. *Nature, 477*(7362), pp. 78–81.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) and Melissa Ha from the following sources:

- Biogeochemical Cycles, Energy, and Energy Enters Ecosystems Through Photosynthesis from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Nitrogen Cycle from *Biology* by John W. Kimball (licensed under CC-BY)
- Soil and Sustainability and Biogeochemical Cycles and the Flow of Energy in the Earth System from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Cycling of Matter from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Nutrient Cycles from *Life Sciences Grade 10* by Siyavula (CC-BY)

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY
- Biogeochemical Cycles and the Flow of Energy in the Earth System from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

20.5: The Phosphorus Cycle

Key Points

- Phosphorus, a major component of nucleic acid and phospholipids, also makes up the supportive components of our bones; it is often necessary for growth in aquatic ecosystems.
- Phosphates (PO_4^{3-}) are sent into rivers, lakes, and the ocean by leaching and natural surface runoff.
- Phosphate-containing ocean sediments slowly move to land by the uplifting of areas of the earth's surface.

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes. It is a major component of nucleic acids, both DNA and RNA; of phospholipids, the major component of cell membranes; and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems.

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the earth's surface (Figure $20.5.1$). Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

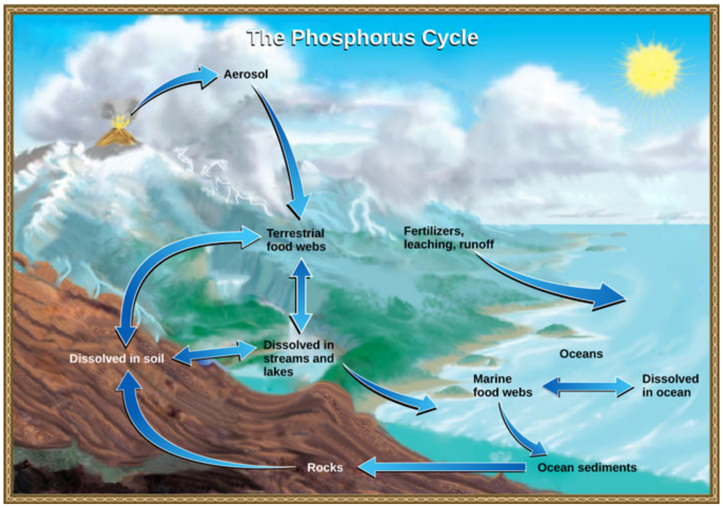


Figure $20.5.1$: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment.

Marine birds play a unique role in the phosphorous cycle. These birds take up phosphorous from ocean fish. Their droppings on land (**guano**) contain high levels of phosphorous and are sometimes mined for commercial use. A 2020 study estimated that the **ecosystem services** (natural processes and products that benefit humans) provided by guano are worth $470 million per year.

Weathering of rocks releases phosphates into the soil and bodies of water. Plants can assimilate phosphates in the soil and incorporate it into organic molecules, making phosphorus available to consumers in terrestrial food webs. Waste and dead organisms are decomposed by fungi and bacteria, releasing phosphates back into the soil. Some phosphate is leached from the soil, entering into rivers, lakes, and the ocean. Primary producers in aquatic food webs, such as algae and photosynthetic bacteria, assimilate phosphate, and organic phosphate is thus available to consumers in aquatic food webs. Similar to terrestrial food webs, phosphorus is reciprocally exchanged between phosphate dissolved in the ocean and organic phosphorus in marine organisms.

The movement of phosphorus from rock to living organisms is normally a very slow process, but some human activities speed up the process. Phosphate-bearing rock is often mined for use in the manufacture of fertilizers and detergents. This commercial production greatly accelerates the phosphorous cycle. In addition, runoff from agricultural land and the release of sewage into water systems can cause a local overload of phosphate. The increased availability of phosphate can cause overgrowth of algae. This reduces the oxygen level, causing eutrophication and the destruction of other aquatic species.

The processes of plant production and decomposition are important for biogeochemical cycling of phosphorus within terrestrial and aquatic ecosystems, just as they are for the nitrogen and carbon cycles. Figure $20.5.2$ shows a close up of the phosphorus (and nitrogen) cycling within a wetland controlled by plant productivity and decomposition.

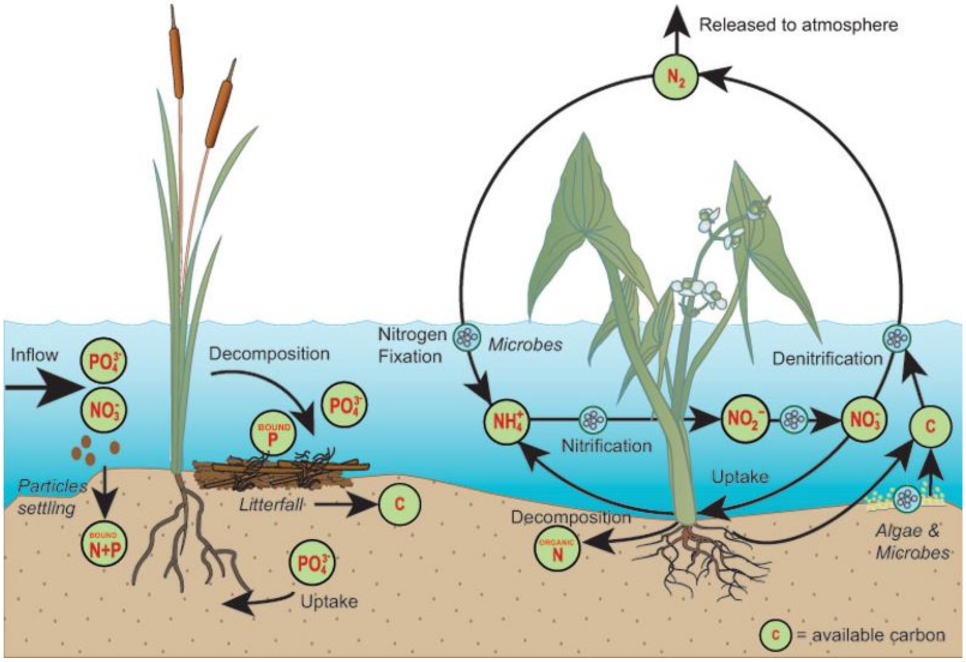


Figure $20.5.2$: A simplified diagram of phosphorus and nitrogen cycles in a wetland. *Source: Kadlec and Knight (1996), CC BY-SA 4.0, via Wikimedia Commons.*

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) and Melissa Ha from the following sources:

- Biogeochemical Cycles, Energy, and Energy Enters Ecosystems Through Photosynthesis from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Energy Flow through Ecosystems from *General Biology* by OpenStax (licensed under CC-BY)
- Soil and Sustainability and Biogeochemical Cycles and the Flow of Energy in the Earth System from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Cycling of Matter from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Nutrient Cycles from *Life Sciences Grade 10* by Siyavula (CC-BY)
- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

20.6: Eutrophication and Dead Zones

Key Points

- Excess phosphorus and nitrogen in the ecosystem leads to the death of many organisms, causing dead zones.
- Dead zones are caused by by eutrophication, oil spills, dumping of toxic chemicals, and other human activities.

Key Terms

- **eutrophication**: process whereby excess levels of nitrogen or phosphorus cause excessive growth of microorganisms, depleting dissolved oxygen levels and kill ecosystem fauna
- **dead zone**: an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; caused by excessive nutrient pollution

Eutrophication and Dead Zones

Nutrients in soil and water are generally beneficial when they exist at naturally occurring levels. Nitrogen fertilizers have been applied to farm fields for decades in order to maximize production of agricultural lands. However, an unintended consequence is that the same nutrients can be detrimental to aquatic ecosystems when introduced excessively for agricultural or other purposes. Nitrogen (N) and Phosphorus (P) are introduced by fertilizers that are used intensively in agriculture, as well as golf courses and some lawns and gardens. Farm animal waste and sewage also provide large amounts of reactive N and P. Phosphorus was formerly used heavily as an additive in laundry and dishwater detergents, but since the 1970's it has been phased out in both through a combination of state and federal regulations. Overall, our modern society has altered the global N and P cycles such that there is an overabundance in many settings.

Excessive nutrients (not utilized) are often washed into drainage ways, streams, and rivers during rainfall and storm events. **Eutrophication** occurs when excess phosphorus and nitrogen from fertilizer runoff or sewage causes excessive growth of algae. Algal blooms that block light and therefore kill aquatic plants in rivers, lakes, and seas. The subsequent death and decay of these organisms depletes dissolved oxygen, which leads to the death of aquatic organisms such as shellfish and fish. This process is responsible for **dead zones**, large areas in lakes and oceans near the mouths of rivers that are periodically depleted of their normal flora and fauna, and for massive fish kills, which often occur during the summer months (figure $20.6.1$). There are more than 500 dead zones worldwide. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

One of the worst dead zones is off the coast of the United States in the Gulf of Mexico (figure $20.6.1$). Fertilizer runoff from the Mississippi River basin created a dead zone, which reached its peak size of 8,776 square miles in 2017. The Mississippi River dumps high-nutrient runoff from its drainage basin that includes vast agricultural lands in the American Midwest. Increased algal growth produced by these nutrients has affected important shrimp fishing grounds in the Gulf. The primary source of the nutrients is the heavily tile-drained areas of farmland in the Midwest corn and soybean belt (SW Minnesota, N Iowa, NE Illinois, N Indiana and NW Ohio). Improved soil drainage systems over the past century or more have allowed for effective transport of nitrate compounds as stormwater runoff into drainage basins (Ohio River, Wabash River, Illinois River, Missouri River, etc.) that feed into the Mississippi River. Prior to drainage, these wetlands would also have removed nutrients through denitrification and other biogeochemical processes. In other words, the same drainage tiles that allow for the agricultural benefit of having rich bottomland/wetland soils in production, have the disadvantage of increased and more rapid movements of nitrate solutes to the Gulf of Mexico. Such large-scale problems, across state governmental boundaries, can only be fully addressed in the future with a national system of incentives, regulations, or laws.

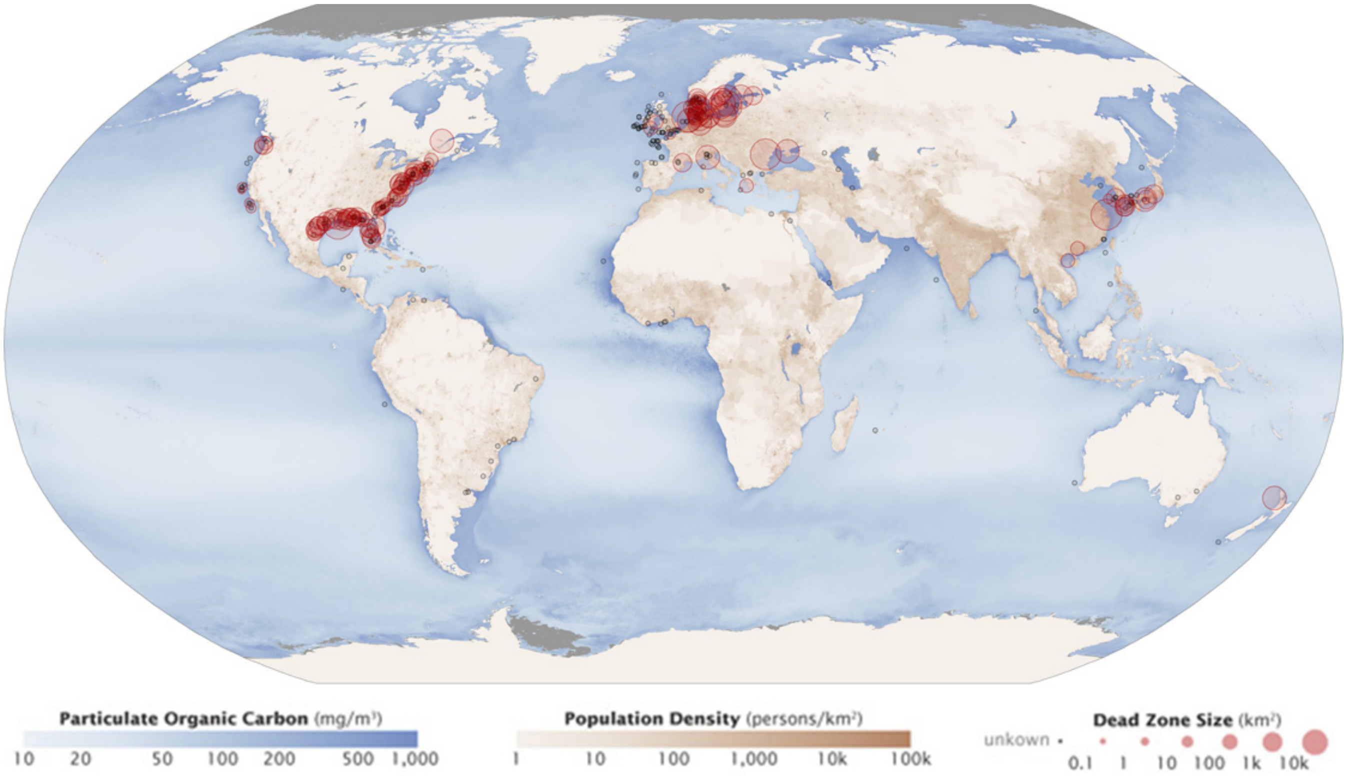


Figure 20.6.1: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. This map shows dead zones around the world in 2008. Worldwide, large dead zones are found in coastal areas of high population density (credit: NASA Earth Observatory).

In addition to fertilizers, nitrogen inputs to watersheds can also include atmospheric deposition, livestock waste, and sewage, but nitrogen fertilizers comprise a significant majority of the input to monitored streams, particularly in springtime when much fertilizer is applied. Possible solutions to this problem include encouraging farmers to apply a more limited quantity of fertilizer in the spring (only as much as necessary), rather than in the fall, to allow for considerably less time for stormwater or meltwater runoff. Other solutions include maintaining cover crops, or restoring wetlands in key locations to contain nitrate losses. An overall strategy that limits the excess capacity of nutrients can simultaneously benefit farmers (by limiting cost), the ecology of stream watersheds and coastal ecosystems (also locally stressed by oil spills and other pollution). Over the long term, more efforts will need to be made in the Mississippi River Basin, and globally in similarly stressed agricultural or urban watersheds (figure 20.6.1), to improve the health and sustainability of our soil, land, and aquatic ecosystems.

Everyday Connection: Chesapeake Bay

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms (Figure 20.6.2). Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

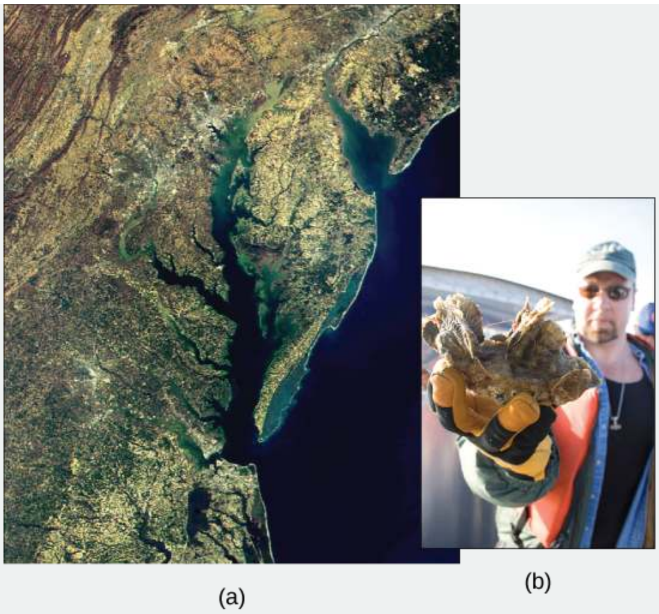


Figure 20.6.2: This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army).

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overexploitation. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Suggested Supplementary Reading

Bruckner, M. 2018. The Gulf of Mexico Dead Zone. [Website]

References

Cell Press. (2020, August 6). Researchers hope to save seabirds by calculating the value of their excrement. Retrieved August 7, 2020 from *ScienceDaily*.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) and Melissa Ha from the following sources:

- Biogeochemical Cycles, Energy, and Energy Enters Ecosystems Through Photosynthesis from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Carbon Cycle and Nitrogen Cycle from *Biology* by John W. Kimball (licensed under CC-BY)
- Energy Flow through Ecosystems from *General Biology* by OpenStax (licensed under CC-BY)
- Soil and Sustainability and Biogeochemical Cycles and the Flow of Energy in the Earth System from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors (licensed under CC-BY). Download for free at CNX.
- Cycling of Matter from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Nutrient Cycles from *Life Sciences Grade 10* by Siyavula (CC-BY)

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

  20.2: Biogeochemical Cycles by OpenStax, is licensed CC BY

20.7: The Sulfur Cycle

Key Points

- Sulfur is an essential element for the macromolecules of living things since it determines the 3-D folding patterns of proteins.
- Chemosynthesis using sulfur is way some autotrophs create sugars.
- On land, sulfur enters the atmosphere via acid rain, fallout, the weathering of rocks, decomposition of organic materials, and geothermal vents.
- Sulfur enters the ocean via runoff, fallout, and underwater geothermal vents; some marine ecosystems also rely on chemoautotrophs as a sulfur source.
- The burning of fossil fuels increases the amount of sulfide in the atmosphere and causes acid rain.
- Acid rain is corrosive rain that causes damage to aquatic ecosystems by lowering the pH of lakes, killing many of the resident fauna; it also degrades buildings and human-made structures.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns and, hence, their functions. As shown in Figure 20.7.1, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), which enters the atmosphere in three ways: first, from the decomposition of organic molecules; second, from volcanic activity and geothermal vents; and, third, from the burning of fossil fuels by humans.

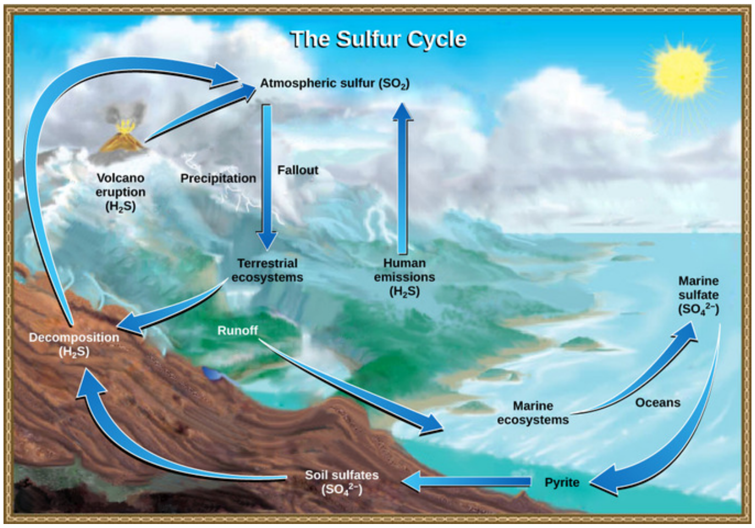


Figure 20.7.1: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil, and atmosphere.

On land, sulfur is deposited in five major ways: precipitation, direct fallout from the atmosphere, rock weathering, decomposition of organic materials, and geothermal vents (Figure 20.7.2). As rain falls through the atmosphere, sulfur dioxide (SO_2) in the atmosphere is dissolved in the form of weak sulfuric acid (H_2SO_4), creating acid rain. Sulfur can also fall directly from the atmosphere in a process called fallout. The weathering of sulfur-containing rocks also releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplift. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{2-}), which enter the food web by being taken up by plant roots. Upon the death and decomposition of these organisms, sulfur is released back into the atmosphere as hydrogen sulfide (H_2S) gas.

Figure 20.7.2: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, fallout, and underwater geothermal vents. Some ecosystems rely on microorganisms using sulfur as a biological energy source (chemoautotrophs) in contrast to ecosystems with photosynthetic producers. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle (Figure 20.7.3). The burning of large quantities of fossil fuels, especially from coal, releases sulfur dioxide, which reacts with the atmosphere to form sulfuric acid. Like nitric acid, sulfuric acid contributes to acid deposition. Acid deposition (sometimes referred to simply as acid rain) damages the natural environment by lowering the pH of lakes, thus killing many of the resident plants and animals. Acid deposition also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

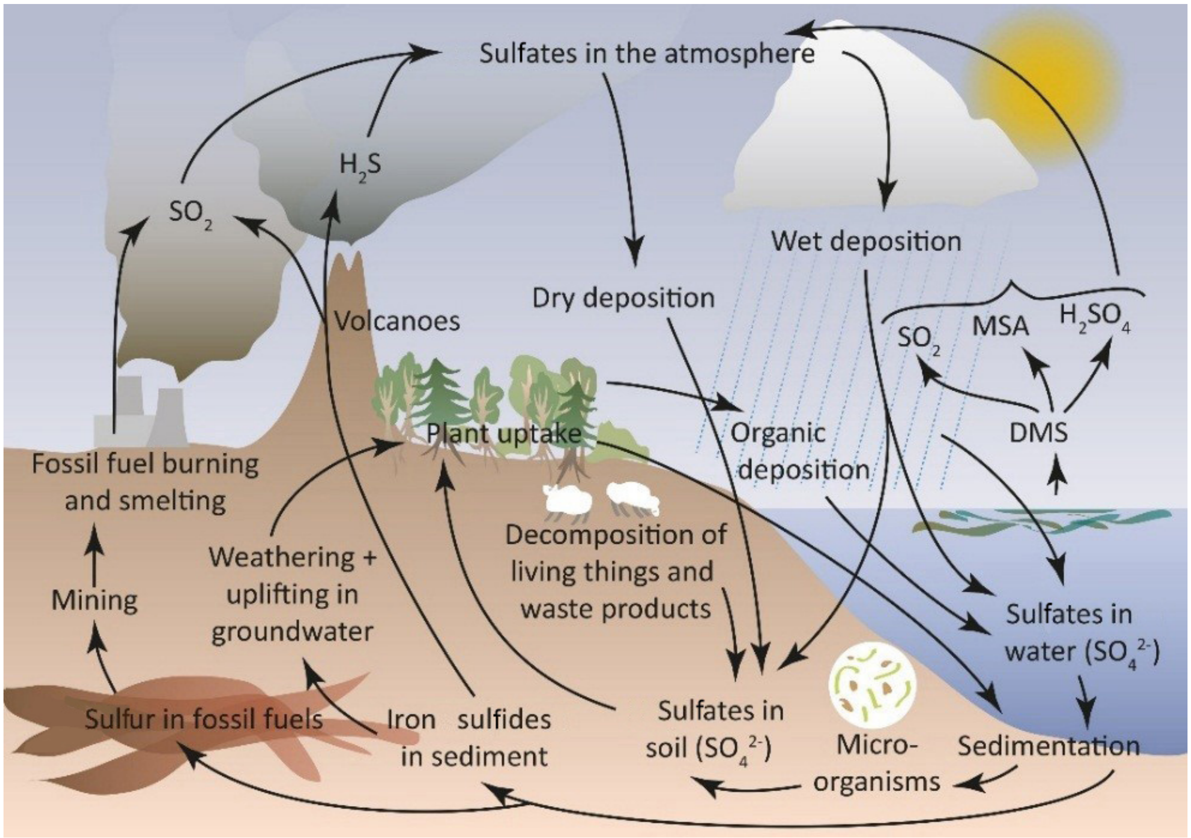


Figure 20.7.3: Schematic figure of the Sulfur cycle including human impacts from mining and burning fossil fuels. *Source: Hanna K. Lappalainen, Veli-Matti Kerminen, Tuukka Petäjä, Theo Kurten, Aleksander Baklanov, Anatoly Shvidenko, Jaana Bäck, Timo Vihma, Pavel Alekseychik, Meinrat O. Andreae, Stephen R. Arnold, Mikhail Arshinov, Eija Asmi, Boris Belan, Leonid Bobylev, Sergey Chalov, Yafang Cheng, Natalia Chubarova, Gerrit de Leeuw, Aijun Ding, Sergey Dobrolyubov, Sergei Dubtsov, Egor Dyukarev, Nikolai Elansky, Kostas Eleftheriadis, Igor Esau, Nikolay Filatov, Mikhail Flint, Congbin Fu, Olga Glezer, Aleksander Gliko, Martin Heimann, Albert A. M. Holtslag, Urmas Hõrrak, Juha Janhunen, Sirkku Juhola, Leena Järvi, Heikki Järvinen, Anna Kanukhina, Pavel Konstantinov, Vladimir Kotlyakov, Antti-Jussi Kieloaho, Alexander S. Komarov, Joni Kujansuu, Ilmo Kukkonen, Ella-Maria Duplissy, Ari Laaksonen, Tuomas Laurila, Heikki Lihavainen, Alexander Lisitzin, Alexsander Mahura, Alexander Makshtas, Evgeny Mareev, Stephany Mazon, Dmitry Matishov, Vladimir Melnikov, Eugene Mikhailov, Dmitri Moisseev, Robert Nigmatulin, Steffen M. Noe, Anne Ojala, Mari Pihlatie, Olga Popovicheva, Jukka Pumpanen, Tatjana Regerand, Irina Repina, Aleksei Shcherbinin, Vladimir Shevchenko, Mikko Sipilä, Andrey Skorokhod, Dominick V. Spracklen, Hang Su, Dmitry A. Subetto, Junying Sun, Arkady Y. Terzhevik, Yuri Timofeyev, Yuliya Troitskaya, Veli-Pekka Tynkkynen, Viacheslav I. Kharuk, Nina Zaytseva, Jiahua Zhang, Yrjö Viisanen, Timo Vesala, Pertti Hari, Hans Christen Hansson, Gennady G. Matvienko, Nikolai S. Kasimov, Huadong Guo, Valery Bondur, Sergej Zilitinkevich, Markku Kulmala, CC BY 3.0, via Wikimedia Commons.*

Chemosynthesis

Why do bacteria that live deep below the ocean's surface rely on chemical compounds instead of sunlight for energy to make food?

Most autotrophs make food by photosynthesis, but this isn't the only way that autotrophs produce food. Some bacteria make food by another process, which uses chemical energy instead of light energy. This process is called **chemosynthesis**. In chemosynthesis, one or more carbon molecules (usually carbon dioxide or methane, CH_4) and nutrients is converted into organic matter, using the oxidation of inorganic molecules (such as hydrogen gas, hydrogen sulfide (H_2S) or ammonia (NH_3)) or methane as a source of energy, rather than sunlight. In hydrogen sulfide chemosynthesis, in the presence of carbon dioxide and oxygen, carbohydrates (CH_2O) can be produced:

$CO_2 + O_2 + 4H_2S \rightarrow CH_2O + 4S + 3H_2O$

Many organisms that use chemosynthesis are **extremophiles,** living in harsh conditions, such as in the absence of sunlight and a wide range of water temperatures, some approaching the boiling point. Some chemosynthetic bacteria live around deep-ocean vents known as "black smokers." Compounds such as hydrogen sulfide, which flow out of the vents from Earth's interior, are used by the bacteria for energy to make food. These organisms are known as **chemoautotrophs.** Many chemosynthetic microorganisms are consumed by other organisms in the ocean, and symbiotic associations between these organisms and respiring heterotrophs are quite common. Consumers that depend on these bacteria to produce food for them include giant tubeworms (Figure 20.7.4), and Pompeii worms ((Figure 20.7.5).

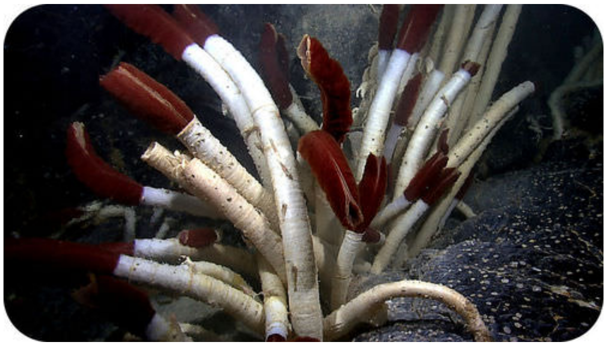


Figure 20.7.4: Tubeworms deep in the Galapagos Rift get their energy from chemosynthetic bacteria. Tubeworms have no mouth, eyes or stomach. Their survival depends on a symbiotic relationship with the billions of bacteria that live inside them. These bacteria convert the chemicals that shoot out of the hydrothermal vents into food for the worm.

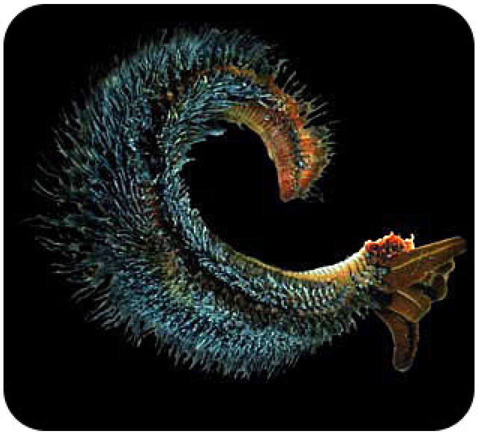


***Figure 20.7.5**: Is it possible to live in temperatures over 175°F? It is if you're a Pompeii worm. The Pompeii worm, the most heat-tolerant animal on Earth, lives in the deep ocean at super-heated hydrothermal vents. Covering this deep-sea worm's back is a fleece of bacteria. These microbes contain all the genes necessary for life in extreme environments.*

Contributors and Attributions

This section was modified from the original by Kyle Whittinghill

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

- **20.2: Biogeochemical Cycles** by OpenStax, is licensed CC BY
- **2.24: Chemosynthesis** by CK-12: Biology Concepts, is licensed CC BY-NC
- General Microbiology **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***
- Atmosphere-Biosphere-Hydrosphere-Lithosphere. **Provided by**: Wikimedia. **Located at**: **commons.wikimedia.org/wiki/Fi...ithosphere.png**. **License**: ***CC BY: Attribution***

- **20.2: Biogeochemical Cycles** by OpenStax is licensed CC BY 4.0.
- **2.24: Chemosynthesis** by CK-12 Foundation is licensed CK-12. Original source: http://www.ck12.org/book/CK-12-Biology-Concepts.

CHAPTER OVERVIEW

21: Landscape Ecology and Island Biogeography

Learning Objectives

- Understand the origins and aims of Landscape Ecology
- Learn some of the important terms used in Landscape Ecology
- Understand the basics of the Theory of Island Biogeography
- Make connections between the Theory of Island Biogeography and its application in Ecology

Topic hierarchy

Summary

Landscape ecology is the science of studying and improving relationships between ecological processes in the environment and particular ecosystems. This is done within a variety of landscape scales, development spatial patterns, and organizational levels of research and policy. Landscape ecology often focuses on the composition of landscapes, and how the size, shape, and adjacency of different habitat patches affect ecological processes. The development of the Theory of Island Biogeography in the 1960s was fundamental to our understanding of how the size and isolation of habitat patches affect the life histories of species found within them. This, in turn, resulted in a strong focusses on habitat fragmentation within the subfield of Landscape Ecology.

21.1: What is Landscape Ecology?

Landscape Ecology

Landscape ecology is the science of studying and improving relationships between ecological processes in the environment and particular ecosystems. This is done within a variety of landscape scales, development spatial patterns, and organizational levels of research and policy.[1][2][3] Concisely, landscape ecology can be described as the science of landscape diversity as the synergetic result of biodiversity and geodiversity.[4]

As a highly interdisciplinary field in systems science, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across the natural sciences and social sciences. Landscapes are spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems, ranging from relatively natural terrestrial and aquatic systems such as forests, grasslands, and lakes to human-dominated environments including agricultural and urban settings.[2][5][6]

The most salient characteristics of landscape ecology are its emphasis on the relationship among pattern, process and scale, and its focus on broad-scale ecological and environmental issues. These necessitate the coupling between biophysical and socioeconomic sciences. Key research topics in landscape ecology include ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, and landscape conservation and sustainability.[7] Landscape ecology also studies the role of human impacts on landscape diversity in the development and spreading of new human pathogens that could trigger epidemics.[8][9]

Heterogeneity is the measure of how parts of a landscape differ from one another. Landscape ecology looks at how this spatial structure affects organism abundance at the landscape level, as well as the behavior and functioning of the landscape as a whole. This includes studying the influence of pattern, or the internal order of a landscape, on process, or the continuous operation of functions of organisms.[11] Landscape ecology also includes geomorphology as applied to the design and architecture of landscapes.[12] Geomorphology is the study of how geological formations are responsible for the structure of a landscape.

History

Terminology

The German term Landschaftsökologie–thus landscape ecology–was coined by German geographer Carl Troll in 1939.[10] He developed this terminology and many early concepts of landscape ecology as part of his early work, which consisted of applying aerial photograph interpretation to studies of interactions between environment and vegetation.

Evolution of theory

One central landscape ecology theory originated from MacArthur & Wilson's The Theory of Island Biogeography (see 21.4: Island Biogeography). This work considered the biodiversity on islands as the result of competing forces of colonization from a mainland stock and stochastic extinction. The concepts of island biogeography were generalized from physical islands to abstract patches of habitat by Levins' metapopulation model (which can be applied e.g. to forest islands in the agricultural landscape[13]). A **metapopulation** is a group of smaller populations of an organism in distinct habitat patches or islands which have individuals moving between patches. This generalization spurred the growth of landscape ecology by providing conservation biologists a new tool to assess how habitat fragmentation affects population viability. Recent growth of landscape ecology owes much to the development of geographic information systems (GIS)[14] and the availability of large-extent habitat data (e.g. remotely sensed datasets) Figure 21.1.1.

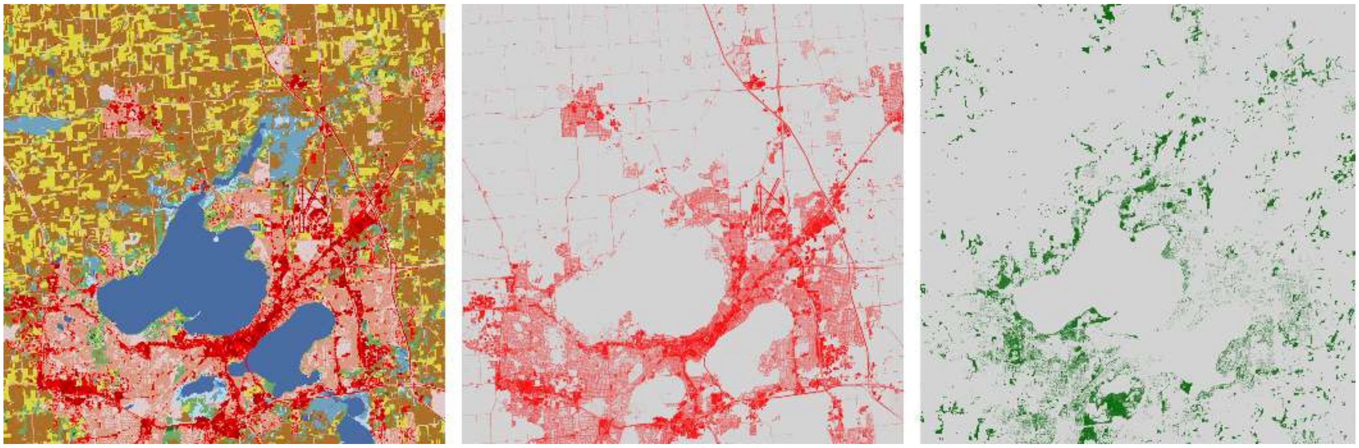


Figure 21.1.1 : Land cover surrounding Madison, WI. Left: fields are colored yellow and brown, water is colored blue, and urban surfaces are colored red. Center: impervious surfaces. Right: canopy cover.

Development as a discipline

Landscape ecology developed in Europe from historical planning on human-dominated landscapes. Concepts from general ecology theory were integrated in North America. While general ecology theory and its sub-disciplines focused on the study of more homogenous, discrete community units organized in a hierarchical structure (typically as ecosystems, populations, species, and communities), landscape ecology built upon heterogeneity in space and time. It frequently included anthropogenic (human-caused) landscape changes in theory and application of concepts.[15]

By 1980, landscape ecology was a discrete, established discipline. It was marked by the organization of the International Association for Landscape Ecology (IALE) in 1982. Landmark book publications defined the scope and goals of the discipline, including Naveh and Lieberman[16] and Forman and Godron[17]. Forman[6] wrote that although study of "the ecology of spatial configuration at the human scale" was barely a decade old, there was strong potential for theory development and application of the conceptual framework.Today, the theory and application of landscape ecology continue to develop through a need for innovative applications in a changing landscape and environment. Landscape ecology relies on advanced technologies such as remote sensing, GIS, and models. There has been associated development of powerful quantitative methods to examine the interactions of patterns and processes.[5] An example would be determining the amount of carbon present in the soil based on landform over a landscape, derived from GIS maps, vegetation types, and rainfall data for a region. Remote sensing work has been used to extend landscape ecology to the field of predictive vegetation mapping, for instance by Janet Franklin.

Sources

1. Wu, J. (2006). Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology, 21*(1), pp. 1-4. doi:10.1007/s10980-006-7195-2. S2CID 27192835.
2. Wu, J., & Hobbs, R., eds. (2007). Key topics in landscape ecology. *Cambridge: Cambridge University Press*.
3. Wu, J. (2008). Landscape ecology. In Jorgensen, S.E. (Eds.), *Encyclopedia of ecology*. Oxford: Elsevier.
4. Leser, H., & Nagel, P. (2001). Landscape diversity -- a holistic approach. Biodiversity. Springer, pp. 129-143. doi:10.1007/978-3-662-06071-1_9. ISBN 978-3-642-08370-9.
5. Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2001). Landscape ecology in theory and practice. *New York, NY, USA: Springer-Verlag.*
6. Forman, R.T. (1995). Land mosaics: The ecology of landscapes and regions. *Cambridge, UK: Cambridge University Press.*
7. Wu & Hobbs 2002
8. Bloomfield, L.S., McIntosh, T.L., & Lambin, E.F. (2020). Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa. *Landscape Ecology, 35*(4), pp. 985-1000. doi:10.1007/s10980-020-00995-w. ISSN 1572-9761. S2CID 214731443.
9. Bausch, D.G., & Scwarz, L. (2014). Outbreak of ebola virus disease in Guinea: Where ecology meets economy. *PLOS Neglected Tropical Diseases, 8*(7), *e3056*. doi:10.1371/journal.pntd.0003056. PMC 4117598. PMID 25079231.
10. Troll, C. (1939). Luftbildplan und ökologische Bodenforschung [Aerial photography and ecological studies of the earth]. *Zeitschrift der Gesellschaft für Erdkunde (in German). Berlin: pp. 241–298.*

11. Turner, M.G. (1989). Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics, 20*, pp. 171-197. *doi:10.1146/annurev.es.20.110189.001131*.
12. Allaby, M. (1998). Oxford dictionary of ecology. *New York, NY: Oxford University Press.*
13. Banaszak, J., ed. (2000). Ecology of forest islands. *Bydgoszcz, Poland: Bydgoszcz University Press. p. 313.*
14. Steiniger, S., & Hay, G.J. (2009). Free and open source geographic information tools for landscape ecology. *Ecological Informatics*, *4*(4), pp, 183-95. *doi:10.1016/j.ecoinf.2009.07.004*.
15. Sanderson, J., Harris, L.D., eds. (2000). Landscape ecology: A top-down approach. *Boca Raton, Florida, USA: Lewis Publishers.*
16. Naveh, Z., & Lieberman, A. (1984). Landscape ecology: Theory and application. *New York, NY, USA: Springer-Verlag.*
17. Forman, R.T., & Godron, M. (1986). Landscape ecology. *New York, NY, USA: John Wiley and Sons, Inc.*
18. Ryszkowski, L., ed. (2002). Landscape ecology in agroecosystems management. *Florida, USA: CRC Press, Boca Raton.*

Contributors and Attributions

Modified by Andy Wilson (Gettysburg College) and Kyle Whittinghill (University of Vermont) from the following sources:

- Wikipedia, the free encyclopedia https://en.Wikipedia.org/wiki/Landscape_ecology

---

21.2: Important Terms in Landscape Ecology

Landscape

Certainly, 'landscape' is a central concept in landscape ecology. It is, however, defined in quite different ways. For example:[19] Carl Troll conceives of landscape not as a mental construct but as an objectively given 'organic entity', a *harmonic individuum of space*.[34] Ernst Neef[20][21] defines landscapes as sections within the uninterrupted earth-wide interconnection of geofactors which are defined as such on the basis of their uniformity in terms of a specific land use, and are thus defined in an anthropocentric and relativistic way. According to Richard Forman and Michel Godron,[22] a landscape is a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout, whereby they list woods, meadows, marshes and villages as examples of a landscape's ecosystems, and state that a landscape is an area at least a few kilometers wide. John A. Wiens defines 'landscape'—regardless of scale—as "the template on which spatial patterns influence ecological processes".[25][35] Some define 'landscape' as an area containing two or more ecosystems in close proximity.[15]

Scale and heterogeneity (incorporating composition, structure, and function)

A main concept in landscape ecology is *scale*. Scale represents the real world as translated onto a map, relating distance on a map image and the corresponding distance on earth.[36] Scale is also the spatial or temporal measure of an object or a process,[33] or amount of spatial resolution.[6] Components of scale include composition, structure, and function, which are all important ecological concepts. Applied to landscape ecology, *composition* refers to the number of patch types (see below) represented on a landscape and their relative abundance. For example, the amount of forest or wetland, the length of forest edge, or the density of roads can be aspects of landscape composition. *Structure* is determined by the composition, the configuration, and the proportion of different patches across the landscape, while *function* refers to how each element in the landscape interacts based on its life cycle events.[33] *Pattern* is the term for the contents and internal order of a heterogeneous area of land.[17]

A landscape with structure and pattern implies that it has spatial *heterogeneity*, or the uneven distribution of objects across the landscape.[6] Heterogeneity is a key element of landscape ecology that separates this discipline from other branches of ecology.

Patch and mosaic

Patch, a term fundamental to landscape ecology, is defined as a relatively homogeneous area that differs from its surroundings.[6] Patches are the basic unit of the landscape that change and fluctuate, a process called *patch dynamics*. Patches have a definite shape and spatial configuration, and can be described compositionally by internal variables such as number of trees, number of tree species, height of trees, or other similar measurements.[6]

Matrix is the "background ecological system" of a landscape with a high degree of connectivity. *Connectivity* is the measure of how connected or spatially continuous a corridor, network, or matrix is.[6] For example, a forested landscape (matrix) with fewer gaps in forest cover (open patches) will have higher connectivity. *Corridors* have important functions as strips of a particular type of landscape differing from adjacent land on both sides.[6] A *network* is an interconnected system of corridors while *mosaic* describes the pattern of patches, corridors, and matrix that form a landscape in its entirety.[6]

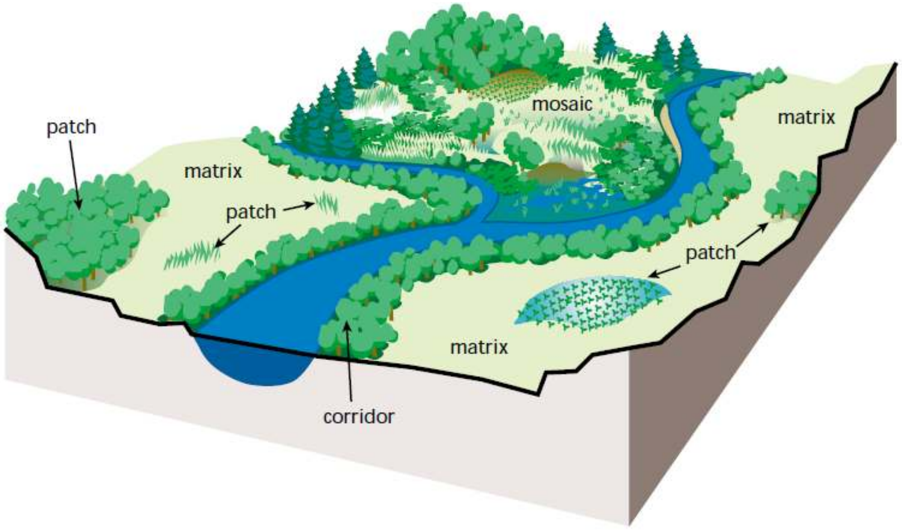


Figure 21.2.1 : Basic terms to define landscape ecology (FISGRW 1998) from Understanding Landscape Structure Using Landscape Metrics (Ercan Gökyer) (DOI: 10.5772/55758).

Boundary and edge

Landscape patches have a boundary between them which can be defined or fuzzy.[15] The zone composed of the edges of adjacent ecosystems is the *boundary*.[6] *Edge* means the portion of an ecosystem near its perimeter, where influences of the adjacent patches can cause an environmental difference between the interior of the patch and its edge. This edge effect includes a distinctive species composition or abundance.[6] For example, when a landscape is a mosaic of perceptibly different types, such as a forest adjacent to a grassland, the edge is the location where the two types adjoin. In a continuous landscape, such as a forest giving way to open woodland, the exact edge location is fuzzy and is sometimes determined by a local gradient exceeding a threshold, such as the point where the tree cover falls below thirty-five percent.[33]

Ecotones, ecoclines, and ecotopes

A type of boundary is the *ecotone*, or the transitional zone between two communities.[12] Ecotones can arise naturally, such as a lakeshore, or can be human-created, such as a cleared agricultural field from a forest.[12] The ecotonal community retains characteristics of each bordering community and often contains species not found in the adjacent communities. Classic examples of ecotones include fencerows, forest to marshlands transitions, forest to grassland transitions, or land-water interfaces such as riparian zones in forests. Characteristics of ecotones include vegetational sharpness, physiognomic change, occurrence of a spatial community mosaic, many exotic species, ecotonal species, spatial mass effect, and species richness higher or lower than either side of the ecotone.[38]

An *ecocline* is another type of landscape boundary, but it is a gradual and continuous change in environmental conditions of an ecosystem or community. Ecoclines help explain the distribution and diversity of organisms within a landscape because certain organisms survive better under certain conditions, which change along the ecocline. They contain heterogeneous communities which are considered more environmentally stable than those of ecotones.[39] An *ecotope* is a spatial term representing the smallest ecologically distinct unit in mapping and classification of landscapes.[6] Relatively homogeneous, they are spatially explicit landscape units used to stratify landscapes into ecologically distinct features. They are useful for the measurement and mapping of landscape structure, function, and change over time, and to examine the effects of disturbance and fragmentation.

Figure 21.2.2: An ecotone between grassland and woodland. "Ecotone" by Nicholas A. Tonelli is licensed under CC BY 2.0.

Disturbance and fragmentation

Disturbance is an event that significantly alters the pattern of variation in the structure or function of a system. *Fragmentation* is the breaking up of a habitat, ecosystem, or land-use type into smaller parcels.[6] Disturbance is generally considered a natural process. Fragmentation causes land transformation, an important process in landscapes as development occurs.

An important consequence of repeated, random clearing (whether by natural disturbance or human activity) is that contiguous cover can break down into isolated patches. This happens when the area cleared exceeds a critical level, which means that landscapes exhibit two phases: connected and disconnected.[40]

Figure 21.2.3: Rapid deforestation in Cambodia resulted in habitat loss and fragmentation (credit: Global Forest Watch. World Resources Institute. Accessed on 1/5/2022. www.globalforestwatch.org).

Sources

1. Wu, J. (2006). Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology, 21*(1), pp. 1-4. *doi:10.1007/s10980-006-7195-2. S2CID 27192835*.
2. Wu, J., Hobbs, R., eds. (2007). Key topics in landscape ecology. *Cambridge: Cambridge University Press.*
3. Wu, J. (2008). Landscape ecology. In Jorgensen, S.E. (Eds.), Encyclopedia of ecology. *Oxford: Elsevier.*
4. Leser, H., & Nagel, P. (2001). Landscape diversity -- a holistic approach. *Biodiversity, Springer,* pp. 129-143. *doi:10.1007/978-3-662-06071-1_9. ISBN 978-3-642-08370-9.*
5. Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2001). Landscape ecology in theory and practice. *New York, NY, USA: Springer-Verlag.*
6. Forman, R.T. (1995). Land mosaics: The ecology of landscapes and regions. *Cambridge, UK: Cambridge University Press.*
7. Wu & Hobbs 2002
8. Bloomfield, L.S., McIntosh, T.L., & Lambin, E.F. (2020). Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa. *Landscape ecology, 35*(4), pp. 985-1000. *doi:10.1007/s10980-020-00995-w. ISSN 1572-9761. S2CID 214731443.*
9. Bausch, D.G., & Scwarz, L. (2014). Outbreak of ebola virus disease in Guinea: Where ecology meets economy. *PLOS Neglected Tropical Diseases, 8*(7), *e3056. doi:10.1371/journal.pntd.0003056. PMC 4117598. PMID 25079231.*
10. Troll, C. (1939). Luftbildplan und ökologische Bodenforschung [Aerial photography and ecological studies of the earth. *Zeitschrift der Gesellschaft für Erdkunde (in German). Berlin: pp. 241–298.*
11. Turner, M.G. (1989). Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics, 20*, pp. 171-197. *doi:10.1146/annurev.es.20.110189.001131.*
12. Allaby, M. (1998). Oxford dictionary of ecology. *New York, NY: Oxford University Press.*
13. Banaszak, J., ed. (2000). Ecology of forest islands. *Bydgoszcz, Poland: Bydgoszcz University Press. p. 313.*
14. Steiniger, S., & Hay, G.J. (2009). Free and open source geographic information tools for landscape ecology. *Ecological Informatics, 4*(4), pp. 183-95. *doi:10.1016/j.ecoinf.2009.07.004.*
15. Sanderson, J., Harris, L.D., eds. (2000). Landscape ecology: A top-down approach. *Boca Raton, Florida, USA: Lewis Publishers.*
16. Naveh, Z., & Lieberman, A. (1984). Landscape ecology: Theory and application. *New York, NY, USA: Springer-Verlag.*
17. Forman, R.T., & Godron, M. (1986). Landscape ecology. *New York, NY, USA: John Wiley and Sons, Inc.*
18. Ryszkowski, L., ed. (2002). Landscape ecology in agroecosystems management. *Florida, USA: CRC Press, Boca Raton.*

19. Kirchhoff, T., Trepl, L., & Vicenzotti, V. (2013). What is landscape ecology? An analysis and evaluation of six different conceptions. *Landscape Research, 38*(1), pp. 33-51. doi:10.1080/01426397.2011.640751. S2CID 145421450.
20. Neef, E. (1967). Die theoretischen Grundlagen der Landschaftslehre [The theoretical basics of. landscape science]. *Gotha: Haack.*
21. Haase, G. (1990). Approaches to, and methods of landscape diagnosis as a basis of landscape planing and landscape management. *Ekológia, 9*(1), pp. 31-44.
22. Forman, R.T., & Godron, M. (1981). Patches and structural components for a landscape ecology. *BioScience, 31*(10), pp. 733-740. doi:10.2307/1308780. JSTOR 1308780.
23. Wiens, J.A., & Milne, B.T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology, 3*(2), pp. 87-96. doi:10.1007/BF00131172. S2CID 15683804.
24. Wiens, J.A. (1999). The science and practice of landscape ecology. In Klopatek, J.M., Gardner, R.H. (Eds.), *Landscape ecological analyses: Issues and applications* (pp. 371-383). NY: Springer.
25. Urban, D.L., O'Neill, R.V., & Shugart, H.H., Jr. (1987). A hierarchical perspective can help scientists understand spatial patterns. *BioScience, 37*(2), pp. 119-127. doi:10.2307/1310366. JSTOR 1310366.
26. Leser, H. (1991). Landschaftsökologie. *Ansatz, Modelle, Methodik, Anwendung. Stuttgart: Ulmer.*
27. Naveh, Z., & Lieberman, A.S. (1984). Landscape ecology.*Theory and application. NY: Springer.*
28. Naveh, N. (2000). What is holistic landscape ecology? A conceptual introduction. *Landscape and Urban Planning, 50*(1-3), pp. 7-26. doi:10.1016/S0169-2046(00)00077-3.
29. Zonneveld, I.S. (1995). Land ecology: An introduction to landscape ecology as a base for land evaluation, land management and conservation. *Amsterdam: SPB.*
30. However, not always under the designation 'landscape ecology', but as part of landscape stewardship, landscape architecture and, first and foremost, environmental or urban and landscape planning.
31. Hard, G (1973). *Die Geographie. Eine wissenschaftstheoretische Einführung. Berlin: deGruyter. pp. 92–95.*
32. Turner, M.G., & Gardner, R.H., eds. (1991). Quantitative methods in landscape ecology. *New York, NY, USA: Springer-Verlag.*
33. Troll, C. (2007). The geographic landscape and its investigation. In Wiens, J.A., Moss, M.R., Turner, M.G., & Mladenoff, D.J. (Eds.), Foundation papers in landscape ecology (pp. 71-101). New York: Columbia University Press. First published as: *Troll C (1950). "Die geographische Landschaft und ihre Erforschung". Studium Generale. Vol. 3. pp. 163–181.* doi:10.1007/978-3-662-38240-0_20. ISBN 978-3-662-37475-7.
34. Wiens, J.A. (2005). Toward a unified landscape ecology. In Wiens, J.A., & Moss, M.R. (Eds.), *Issues and perspectives in landscape ecology* (pp. 365-373). Cambridge University Press.
35. Malczewski, J. 1999). GIS and multicriteria decision analysis. *New York, NY, USA: John Wiley and Sons, Inc.*
36. Wirth, E., Szabó, G., & Czinkóczky, A. (2016). Measure of landscape heterogeneity by agent-based methodology. *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences. III-8: 145–151.* Bibcode:2016ISPAnIII8..145W. doi:10.5194/isprs-annals-iii-8-145-2016. ISSN 2194-9042.
37. Walker, S., Wilson, J.B., Steel, J.B., Rapson, G.L., Smith, B., King, W.M., & Cottam, Y.H. (2003). Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient. *Journal of Vegetation Science, 14*(4), pp. 579-90. doi:10.1111/j.1654-1103.2003.tb02185.x.
38. Attrill, M.J., & Rundle, S.D. (2002). Ecotone or ecocline: Ecological boundaries in estuaries. Esturaine, Coastal and Shelf Science, 55(6), pp. 929-936. Bibcode:2002ECSS...55..929A. doi:10.1006/ecss.2002.1036.
39. Green, D.G., Klomp, N.I., Rimmington, G.R., & Sadedin, S. (2006). Complexity in landscape ecology. *Amsterdam: Springer. Archived from the original on 2008-06-19. Retrieved 2008-03-22.*

Contributors and Attributions

Modified by Andy Wilson (Gettysburg College) and Kyle Whittinghill (University of Vermont) from the following sources:

- Wikipedia, the free encyclopedia https://en.Wikipedia.org/wiki/Landscape_ecology

---

21.3: Applications of Landscape Ecology

Research directions

Developments in landscape ecology illustrate the important relationships between spatial patterns and ecological processes. These developments incorporate quantitative methods that link spatial patterns and ecological processes at broad spatial and temporal scales. This linkage of time, space, and environmental change can assist managers in applying plans to solve environmental problems.[5] The increased attention in recent years on spatial dynamics has highlighted the need for new quantitative methods that can analyze patterns, determine the importance of spatially explicit processes, and develop reliable models.[33] Multivariate analysis techniques are frequently used to examine landscape level vegetation patterns. **Vegetation classification** is the process of classifying and mapping the vegetation over an area of the earth's surface and is often performed by state based agencies as part of landuse, resource and environmental management.

Many different methods of vegetation classification have been used but vegetation classification mapping is usually now done using geographic information systems (GIS) software. Studies use statistical techniques for classifying vegetation based on a combination of remote sensing variables. For an example of a vegetation classification system see the United States Geological Survey Land Cover website. Gradient analysis is another way to determine the vegetation structure across a landscape or to help delineate critical wetland habitat for conservation or mitigation purposes (Choesin & Boerner, 2002).[41]

Climate change is another major component in structuring current research in landscape ecology.[42] Ecotones, as a basic unit in landscape studies, may have significance for management under climate change scenarios, since change effects are likely to be seen at ecotones first because of the unstable nature of a fringe habitat.[38] Research in northern regions has examined landscape ecological processes, such as the accumulation of snow, melting, freeze-thaw action, percolation, soil moisture variation, and temperature regimes through long-term measurements in Norway.[43] The study analyzes gradients across space and time between ecosystems of the central high mountains to determine relationships between distribution patterns of animals in their environment. Looking at where animals live, and how vegetation shifts over time, may provide insight into changes in snow and ice over long periods of time across the landscape as a whole.

Other landscape-scale studies maintain that human impact is likely the main determinant of landscape pattern over much of the globe.[44] Landscapes may become substitutes for biodiversity measures because plant and animal composition differs between samples taken from sites within different landscape categories. Taxa, or different species, can “leak” from one habitat into another, which has implications for landscape ecology. As human land use practices expand and continue to increase the proportion of edges in landscapes, the effects of this leakage across edges on assemblage integrity may become more significant in conservation. This is because taxa may be conserved across landscape levels, if not at local levels.[45]

Land change modeling

Land change modeling is an application of landscape ecology designed to predict future changes in land use. Land change models are used in urban planning, geography, GIS, and other disciplines to gain a clear understanding of the course of a landscape.[46] In recent years, much of the Earth's land cover has changed rapidly, whether from deforestation or the expansion of urban areas.[47]

Relationship to other disciplines

Landscape ecology has been incorporated into a variety of ecological subdisciplines. For example, it is closely linked to land change science, the interdisciplinary of land use and land cover change and their effects on surrounding ecology. Another recent development has been the more explicit consideration of spatial concepts and principles applied to the study of lakes, streams, and wetlands in the field of landscape limnology. Seascape ecology is a marine and coastal application of landscape ecology.[48] In addition, landscape ecology has important links to application-oriented disciplines such as agriculture and forestry. In agriculture, landscape ecology has introduced new options for the management of environmental threats brought about by the intensification of agricultural practices. Agriculture has always been a strong human impact on ecosystems.[18]

In forestry, from structuring stands for fuelwood and timber to ordering stands across landscapes to enhance aesthetics, consumer needs have affected conservation and use of forested landscapes. Landscape forestry provides methods, concepts, and analytic procedures for landscape forestry.[49] Landscape ecology has been cited as a contributor to the development of fisheries biology as a distinct biological science discipline,[50] and is frequently incorporated in study design for wetland delineation in hydrology.[39] It has helped shape integrated landscape management.[51] Lastly, landscape ecology has been very influential for progressing sustainability science and sustainable development planning. For example, a recent study assessed sustainable urbanization across Europe using evaluation indices, country-landscapes, and landscape ecology tools and methods.[52]

Landscape ecology has also been combined with population genetics to form the field of landscape genetics, which addresses how landscape features influence the population structure and gene flow of plant and animal populations across space and time[53] and on how the quality of intervening landscape, known as "matrix," influences spatial variation.[54] After the term was coined in 2003, the field of landscape genetics had expanded to over 655 studies by 2010,[55] and continues to grow today. As genetic data has become more readily accessible, it is increasingly being used by ecologists to answer novel evolutionary and ecological questions,[56] many with regard to how landscapes effect evolutionary processes, especially in human-modified landscapes, which are experiencing biodiversity loss.[57]

References

1. Wu, J. (2006). Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology, 21*(1), pp. 1-4. *doi:10.1007/s10980-006-7195-2. S2CID 27192835.*
2. Wu, J., & Hobbs, R., eds. (2007). Key topics in landscape ecology. *Cambridge: Cambridge University Press.*
3. Wu, J. (2008). Landscape ecology. In Jorgensen, S.E. (Eds.), *Encyclopedia of ecology.* Oxford: Elsevier.
4. Leser, H., & Nagel, P. (2001). Landscape diversity -- a holistic approach. *Biodiversity, Springer*, pp. 129-143. *doi:10.1007/978-3-662-06071-1_9. ISBN 978-3-642-08370-9.*
5. Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2001). Landscape ecology in theory and practice. *New York, NY, USA: Springer-Verlag.*
6. Forman, R.T. (1995). Land mosaics: The ecology of landscapes and regions. *Cambridge, UK: Cambridge University Press.*
7. Wu & Hobbs 2002
8. Bloomfield, L.S., McIntosh, T.L., & Lambin, E.F. (2020). Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa. *Landscape Ecology, 35*(4), pp. 985-1000. *doi:10.1007/s10980-020-00995-w. ISSN 1572-9761. S2CID 214731443.*
9. Bausch, D.G., & Schwarz, L. (2014). Outbreak of ebola virus disease in Guinea: Where ecology meets economy. PLOS Neglected Tropical Diseases, 8(7),
10. *Bausch DG, Schwarz L (2014-07-31). "Outbreak of ebola virus disease in Guinea: where ecology meets economy". PLOS Neglected Tropical Diseases.* ***8*** *(7): e3056. doi:10.1371/journal.pntd.0003056. PMC 4117598. PMID 25079231.*
11. *Troll C (1939). "Luftbildplan und ökologische Bodenforschung" [Aerial photography and ecological studies of the earth]. Zeitschrift der Gesellschaft für Erdkunde (in German). Berlin: 241–298.*
12. *Turner MG (1989). "Landscape ecology: the effect of pattern on process". Annual Review of Ecology and Systematics.* ***20****: 171–197. doi:10.1146/annurev.es.20.110189.001131.*
13. *Allaby M (1998). Oxford Dictionary of Ecology. New York, NY: Oxford University Press.*
14. *Banaszak J, ed. (2000). Ecology of Forest Islands. Bydgoszcz, Poland: Bydgoszcz University Press. p. 313.*
15. *Steiniger S, Hay GJ (September 2009). "Free and open source geographic information tools for landscape ecology" (PDF). Ecological Informatics.* ***4*** *(4): 183–195. doi:10.1016/j.ecoinf.2009.07.004.*
16. *Sanderson J, Harris LD, eds. (2000). Landscape Ecology: A Top-Down Approach. Boca Raton, Florida, USA: Lewis Publishers.*
17. *Naveh Z, Lieberman A (1984). Landscape ecology: theory and application. New York, NY, USA: Springer-Verlag.*
18. *Forman RT, Godron M (1986). Landscape Ecology. New York, NY, USA: John Wiley and Sons, Inc.*
19. *Ryszkowski L, ed. (2002). Landscape Ecology in Agroecosystems Management. Florida, USA: CRC Press, Boca Raton.*
20. *Kirchhoff T, Trepl L, Vicenzotti V (February 2013). "What is landscape ecology? An analysis and evaluation of six different conceptions". Landscape Research.* ***38*** *(1): 33–51. doi:10.1080/01426397.2011.640751. S2CID 145421450.* All the following quotations and descriptions come from this source.
21. *Neef E (1967). Die theoretischen Grundlagen der Landschaftslehre [The theoretical basics of landscape science] (in German). Gotha: Haack.*
22. *Haase G (1990). "Approaches to, and methods of landscape diagnosis as a basis of landscape planning and landscape management". Ekológia.* ***9*** *(1): 31–44.*
23. *Forman RT, Godron M (November 1981). "Patches and structural components for a landscape ecology". BioScience.* ***31*** *(10): 733–740. doi:10.2307/1308780. JSTOR 1308780.*
24. *Forman RT, Godron M (1986). Landscape ecology. NY: Wiley.*

25. *Wiens JA, Milne BT (December 1989). "Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective". Landscape Ecology.* **3** *(2): 87–96. doi:10.1007/BF00131172. S2CID 15683804.*
26. *Wiens JA (1999). "The science and practice of landscape ecology.". In Klopatek JM, Gardner RH (eds.). Landscape ecological analyses: Issues and applications. NY: Springer. pp. 371–383.*
27. *Urban DL, O'Neill RV, Shugart Jr HH (February 1987). "A hierarchical perspective can help scientists understand spatial patterns"* (PDF). BioScience. **37** (2): 119–127. *doi:10.2307/1310366. JSTOR 1310366.*
28. *Leser H (1991). Landschaftsökologie. Ansatz, Modelle, Methodik, Anwendung. Stuttgart: Ulmer.*
29. *Naveh Z, Lieberman AS (1984). Landscape ecology. Theory and application. NY: Springer.*
30. *Naveh N (2000). "What is holistic landscape ecology? A conceptual introduction". Landscape and Urban Planning.* **50** *(1–3): 7–26. doi:10.1016/S0169-2046(00)00077-3.*
31. *Zonneveld IS (1995). Land ecology: an introduction to landscape ecology as a base for land evaluation, land management and conservation. Amsterdam: SPB.*
32. However, not always under the designation 'landscape ecology', but as part of landscape stewardship, landscape architecture and, first and foremost, environmental or urban and landscape planning.
33. *Hard G (1973). Die Geographie. Eine wissenschaftstheoretische Einführung. Berlin: deGruyter. pp. 92–95.*
34. *Turner MG, Gardner RH, eds. (1991). Quantitative Methods in Landscape Ecology. New York, NY, USA: Springer-Verlag.*
35. *Troll C (2007). "The geographic landscape and its investigation.". In Wiens JA, Moss MR, Turner MG, Mladenoff DJ (eds.). Foundation papers in landscape ecology. New York: Columbia University Press. pp. 71–101.* First published as: *Troll C (1950). "Die geographische Landschaft und ihre Erforschung". Studium Generale. Vol. 3. pp. 163–181. doi:10.1007/978-3-662-38240-0_20. ISBN 978-3-662-37475-7.*
36. *Wiens JA (2005). "Toward a unified landscape ecology". In Wiens JA, Moss MR (eds.). Issues and perspectives in landscape ecology. Cambridge: Cambridge University Press. pp. 365–373.*
37. *Malczewski J (1999). GIS and Multicriteria Decision Analysis. New York, NY, USA: John Wiley and Sons, Inc.*
38. *Wirth E, Szabó G, Czinkóczky A (2016-06-07). "Measure of Landscape Heterogeneity by Agent-Based Methodology". ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences. III-8: 145–151. Bibcode:2016ISPAnIII8..145W. doi:10.5194/isprs-annals-iii-8-145-2016. ISSN 2194-9042.*
39. *Walker S, Wilson JB, Steel JB, Rapson GL, Smith B, King WM, Cottam YH (August 2003). "Properties of ecotones: evidence from five ecotones objectively determined from a coastal vegetation gradient". Journal of Vegetation Science.* **14** *(4): 579–90. doi:10.1111/j.1654-1103.2003.tb02185.x.*
40. *Attrill MJ, Rundle SD (December 2002). "Ecotone or ecocline: ecological boundaries in estuaries". Estuarine, Coastal and Shelf Science.* **55** *(6): 929-936. Bibcode:2002ECSS...55..929A. doi:10.1006/ecss.2002.1036.*
41. *Green DG, Klomp NI, Rimmington GR, Sadedin S (2006). Complexity in Landscape Ecology. Amsterdam: Springer. Archived from the original on 2008-06-19. Retrieved 2008-03-22.*
42. *Lyon J, Sagers CL (September 1998). "Structure of herbaceous plant assemblages in a forested riparian landscape". Plant Ecology.* **138** *(1): 1–6. doi:10.1023/A:1009705912710. S2CID 28628830.*
43. *Ochoa-Hueso R, Delgado-Baquerizo M, King PT, Benham M, Arca V, Power SA (February 2019). "Ecosystem type and resource quality are more important than global change drivers in regulating early stages of litter decomposition". Soil Biology and Biochemistry.* **129***: 144–152. doi:10.1016/j.soilbio.2018.11.009. S2CID 92606851.*
44. *Löffler J, Finch OD (November 2005). "Spatio-temporal gradients between high mountain ecosystems of central Norway". Arctic, Antarctic, and Alpine Research.* **37** *(4): 499–513. doi:10.1657/1523-0430(2005)037[0499:sgbhme]2.0.co;2. S2CID 131326887.*
45. *Ellis, Erle C.; Gauthier, Nicolas; Klein Goldewijk, Kees; Bliege Bird, Rebecca; Boivin, Nicole; Díaz, Sandra; Fuller, Dorian Q.; Gill, Jacquelyn L.; Kaplan, Jed O.; Kingston, Naomi; Locke, Harvey; McMichael, Crystal N. H.; Ranco, Darren; Rick, Torben C.; Shaw, M. Rebecca (2021-04-27). "People have shaped most of terrestrial nature for at least 12,000 years". Proceedings of the National Academy of Sciences.* **118** *(17):* e2023483118. *doi:10.1073/pnas.2023483118. ISSN 0027-8424. PMC 8092386. PMID 33875599.*
46. *Wilson JB, King WM (August 1995). "Human-mediated vegetation switches as processes in landscape ecology". Landscape Ecology.* **10** *(4): 191–6. doi:10.1007/BF00129253. S2CID 772430.*
47. *Dangerfield JM, Pik AJ, Britton D, Holmes A, Gillings M, Oliver IA, Briscoe D, Beattie AJ (June 2003). "Patterns of invertebrate biodiversity across a natural edge". Austral Ecology.* **28** *(3): 227–36. doi:10.1046/j.1442-9993.2003.01240.x.*
48. *National Research Council (2014). Advancing Land Change Modeling: Opportunities and Research Requirements. National Academies Press. pp. Chapter 1. doi:10.17226/18385. ISBN 978-0-309-28833-0.*

49. *University of Maryland. "GLCF: Global Land Cover Change". glcf.umd.edu. Archived from the original on 2019-06-09. Retrieved 2018-12-27.*
50. *Pittman SJ, ed. (2017). Seascape Ecology. Wiley & Sons.*
51. *Boyce SG (1995). Landscape Forestry. New York, NY: John Wiley and Sons, Inc.*
52. *Magnuson JJ (February 1991). "Fish and fisheries ecology". Ecological Applications.* ***1*** *(1): 13–26. doi:10.2307/1941844. JSTOR 1941844. PMID 27755677.*
53. *Sayer J (2009). "Reconciling conservation and development: are landscapes the answer?". Biotropica.* ***41*** *(6): 649–652. doi:10.1111/j.1744-7429.2009.00575.x. S2CID 85171847.*
54. *Shaker RR (September 2015). "The well-being of nations: an empirical assessment of sustainable urbanization for Europe". International Journal of Sustainable Development & World Ecology.* ***22*** *(5): 375–87. doi:10.1080/13504509.2015.1055524. S2CID 154904536.*
55. *Manel S, Schwartz MK, Luikart G, Taberlet P (April 2003). "Landscape genetics: combining landscape ecology and population genetics". Trends in Ecology & Evolution.* ***18*** *(4): 189–197. doi:10.1016/S0169-5347(03)00008-9. S2CID 2984426.*
56. *Storfer A, Murphy MA, Evans JS, Goldberg CS, Robinson S, Spear SF, et al. (March 2007). "Putting the "landscape" in landscape genetics". Heredity.* ***98*** *(3): 128–42. doi:10.1038/sj.hdy.6800917. PMID 17080024.*
57. *Storfer A, Murphy MA, Spear SF, Holderegger R, Waits LP (September 2010). "Landscape genetics: where are we now?". Molecular Ecology.* ***19*** *(17): 3496–514. doi:10.1111/j.1365-294X.2010.04691.x. PMID 20723061. S2CID 16435893.*
58. *Balkenhol N, Cushman S, Storfer A, Waits L (2015-11-09). Landscape Genetics: Concepts, Methods, Applications. John Wiley & Sons. ISBN 9781118525296.*
59. *Manel S, Holderegger R (October 2013). "Ten years of landscape genetics". Trends in Ecology & Evolution.* ***28*** *(10): 614–21. doi:10.1016/j.tree.2013.05.012. PMID 23769416.*

Contributors and Attributions

Modified by Andy Wilson (Gettysburg College) and Kyle Whittinghill (University of Vermont) from the following sources:

- Wikipedia, the free encyclopedia: https://en.Wikipedia.org/wiki/Landscape_ecology
- Wikipedia, the free encyclopedia: https://en.wikipedia.org/wiki/Vegeta...classification

21.4: Island Biogeography

Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. Organisms and biological communities often vary in a regular fashion along geographic gradients of latitude, elevation, isolation, and habitat area. The latter pattern, often called the **species-area relationship**, has long been a fascination for biogeographers. Figure 21.4.1 demonstrates this species-area relationship for amphibians and reptiles in the West Indies. A study from around 1957 was included in Robert H. MacArthur and Edward O. Wilson's famous book "The Theory of Island Biogeography", and showed that among seven islands studied, the largest, Cuba, had the most species, and the smallest, Redonda, had the fewest. This general pattern has been found in many different islands groups, and across various different taxa.

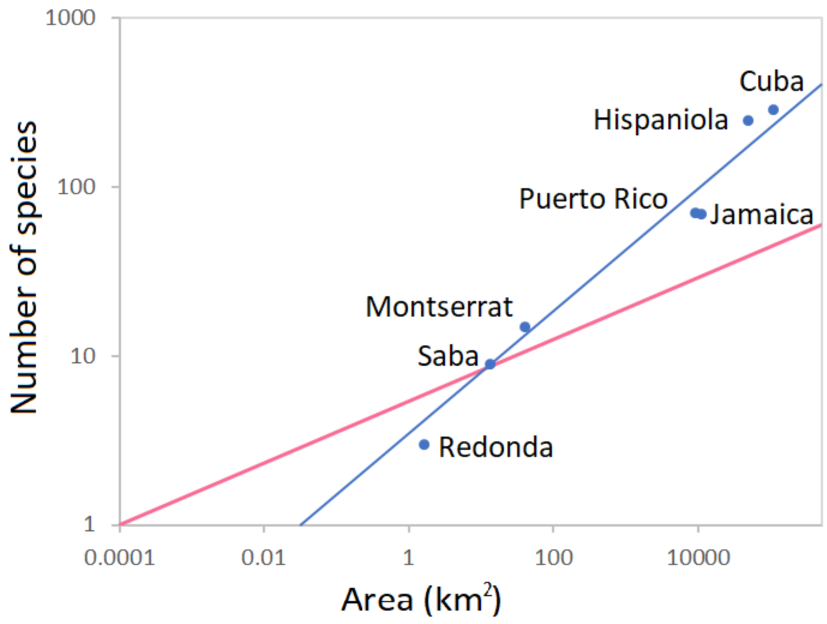


Figure 21.4.1: Species-area relationship for amphibians and reptilians on seven different islands in the West Indies. An original study (Darlington c. 1957), published in "The Theory of Island biogeography", showed a strong positive correlation between island size and number of species (blue line). A more recent study by Gao and Perry (2016) included data for many additional small islands (smaller than Redonda) and found that while the pattern holds, the relationship is flatter than in the original study--indicated by the pink line. Figure drawn by Andy Wilson, based on Figure 4 in Gao and Perry (2016).

While studying these species-area relationships for their seminal book, MacArthur and Wilson were drawn to another of the four geographic gradients--that of isolation. They observed that some large Islands had fewer species than would be expected for their size, while conversely, some small islands had more species than expected.

While studying patterns of species richness on islands, two ecologists, Robert H. MacArthur and Edward O. Wilson, noted some exceptions to the **species-area relationship**. For example, some large islands had fewer species than expected due to their size, while some small islands had more species than expected. These patterns were explained by MacArthur and Wilson's **Equilibrium Theory of Island Biogeography**, which takes into account the fact that islands are colonized by species from elsewhere, and natural extinctions will occur on those islands, over long periods of time.

Imagine there are two islands (**a** and **b**) located off the coast of the mainland. Although the two islands are about the same size, island **a** is located much farther away than island **b**. If you are a bird that lives on the mainland, which island are you most likely to find? The answer is generally island **b**. This means immigration (or colonization) is influenced by the distance of an island from the mainland (a source of colonists). Therefore, islands that are closer to the island are more likely to receive immigrants than islands that are further away.

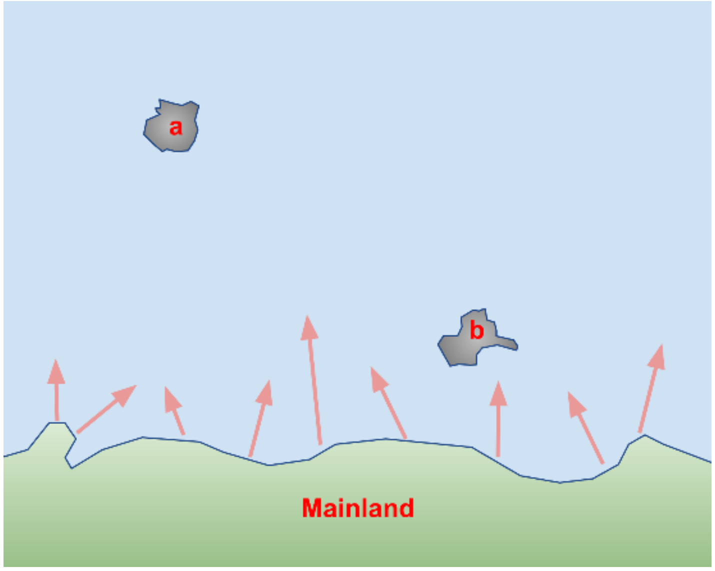


Figure 21.4.2: Two offshore islands--the Theory of Island Biogeography suggests that fewer species will colonize the more distant island **a**, in comparison to island **b** (credit: Andy Wilson, redrawn from Hdelucalowell15 (CC BY-SA 4.0)).

Once a species manages to reach and colonize an island, the rate of extinction is largely influenced by size of the island. This is because smaller islands tend to hold smaller populations (which are more likely to experience extinction due to stochastic effects like genetic drift). Larger habitat size reduces the probability of extinction of the colonized species due to chance events. Smaller islands are also likely to hold fewer populations in general because they have fewer resources and less diversity of resources. Larger islands have larger and more habitat areas, which typically leads to more differences in habitat or *habitat heterogeneity*. Higher heterogeneity means that there are more opportunities for a variety of species to find their suitable niches. Habitat heterogeneity also helps increase the number of species to successfully colonize after immigration.

Now let's consider the situation if we had two different islands sizes in our offshore archipelago, with **c** and **d**, much bigger than **a** and **b** Figure 21.4.3. We would expect extinction rates to be much lower on islands **c** and **d** than on the two smaller islands.

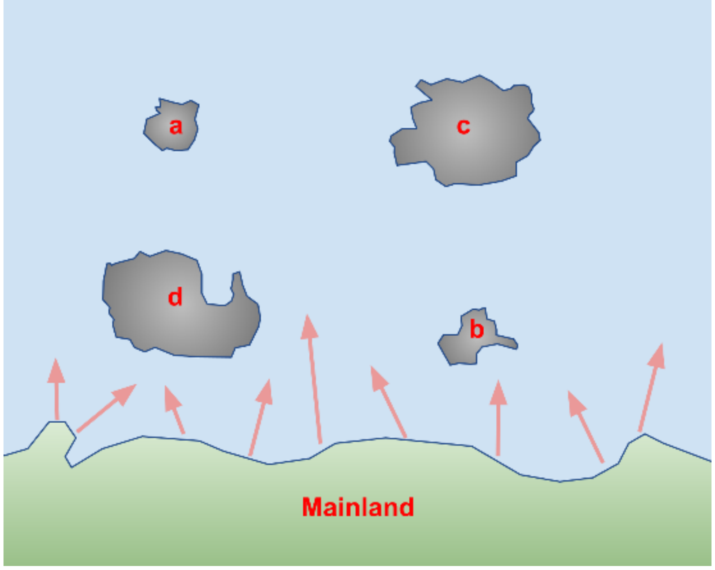


Figure 21.4.3: Four offshore islands--the Theory of Island Biogeography suggests that fewer species will go extinct on the larger islands **c** and **d**, in comparison to islands **a** and **b** (credit: Andy Wilson, redrawn from Wikipedia (CC BY-SA 4.0)).

We could plot both immigration and extinction relationships on a single image, as in Figure 21.4.4. Note the y-axis is the number of species (either colonizing or going extinct). Now we see that of the four islands in Figure 21.4.3, island **a** (small and far) would likely have the fewest species, island **d** (large and close), would have the most, and islands **b** and **c** would fall between the two extremes.

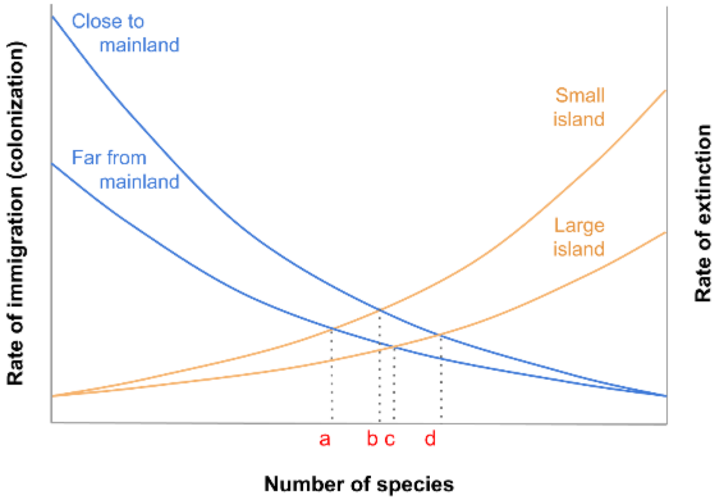


Figure 21.4.4: Equilibrium Theory of Island Biogeogaphy (credit: Andy Wilson, redrawn from Wikipedia (CC BY-SA 4.0)).

This basic graph makes a lot of assumptions but also offers a lot of insight. In this graph, immigration rates (blue lines) depend on proximity to mainland. Immigration rates also decline with species richness. That's becasuse its' easiest to immigrate to an island when it is empty because all the resources on the island are available. As the islands get more and more full, colonizing the island becomes more difficult.

Extinction rates (orange lines), as noted above, depend on island size. We also see that extinction rates tend to increase with the number of species. This should make sense: If there are no species on an island, extinction is impossible, but as more and more species arrive (and compete!) extinction becomes more likely.

Figure 21.4.4 shows the basic Equilibrium Theory of Island Biogeography. It suggests that islands will reach an equilibrium, or stable, number of species when immigration and extinction rates are equal! Note this model could be modified in multiple ways. Size of an island, for example, likely also impacts immigration rate (larger islands are easier to hit!), and islands that are close together may also share individuals (the Rescue effect!), but even this simple conceptualization has proven useful for understanding global species richness patterns.

One interesting point to note is that an equilibrium number of species is reached when immigration and extinction rates are equal, not when those processes stop! This means islands may consistently be changing species composition but should maintain fairly consistent levels of species richness. As odd as this sounds, early tests of the Equilibrium Theory of Island Biogeography supported these assumptions. When mangrove islands off the coast of Florida were fully cleared of their invertebrate (insect and arachnid) communities and allowed to recolonize, islands eventually stabilized with communities of about the same richness as they had before disturbance.

Conservation in Preserves as an application of Island Biogeography

The island biogeography model has crucial applications for wildlife management because wildlife reserves or patches of habitat can be considered “islands” of habitat in “an ocean” of an inhabitable area. For this reason, the Theory Island Biogeography has become central to our understanding of how habitat fragmentation leads to biodiversity loss. For a more detailed description of how habitat fragmentation leads to biodiversity loss, see the section on "Threats to Biodiversity" in the chapter on Conservation Biology from this book or see the section on "The Scramble for Space" in Conservation Biology in Sub-Saharan Africa (Wilson and Primack 2019).

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts (Figure $21.4.5$). A **preserve** is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. There has been extensive research into optimal preserve designs for maintaining biodiversity. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. In general, large preserves are better because they support more species, including species with large home ranges; they have more core area of optimal habitat for individual species; they have more niches to support more species; and they attract more species because they can be found and reached more easily. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing **wildlife corridors** (narrow strips of protected land) between two preserves is important so that species and their genes can move between them. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

Figure $21.4.5$: Mequon Nature Preserve in Wisconsin. Image by Jennifer Tomaloff (CC-BY-NC-SA).

Contributors and Attributions

Modified by Andy Wilson (Gettysburgh College), Kyle Whittinghill (University of Vermont) and Natasha Gownaris (Gettysburg College) from the following sources:

- https://sites.google.com/view/env10031004/lab/module-library/simulation-and-data-based-learning-activities/island-biogeography-simulation-simulation
- Preserving Biodiversity by OpenStax is licensed under CC BY 4.0 by Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- Threatened and Endangered Species by California Department of Fish and Wildlife (public domain)
- Marine Mammal Protection by NOAA Fisheries (public domain)
- Ecotourism from *Life Sciences Grade 10* by Siyavula (licensed under CC-BY)
- Issues and Opinions, Biological and Land from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.

CHAPTER OVERVIEW

22: Biodiversity

Learning Objectives

- Differentiate among the types of biodiversity
- Learn how to measure diversity using indices
- Understand why biodiversity is not evenly distributed
- Learn how rarefaction curves are used to estimate species richness

Summary

Genetic diversity, ecosystem diversity, and human-derived diversity are measures of biodiversity that currently define life on earth. Because it is often difficult to obtain a full list of species in any given location, various metrics are used to measure biodiversity, including Alpha, Beta, and Gamma diversity, and rarefaction curves. While around 2 million species have been scientifically described globally, estimates of the actual number of species on earth range from 10s of millions to billions.

22.1: What is Biodiversity?

Genetic diversity, ecosystem diversity, and human-derived diversity are measures of biodiversity that currently define life on earth.

Key Points

- A genus with a high variety of species will have more genetic diversity; the most genetically-diverse species will have the greatest potential for evolution and preservation.
- The loss of ecosystem diversity results in the loss of interactions between species, unique features of co-adaptation, and biological productivity.
- Human-generated species diversity has decreased due to migration, market forces, and agriculture.
- Humans have only been able to estimate the number of species that inhabit Earth; this estimate only accounts for 20 percent of predicted species on the planet.

Key Terms

- **genetic diversity**: variety of genes in a species or other taxonomic group or ecosystem; can refer to allelic diversity or genome-wide diversity
- **ecosystem diversity**: variety of ecosystems in a biosphere or the variety of species and ecological processes that occur in different physical settings
- **chemical diversity**: variety of metabolic compounds in an ecosystem

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. Genetic diversity or variation is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically-diverse one. It would be ideal not to have to make such choices, but, increasingly, this may be the norm.

Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as chemical diversity in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and by-products of metabolism. This chemical diversity has potential benefits for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily-populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source; its decline is troubling to biologists and agricultural scientists.

It is also useful to define ecosystem diversity: the number of different ecosystems on the planet or in a given geographic area. Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of co-adaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely-extinct ecosystem in North America is the prairie ecosystem. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. Now, they have mostly disappeared, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely-productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.

Figure \(\PageIndex{1}\): Ecosystem diversity - The variety of ecosystems on earth, from (a) coral reef to (b) prairie, enables a great diversity of species to exist.

✓ Functional Diversity and Indigenous Land Use Practices 22.1.1

Case Study Modified from Armstrong, C. G., Miller, J. E., McAlvay, A. C., Ritchie, P. M., & Lepofsky, D. (2021). Historical indigenous land-use explains plant functional trait diversity. Ecology and Society. 26: 6. This article was published under CC BY 4.0.

In addition to species diversity, ecologists are often interested in the trait or functional diversity of a community. A trait is simply any morphological, physiological or phenological feature measurable at the individual level (Reiss et al., 2009). Functional traits are those that define species in terms of their ecological roles - how they interact with the environment and with other species (Diaz & Cabido, 2001).

Functional diversity is a biodiversity measure based on functional traits of the species present in a community. In ocean phytoplankton, for example, these traits usually include body size, tolerance and sensitivity to environmental conditions, motility, shape, and N-fixation ability (Reynolds et al., 2002; Weithoff G., 2003). In terrestrial plant communities, researchers have included more complex traits like rates of growth, nutrient requirements and water uptake (Walker & Langridge, 2002; Barnett et al, 2007). Functional traits are a critical tool for understanding ecological communities because they give insights into community assembly processes as well as potential species interactions and other ecosystem functions. Because there are a greater variety of “roles” being played in a system with higher functional diversity, this measure of diversity has often been linked to higher ecosystem productivity and stability.

Human land-use legacies have long-term effects on plant community composition and ecosystem function and on the diversity of functional traits. Armstrong et al. (2021) studied how plant functional trait distributions and functional diversity are affected by ancient and historical Indigenous forest management in the Pacific Northwest.

Figure 22.1.2: The Village complex of Dałk Gyilakyaw consists of three discrete villages and is the ancestral home of Gitsm'geelm (Ts'msyen) people. Note the dramatic vegetation change between the forest garden and encroaching conifers ("periphery forests"). Photograph: S. Carroll.

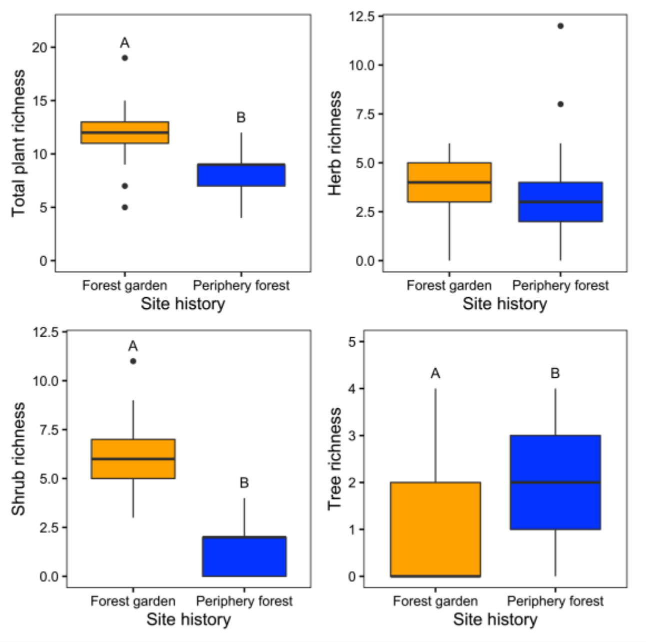


Figure 22.1.3: Total Species Richness and Species Richness by Lifeform. Richness is indicated overall between forest gardens and periphery forests (averaged across the four of the study areas) and among the three growth forms (trees, shrubs and herbs).

For their research into plant functional diversity, Armstrong et al. (2021) compared forest garden ecosystems - managed perennial fruit and nut communities associated exclusively with archaeological village sites - with surrounding periphery conifer forests. To characterize the functional diversity of understory plant communities, they focused on four functional traits: seed mass, shade tolerance, pollination syndrome, and dispersal syndrome. These traits represent important axes of plant life-history variation and can also have important consequences for ecosystem functioning, while also having relevance to ethnobotanical plant uses (Pérez-Harguindeguy et al., 2013). For example, plants with animal-dispersed seeds may be able to disperse long distances and may also contribute to wildlife habitat by providing edible fruits; these plants are also more likely to be eaten by people.

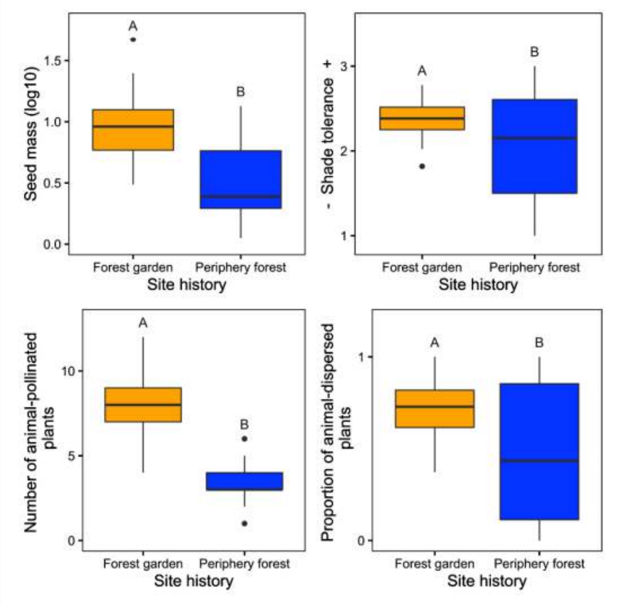


Figure 22.1.4: Functional Trait Measures between Forest Gardens and Periphery Forests. Comparisons of average seed mass, shade tolerance, pollination syndrome, and dispersal syndrome traits for herbs and shrubs across forest gardens and peripheral forests — all are significantly higher in the forest gardens.

Armstrong et al. (2021) found that forest gardens have substantially greater plant and functional trait diversity than periphery forests, even more than 150 years after management ceased. Forests managed by Indigenous peoples in the past now provide diverse resources and habitat for animals and other pollinators and are more rich than naturally forested ecosystems. Although ecological studies rarely incorporate Indigenous land-use legacies, the positive effects of Indigenous land use on contemporary functional and taxonomic diversity found by Armstrong et al. (2021) suggest that Indigenous management practices are tied to ecosystem health and resilience.

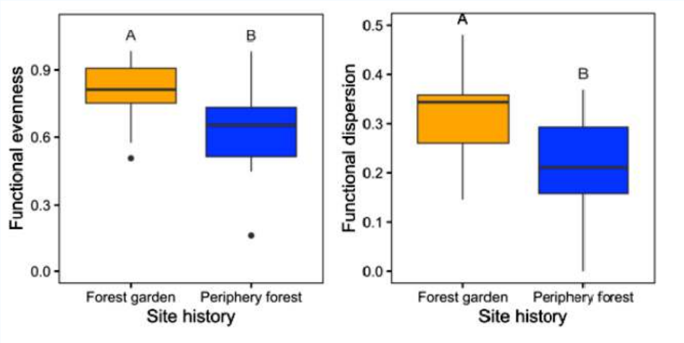


Figure 22.1.5: Functional Diversity Measures between Forest Gardens and Periphery Forests. Functional evenness (the evenness of functional trait distribution in niche space; Villéger et al. 2008) and functional dispersion (the average distance to the abundance-weighted centroid of functional trait values; Laliberté, and Legendre 2010) were significantly greater in forest gardens as compared to periphery forests. Comparisons of functional diversity at forest gardens and peripheral forests.

References

Barnett, A.J., & Beisner, B.E. (2007). Zooplankton biodiversity and lake tropic state: Explanations invoking resource abundance and distribution. *Ecology, 88*, pp. 1675-1686

Diaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution, 16*, pp. 646-655

Pérez-Harguindeguy N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, N. Buchmann, A.C., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., & Cornelissen, J.H.C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*, pp. 167-234.

Reiss, J., Bridle, J.R., Montoya, J.M. and Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol., 24*, pp. 505-514

Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L. and Melo, S. (2002). Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, *24*, pp. 417–428

Villéger, S., Mason, N.W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology, 89*, pp. 2290-2301.

Walker, B.H., & Langridge, J.L. (2002). Measuring functional diversity in plant communities with mixed lifeforms: A problem of hard and soft attributes. *Ecosystems, 5*, pp. 529–538

Weithoff, G. (2003). The concept of 'plant functional types' and 'functional diversity' in lake phytoplankton – new understanding of phytoplankton ecology? *Freshwater Biology, 48*, pp. 1669–1675

Contributors and Attributions

Written and modified by A. Wilson and N. Gownaris (Gettysburg College) from the following open-access sources

- Chapter 47.1B: Types of Biodiversity in General Biology (Boundless)
- Armstrong, C. G., Miller, J. E., McAlvay, A. C., Ritchie, P. M., & Lepofsky, D. (2021). Historical indigenous land-use explains plant functional trait diversity. Ecology and Society. 26: 6.
- Functional Traits - Coastal Wiki

22.2: Diversity Indices

Diversity Indices

A **diversity index** is a quantitative measure that reflects how many different types (such as species) there are in a dataset (a community). These indices are statistical representations of biodiversity in different aspects (richness, evenness, and dominance). When diversity indices are used in ecology, the types of interest are usually species, but they can also be other categories, such as genera, families, functional types, or haplotypes. The entities of interest are usually individual plants or animals, and the measure of abundance can be, for example, number of individuals, biomass or coverage.

Richness simply quantifies how many different types the dataset of interest contains. For example, species richness (usually noted S) of a dataset is the number of species in the corresponding species list. Richness is a simple measure, so it has been a popular diversity index in ecology, where abundance data are often not available for the datasets of interest.

Although species richness (denoted $\boldsymbol{S}$) is often used as a measure of biodiversity, of more interest to ecologists and conservation biologists are diversity indices that include both species richness *and* measures of abundance. This is because richness alone does not account for evenness across species. In Example $22.2.1$ below, both lakes have the same richness, but Lake B is more diverse because abundance is spread more evenly across the species present.

Many different indices of diversity are used by scientists, but below we cover the most widely used.

Simpson’s Index

Simpson (1949) developed an index of diversity which is a measure of probability--the less diversity, the greater the probability that two randomly selected individuals will be the same species. In the absence of diversity (1 species), the probability that two individuals randomly selected will be the same is 1. Simpson's Index is calculated as follows:

$$D=\sum_{i=1}^{S}\left(\frac{n_i}{N}\right)^2 \tag{22.2.1}$$

where n_i is the number of individuals in species i, N = total number of individuals of all species, and $n_i/N = p_i$ (proportion of individuals of species i), and S = species richness.

The value of Simpson’s $\boldsymbol{D}$ ranges from 0 to 1, with 0 representing infinite diversity and 1 representing no diversity, so the larger the value of $\boldsymbol{D}$, the lower the diversity. For this reason, Simpson’s index is often as its complement (1-$\boldsymbol{D}$). **Simpson's Dominance Index** is the inverse of the Simpson's Index (1/$\boldsymbol{D}$).

Shannon-Weiner Index

Another widely used index of diversity that also considers both species richness and evenness is the Shannon-Weiner Diversity Index, originally proposed by Claude Shannon in 1948. It is also known as **Shannon's Diversity Index.** The index is related to the concept of uncertainty. If for example, a community has very low diversity, we can be fairly certain of the identity of an organism we might choose by random (high certainty or low uncertainty). If a community is highly diverse and we choose an organism by random, we have a greater uncertainty of which species we will choose (low certainty or high uncertainty).

$$H = -\sum_{i=1}^{S} p_i * \ln p_i \tag{22.2.2}$$

where p_i = proportion of individuals of species i, and ln is the natural logarithm, and S = species richness.

The value of ***H*** ranges from 0 to $H_{max.}$ H_{max} is different for each community and depends on species richness. (Note: Shannon-Weiner is often denoted H').

Evenness Index

Species evenness refers to how close in numbers each species in an environment is. So if there are 40 foxes and 1000 dogs, the community is not very even. But if there are 40 foxes and 42 dogs, the community is quite even. The evenness of a community can be represented by Pielou's evenness index (Pielou, 1966):

$$J = \frac{H}{H_{\text{max}}} \tag{22.2.3}$$

The value of J ranges from 0 to 1. Higher values indicate higher levels of evenness. At maximum evenness, ***J*** = 1.

J and ***D*** can be used as measures of **species dominance** (the opposite of diversity) in a community. Low J indicates that 1 or few species dominate the community.

? Exercise 22.2.1

Calculate **Simpson's Index**, **Shannon-Weiner Index**, and the **Evenness Index** for waterbirds on two lakes: Lake A, and Lake B. There are 5 species and 25 individuals on both lakes, but are they equally diverse? Try to check all three indices to decide on your conclusion before you check the answers!

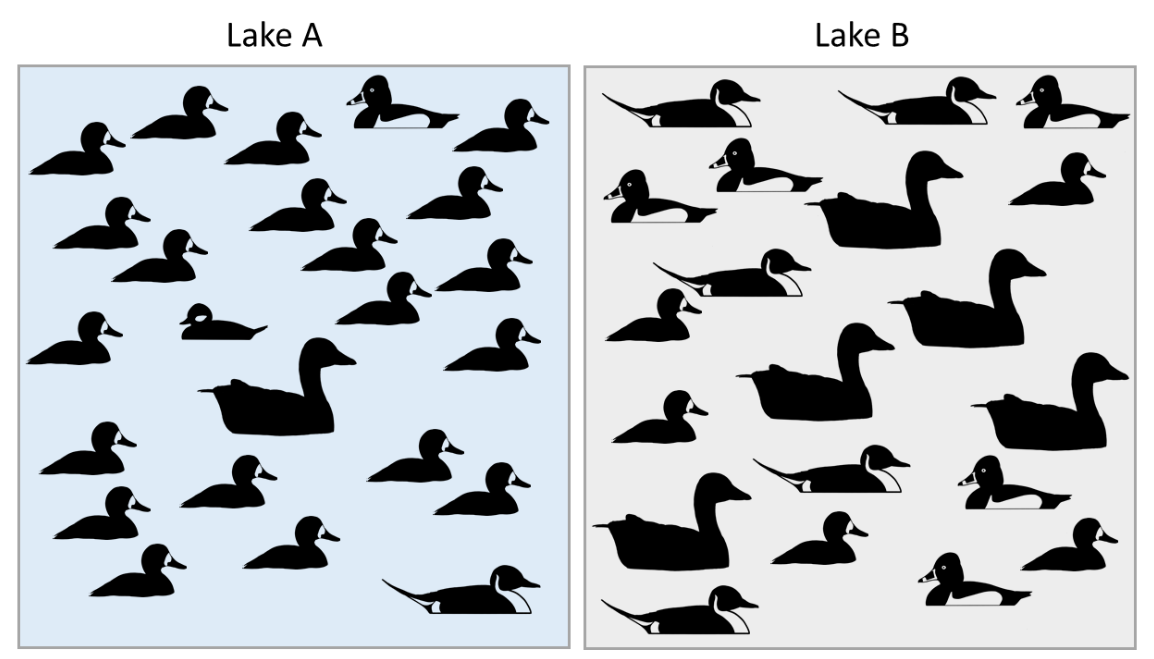
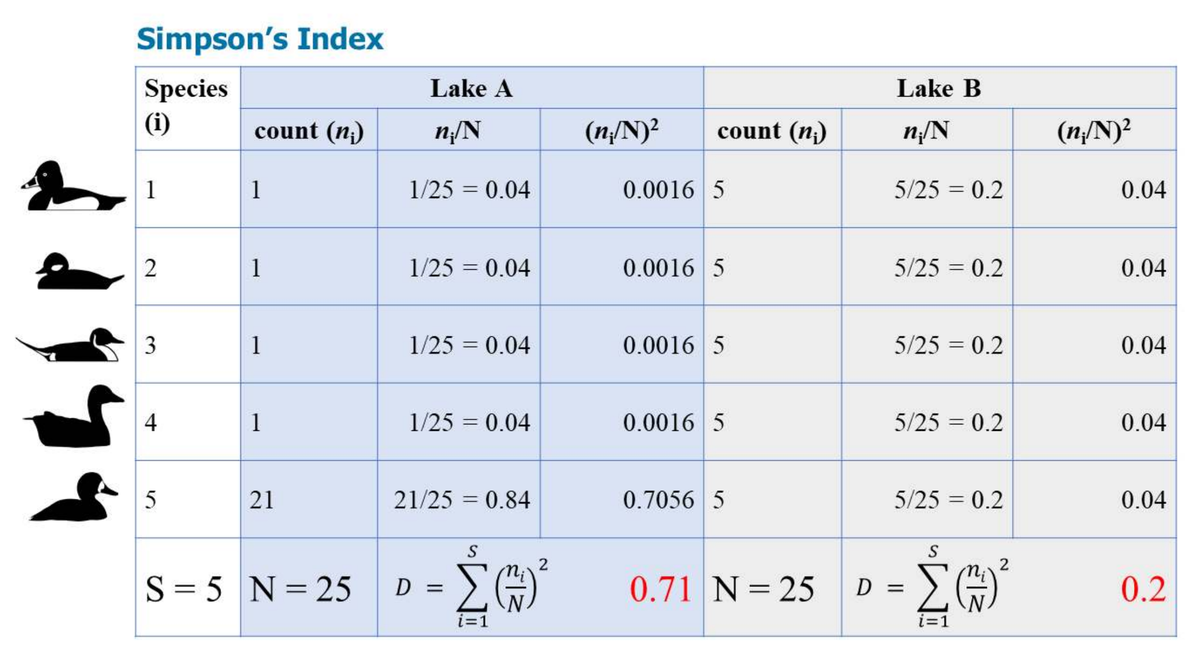


Figure 22.2.1 : Though both Lakes A and B have the same amount of birds and the same number of different species, their diversity is different.

Answer

Solutions for each of the indices are shown below.

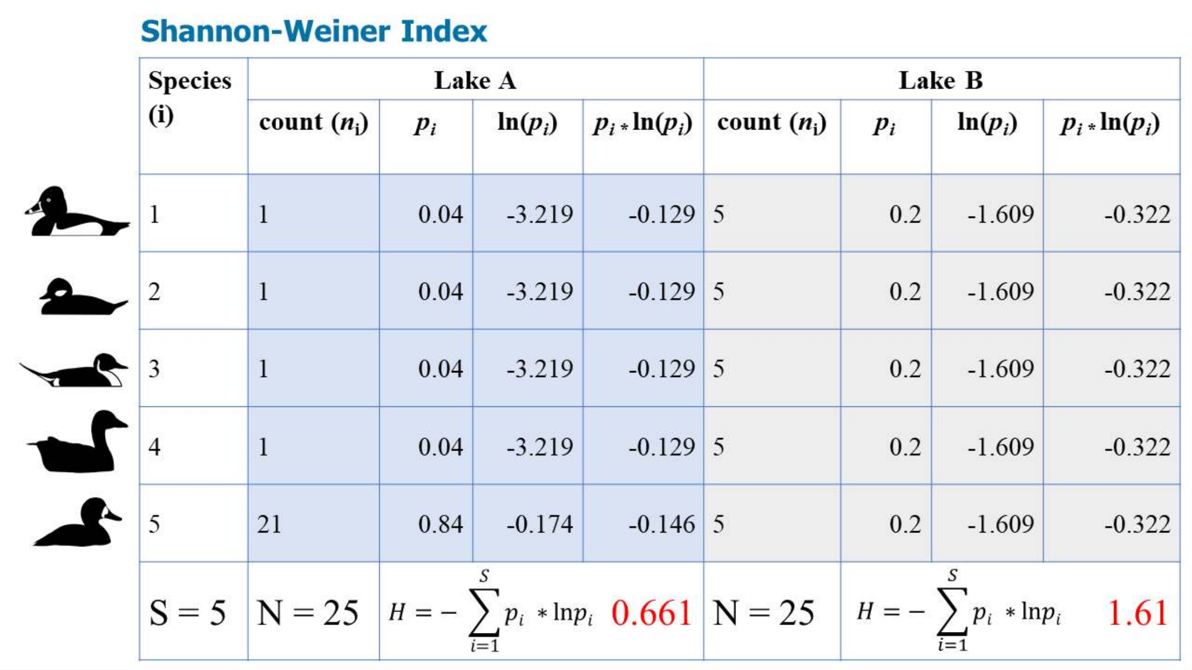


Simpson's Index

Species (i)	Lake A			Lake B		
	count (n_i)	n_i/N	(n_i/N)^2	count (n_i)	n_i/N	(n_i/N)^2
1	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
2	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
3	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
4	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
5	21	21/25 = 0.84	0.7056	5	5/25 = 0.2	0.04
S = 5	N = 25	$D = \sum_{i=1}^{S}\left(\frac{n_i}{N}\right)^2$	0.71	N = 25	$D = \sum_{i=1}^{S}\left(\frac{n_i}{N}\right)^2$	0.2

Figure 22.2.2 The three blue columns show the steps to calculate D for Lake A, while the three gray columns show the steps to calculate D for Lake B. Though the S and N values are the same for both lakes, the proportion of each species in the lakes results in different D values.

Note that Simpson's Index is often expressed (1-*D*), so the final answers are **0.29** and **0.8**. This makes more intuitive sense: a higher D is more diverse--which is Lake B because it is less dominated by one species.

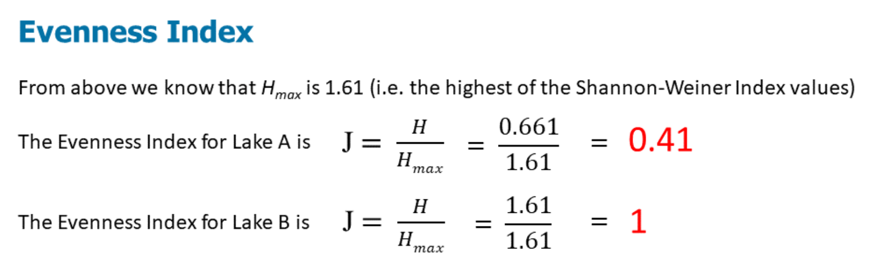


Shannon-Weiner Index

Species (i)	Lake A				Lake B			
	count (n_i)	p_i	$\ln(p_i)$	$p_i * \ln(p_i)$	count (n_i)	p_i	$\ln(p_i)$	$p_i * \ln(p_i)$
1	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
2	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
3	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
4	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
5	21	0.84	-0.174	-0.146	5	0.2	-1.609	-0.322
S = 5	N = 25	$H = -\sum_{i=1}^{S} p_i * \ln p_i$		0.661	N = 25	$H = -\sum_{i=1}^{S} p_i * \ln p_i$		1.61

Figure 22.2.3 The four blue columns show the steps to calculate H for Lake A, while the four gray columns show the steps to calculate H for Lake B.

Again, according to the Shannon-Weiner Index, Lake B is more diverse.



Evenness Index

From above we know that H_{max} is 1.61 (i.e. the highest of the Shannon-Weiner Index values)

The Evenness Index for Lake A is $J = \frac{H}{H_{max}} = \frac{0.661}{1.61} = 0.41$

The Evenness Index for Lake B is $J = \frac{H}{H_{max}} = \frac{1.61}{1.61} = 1$

Figure 22.2.4 J calculates the species evenness for Lakes A and B using the Shannon-Weiner Index calculations.

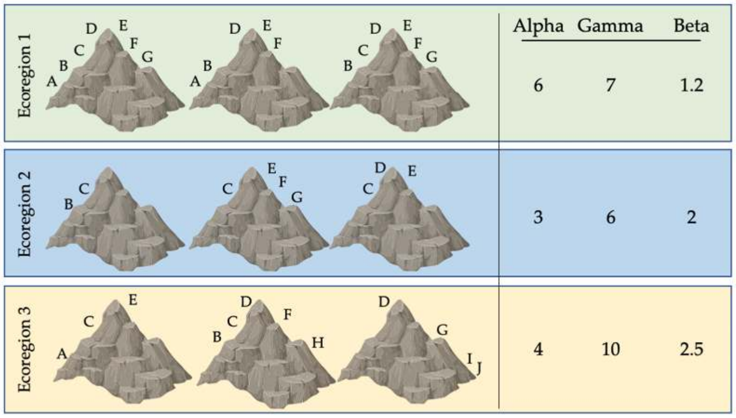
Conclusion

By all three measures, Lake B is more diverse, despite the fact that the two lakes have identical species richness.

Biodiversity at different scales- Alpha, Beta, and Gamma

Biologists have developed three quantitative measures of species diversity as a means of measuring and comparing species diversity:

- Alpha diversity (or species richness), the most commonly referenced measure of species diversity, refers to the total number of species found in a particular biological community, such as a lake or a forest. Bwindi Forest in Uganda, with an estimated 350 bird species, has one of the highest alpha diversities of all African ecosystems.
- Gamma diversity describes the total number of species that occur across an entire region, such as a mountain range or continent, that includes many ecosystems. The Albertine Rift, which includes Bwindi Forest, has more than 1,074 species of birds, a very high gamma diversity for such a small region.
- Beta diversity connects alpha and gamma diversity. It describes the rate at which species composition changes across a region. For example, if every wetland in a region was inhabited by a similar suite of plant species, then the region would have low beta diversity; in contrast, if several wetlands in a region had plants communities that were distinct and had little overlap with one another, the region would have high beta diversity. Beta diversity is calculated as gamma diversity divided by alpha diversity. The beta diversity for forest birds of the Albertine Rift is about 3.0, if each ecosystem in the area has about the same number of species as Bwindi Forest.



	Alpha	Gamma	Beta
Ecoregion 1	6	7	1.2
Ecoregion 2	3	6	2
Ecoregion 3	4	10	2.5

Figure 22.2.5: Biodiversity indices for nine mountain peaks across three ecoregions. Each symbol represents a different species; some species have populations on only one peak, while others are found on two or more peaks. The variation in species richness on each peak results in different alpha, gamma, and beta diversity values for each ecoregion. This variation has implications for how

we divide limited resources to maximise protection. If only one ecoregion can be protected, ecoregion 3 may be a good choice because it has high gamma (total) diversity. However, if only one peak can be protected, should a peak in ecoregion 1 (with many widespread species) or ecoregion 3 (with several unique, range-restricted species) be protected? After Primack, 2012, CC BY 4.0.

It is important to note that alpha, beta, and gamma diversity describe only part of what is meant by biodiversity. For example, none of these three terms completely account for genetic diversity, which allows species to adapt as conditions change. It also neglects the importance of ecosystem diversity, which results from the collective response of species to their dynamic environment. However, these diversity measures are useful for comparing different regions, and identifying locations with high concentrations of native species that should be protected.

References

Pielou, E.C. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology, 13*, pp. 131–144. doi:10.1016/0022-5193(66)90013-0.

Simpson, E.H. (1949). Measurement of diversity. *Nature*, *163*, pp. 688. doi:10.1038/163688a0

Shannon, C.E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, *27*, pp. 379-423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) with material from the following open-access sources:

- Conservation Biology in Sub-Saharan Africa by John W. Wilson and Richard B. Primack
- Diversity Index by Wikipedia, the free Encyclopedia

22.3: Patterns in Biodiversity

Biodiversity is not evenly distributed on the planet. For example, Lake Victoria in Africa (Figure 22.3.1) contained almost 500 species from a family of fishes called cichlids before the introduction of the **invasive** Nile Perch in the 1980s and 1990s caused a mass extinction. Note that this number does not include species of other fish families. Lake Huron, the second largest of North America's Great Lakes, contains about 79 species of fish, all of which are found in many other lakes in North America.

What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These two factors, latitude and age, are two of several hypotheses that biogeographers have suggested explain biodiversity patterns on Earth.

Figure 22.3.1: Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software).

Biogeography is the study of the distribution of the world's species both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species. There are three main subfields of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. **Ecological biogeography** studies the current factors affecting the distribution of plants and animals. **Historical biogeography**, as the name implies, studies the past distribution of species. **Conservation biogeography**, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information.

Understanding the global distribution of biodiversity is one of the most significant objectives for ecologists and biogeographers. Beyond purely scientific goals and satisfying curiosity, this understanding is essential for applied issues of major concern to humankind, such as the spread of invasive species, the control of diseases and their vectors, and the likely effects of global climate change on the maintenance of biodiversity (Gaston, 2000).

22.3.1 Latitudinal Gradients in Biodiversity

Source: https://en.wikipedia.org/wiki/Latitu...cies_diversity

Species richness, or biodiversity, increases from the poles to the tropics for a wide variety of terrestrial and marine organisms Figure 22.3.2 This effect is often referred to as the latitudinal diversity gradient (LDG). The LDG is one of the most widely recognized patterns in ecology. A parallel trend has been found with elevation (elevational diversity gradient), though this is less well-studied. Tropical areas play prominent roles in the understanding of the distribution of biodiversity, as their rates of habitat degradation and biodiversity loss are exceptionally high.

Explaining the latitudinal diversity gradient has been called one of the great contemporary challenges of biogeography and macroecology (e.g. Willig et al., 2003; Pimm & Brown, 2004). There is a lack of consensus among ecologists about the mechanisms underlying the pattern, and many hypotheses have been proposed and debated.

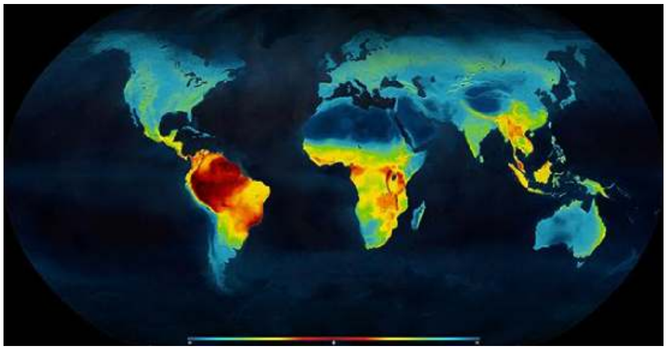


Figure 22.3.2: Map latitudinal gradient of living terrestrial vertebrate species richness (Mannion, 2014).

22.3.2 Hypotheses for Latitudinal Gradients

Although many of the hypotheses exploring the latitudinal diversity gradient are closely related and interdependent, the major hypotheses can be split into three general hypotheses. As you will see below, all of these hypotheses have experienced considerable criticisms and debate among members of the scientific community.

Spatial/Area Hypothesis

Mid-domain effect

Using computer simulations, Cowell and Hurt (1994) and Willig and Lyons (1998) first pointed out that if species' latitudinal ranges were randomly shuffled within the geometric constraints of a bounded biogeographical domain (e.g. the continents of the New World, for terrestrial species), species' ranges would tend to overlap more toward the center of the domain than towards its limits, forcing a mid-domain peak in species richness. Colwell and Lees (2000) called this stochastic phenomenon the mid-domain effect (MDE) and suggested the hypothesis that MDE might contribute to the latitudinal gradient in species richness, together with other explanatory factors considered here, including climatic and historical ones. Mid-domain effects have proven controversial. While some studies have found evidence of a potential role for MDE in latitudinal gradients of species richness, particularly for wide-ranging species, others report little correspondence between predicted and observed latitudinal diversity patterns.

Species-energy hypothesis

The species energy hypothesis suggests that the amount of available energy sets limits to the richness of the system. Thus, increased solar energy (with an abundance of water) at low latitudes causes increased net primary productivity (or photosynthesis). This hypothesis proposes the higher the net primary productivity the more individuals can be supported, and the more species there will be in an area. Put another way, this hypothesis suggests that extinction rates are reduced towards the equator as a result of the higher populations sustainable by the greater amount of available energy in the tropics. Lower extinction rates lead to more species in the tropics.

One critique of this hypothesis has been that increased species richness over broad spatial scales is not necessarily linked to an increased number of individuals, which in turn is not necessarily related to increased productivity (Cardillo et al., 2005). The effect of energy has, however, been supported by several studies in terrestrial and marine taxa (Tittensor et al., 2010). The potential mechanisms underlying the species-energy hypothesis, their unique predictions and empirical support have been assessed in a major review by Currie et al. (2004).

Climate-related hypotheses

Another climate-related hypothesis is the climate harshness hypothesis, which states the latitudinal diversity gradient may exist simply because fewer species can physiologically tolerate conditions at higher latitudes than at low latitudes because higher latitudes are often colder and drier than tropical latitudes. Currie et al. (2004) found fault with this hypothesis by stating that, although it is clear that climatic tolerance can limit species distributions, it appears that species are often absent from areas whose climate they can tolerate.

Similarly to the climate harshness hypothesis, climate stability is suggested to be the reason for the latitudinal diversity gradient. The mechanism for this hypothesis is that while a fluctuating environment may increase the extinction rate or preclude specialization, a constant environment can allow species to specialize on predictable resources, allowing them to have narrower niches and facilitating speciation. The fact that temperate regions are more variable both seasonally and over geological timescales (discussed in more detail below) suggests that temperate regions are thus expected to have less species diversity than the tropics. Critiques for this hypothesis include the fact that there are many exceptions to the assumption that climate stability means higher species diversity. Additionally, many habitats with high species diversity do experience seasonal climates, including many tropical regions that have highly seasonal rainfall (Brown & Lomolino, 1998).

Historical/Evolutionary hypotheses

The historical perturbation hypothesis

The historical perturbation hypothesis proposes the low species richness of higher latitudes is a consequence of an insufficient time period available for species to colonize or recolonize areas because of historical perturbations such as glaciation (Brown & Lomolino, 1998; Gaston & Blackburn, 2000). This hypothesis suggests that diversity in the temperate regions has not yet reached equilibrium and that the number of species in temperate areas will continue to increase until saturated (Clarke & Crame, 2003).

The evolutionary rate hypothesis

The evolutionary rate hypothesis argues that higher evolutionary rates in the tropics have caused higher speciation rates and thus increased diversity at low latitudes (Cardillo et al., 2005; Weir & Schluter, 2007; Rolland et al., 2014). Higher evolutionary rates in the tropics have been attributed to higher ambient temperatures, higher mutation rates, shorter generation time and/or faster physiological processes (Rohde, 1992; Allen et al., 2006), and increased selection pressure from other species that are themselves evolving (Schemske et al., 2009). Faster rates of microevolution in warm climates (i.e. low latitudes and altitudes) have been shown for plants (Wright et al. 2006), mammals (Gillman et al., 2009), and amphibians (Wright et al., 2010). Based on the expectation that faster rates of microevolution result in faster rates of speciation, these results suggest that faster evolutionary rates in warm climates almost certainly have a strong influence on the latitudinal diversity gradient. More research needs to be done to determine whether or not speciation rates actually are higher in the tropics. Understanding whether extinction rate varies with latitude will also be important to whether or not this hypothesis is supported (Rolland et al., 2014).

The hypothesis of effective evolutionary time

The hypothesis of effective evolutionary time assumes that diversity is determined by the evolutionary time under which ecosystems have existed under relatively unchanged conditions, and by evolutionary speed directly determined by effects of environmental energy (temperature) on mutation rates, generation times, and speed of selection (Rohde, 1992). It differs from most other hypotheses in not postulating an upper limit to species richness set by various abiotic and biotic factors, i.e., it is a nonequilibrium hypothesis assuming a largely non-saturated niche space. It does accept that many other factors may play a role in causing latitudinal gradients in species richness as well. The hypothesis is supported by much recent evidence, in particular, the studies of Allen et al. (2006) and Wright et al. (2006).

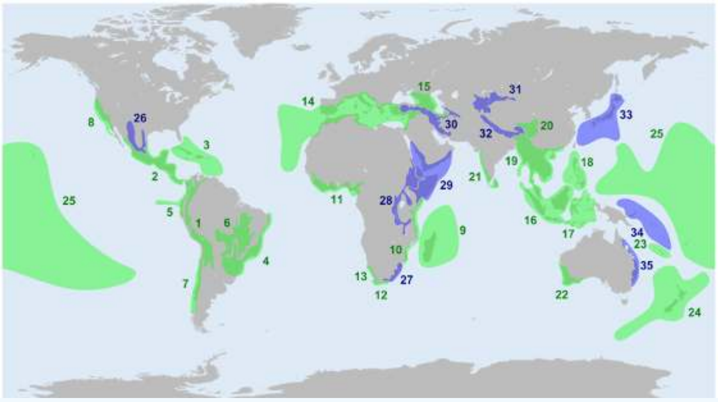
Biotic hypotheses

Biotic hypotheses claim ecological species interactions such as competition, predation, mutualism, and parasitism are stronger in the tropics and these interactions promote species coexistence and specialization of species, leading to greater speciation in the tropics. These hypotheses are problematic because they cannot be the ultimate cause of the latitudinal diversity gradient as they fail to explain why species interactions might be stronger in the tropics. An example of one such hypothesis is the greater intensity of predation and more specialized predators in the tropics has contributed to the increase of diversity in the tropics (Pianka, 1966). This intense predation could reduce the importance of competition (see competitive exclusion) and permit greater niche overlap and promote higher richness of prey. Some recent large-scale experiments suggest predation may indeed be more intense in the tropics,[12][13] although this cannot be the ultimate cause of high tropical diversity because it fails to explain what gives rise to the richness of the predators in the tropics. Interestingly, the largest test of whether biotic interactions are strongest in the tropics, which focused on predation exerted by large fish predators in the world's open oceans, found predation to peak at mid-latitudes. Moreover, this test further revealed a negative association of predation intensity and species richness, thus contrasting the idea that strong predation near the equator drives or maintains high diversity.[14] Other studies have failed to observe consistent changes in ecological interactions with latitude altogether (Lambers et al., 2002),[1] suggesting that the intensity of species interactions is not correlated with the change in species richness with latitude. Overall, these results highlight the need for more studies on the importance of species interactions in driving global patterns of diversity.

✓ Biodiversity Hotspots 22.3.1

With the enormous number of species that exist on Earth, it is remarkable that the distribution of these species is so highly concentrated in specific areas. Species richness, the total number of species found in an area, is not evenly distributed around the globe: two-thirds of all known species occur in tropical areas.

In order to prioritize the areas that should be protected, scientists look for areas that are home to a large number of species, especially those species that are under threat of extinction. or that are currently being destroyed at a fast pace. These areas that are particularly important for biodiversity conservation are called biodiversity hotspots. Two things are crucial when determining that a place is a biodiversity hotspot: (i) the number of different species there; and (ii) whether species in that area are endangered or currently being destroyed. Figure $22.3.3$ shows the location of 36 biodiversity hotspots, according to the Critical Ecosystem Partnership Fund.



North and Central America	
2	Mesoamerica
8	California Floristic Province
26	Madrean pine–oak woodlands
The Caribbean	
3	Caribbean Islands
South America	
1	Tropical Andes
4	Atlantic Forest
5	Tumbes–Chocó–Magdalena
6	Cerrado
7	Chilean Winter Rainfall-Valdivian Forests
Europe	
14	Mediterranean Basin
Africa	
9	Madagascar and the Indian Ocean Islands
10	Coastal Forests of Eastern Africa
11	Guinean Forests of West Africa
12	Cape Floristic Region
13	Succulent Karoo
27	Maputaland-Pondoland-Albany
28	Eastern Afromontane
29	Horn of Africa
Central Asia	
31	Mountains of Central Asia
South Asia	
19	Indo-Burma, India and Myanmar
21	Western Ghats and Sri Lanka
32	Eastern Himalaya
Southeast Asia and Asia-Pacific	
16	Sundaland and Nicobar islands of India
17	Wallacea
18	Philippines
22	Southwest Australia
23	New Caledonia
24	New Zealand
25	Polynesia-Micronesia
34	East Melanesian Islands
35	Eastern Australian temperate forests
East Asia	
20	Mountains of Southwest China
33	Japan
West Asia	
15	Caucasus
30	Irano-Anatolian

Figure $22.3.3$: The names and locations of current biodiversity hotspots around the globe. The original 25 in green, and added regions in purple (Wikipedia, edited by Andy Wilson).

Scientists have observed that, even though biodiversity hotspots make up only approximately 1.4% of land on our planet, they are home to 60% of Earth's plant, bird, mammal, and reptile species (Possingham and Wilson 2005). Just the endangered species in the tropics accounts for 43% of vertebrates (animals with backbones and their close relatives) and 80% of all amphibians (Marchese 2015). Species found only in a certain geographical area are known as endemic species, and biodiversity hotspots are full of them! For example, the Banana Tree Frog can only be found in Ethiopia, and you will only find lemurs in Madagascar (Herrera 2017). Tropical forests are typically biodiversity hotspots and are usually filled with endemic species. The Upper Amazonia/Guyana Shield, the Congo Basin, and the New Guinea/Melanesian Islands have the highest number of endemic terrestrial (land-living) species on Earth (Cincotta et al. 2000). Figure $22.3.4$ shows some examples of biodiversity hotspots and some of their endemic animals and plants.

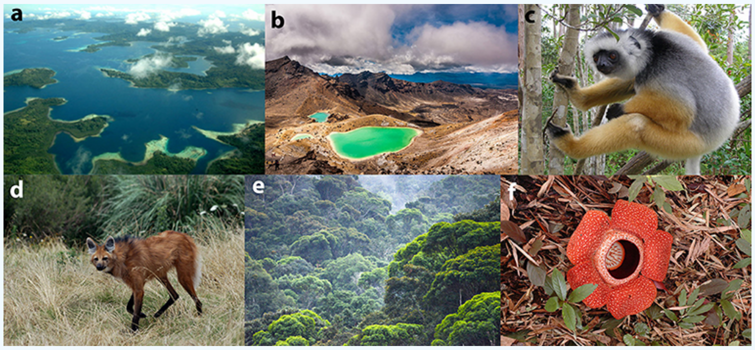


Figure $22.3.4$: Biodiversity hotspots and some of their endemic species. (a) Melanesian Islands ["Solomon Islands" by Jim Lounsbury is available for open access]; (b) Emerald Lakes, New Zealand [Photo by Marcus Holland-Moritz is licensed under CC BY-SA 2.0]; (c) Diademed sifaca, one of the endemic lemur species from Mantadia National Park, Madagascar ["Diademed ready to push off" by Michael Hogan is available in the public domain]; (d) Maned wolf, the largest canid of South America, a species from the Cerrado hotspot [Photo by Aguará is licensed under CC SA 3.0]; (e) Atlantic Forest, Caparaó, Brazil ["Caparaó e a Mata Atlântica" by Heris Luiz Cordeiro Rocha is licensed under CC SA 3.0]; (f) Rafflesia, one of the largest flowers in nature. This particular one, from Borneo, is 80 cm wide ["*Rafflesia keithii* bloom" by Steve Cornish is licensed under CC BY 2.0]

In addition to land, the waters surrounding these tropical regions are just as important, and equally in danger (Marchese, 2015). Tropical coral reefs are currently being threatened by climate change. The change of weather and temperature patterns around the world cause intense habitat destruction, especially of these reefs. These areas are some of the most biodiverse ecosystems on our planet! Scientific studies of 3,235 marine species in these areas, including fishes, corals, snails, and lobsters, show that high percentages of these species are at serious risk of becoming extinct (Roberts et al., 2002). Conservation of species living in fresh or seawater is especially difficult, because many bodies of water are interconnected. For example, all the oceans are connected through sea currents that allow the movement of species, minerals, and pollution across the entire globe (Pimm et al., 2014).

Sources

Allen, A.P., Gillooly, J.F., Savage, V.M., & Brown, J.H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *PNAS, 103*(24), pp. 9130–9135. doi:10.1073/pnas.0603587103. PMC 1474011. PMID 16754845.

Brown, J.H., & Lomolino, M.V. (1998). Biogeography. *Sinauer Associates, Sunderland*.

Cardillo, M., Orme, C.D. L., & Owens, I.P.F. (2005). Testing for latitudinal bias in diversification rates: An example using New World birds. *Ecology, 86*(9), pp. 2278–2287. doi:10.1890/05-0112.

Cincotta, R.P., Wisnewski, J., & Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature, 404*, pp. 990–2. doi: 10.1038/35010105

Clarke, A., & Crame, J.A. (2003). The importance of historical processes in global patterns of diversity. In Blackburn T.M., & Gaston, K.J. (Eds.), *Macroecology concepts and consequences* (pp. 130-151). Blackwell Scientific, Oxford.

Colwell, R.K., & Lees, D.C. (2000). The mid-domain effect: Geometric constraints on the geography of species richness. *Trends in Ecology & Evolution, 15*(2), pp. 70–76. doi:10.1016/s0169-5347(99)01767-x. PMID 10652559.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Kaufman, D.M., Kerr, J.T., & Oberdorff, T. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters, 7*(12), pp. 1121–1134. doi:10.1111/j.1461-0248.2004.00671.x.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature, 405*(6783), pp. 220–227. doi:10.1038/35012228. PMID 10821282. S2CID 4337597.

Gaston, K.J., & Blackburn, T.M. (2000). Pattern and processes in macroecology. *Blackwell Scientific, Oxford*.

Herrera, J.P. (2017). Testing the adaptive radiation hypothesis for the Lemurs of Madagascar. *R. Soc. Open Sci., 4*, 161014. doi: 10.1098/rsos.161014

Lambers, J.H.R., Clark, J.S., & Beckage, B. (2002). Density-dependent mortality and the latitudinal gradient in species diversity. *Nature, 417*(6890), pp. 732–735. doi:10.1038/nature00809.

Marchese, C. (2015). Biodiversity hotspots: A shortcut for a more complicated concept. *Glob. Ecol. Conserv., 3*, pp. 297–309. doi: 10.1016/j.gecco.2014.12.008

Pianka, E.R. (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist, 100*(910), pp. 33–46. doi:10.1086/282398. S2CID 84244127.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., et al. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science, 344*, 1246752. doi: 10.1126/science.1246752.

Possingham, H.P., & Wilson, K.A. (2005). Biodiversity: Turning up the heat on hotspots. *Nature, 436*, pp.919–20. doi: 10.1038/436919a.

Roberts, C.M., McClean, C.J., Veron, J.E., Hawkins, J.P., Allen, G.R., McAllister, D.E., et al. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science, 295*, pp. 1280–4. doi: 10.1126/science.1067728.

Rohde, K. (1997). The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos, 79*(1), pp. 169–172. doi:10.2307/3546102. JSTOR 3546102.

Rolland, J., Condamine, F.L., Jiguet, F., & Morlon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLOS Biology, 12*(1), e1001775. doi:10.1371/journal.pbio.1001775. PMC 3904837. PMID 24492316.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., & Kaustuv, R. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics, 40*(1), pp. 245–269. doi:10.1146/annurev.ecolsys.39.110707.173430.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature, 466*(7310), pp. 1098–1101. doi:10.1038/nature09329.

Weir, J.T., & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science, 315*(5818), pp. 1574–1576. Bibcode:2007Sci...315.1574W. doi:10.1126/science.1135590. PMID 17363673. S2CID 46640620.

Willig, M.R., & Lyons, S.K. (1998). An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos, 81*(1), pp. 93–98. doi:10.2307/3546471. JSTOR 3546471.

Willig, M.R., Kaufmann, D.M., & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale and synthesis. *Annu. Rev. Ecol. Syst., 34*, pp. 273–309. doi:10.1146/annurev.ecolsys.34.012103.144032.

Wright, S., Keeling, J., & Gillman, L. (2006). The road from Santa Rosalia: A faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences, 103*(20), pp. 7718–7722. doi:10.1073/pnas.0510383103.

Wright, S.D., Gillman, L.N., Ross, H.A., & Keeling, D.J. (2010). Energy and the tempo of evolution in amphibians: Energy and the tempo of evolution in amphibians. Global Ecology and Biogeography: no–no. doi:10.1111/j.1466-8238.2010.00549.x.

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) from the following open-access sources:

- Chapter 9.4 in Environmental Science by Melissa Ha and Rachel Schleiger, licensed under CC BY - SA
- Latitudinal Gradients in Species Diversity by Wikipedia, the Free Encyclopedia
- What are Biodiversity Hotspots? on Frontiers for Young Minds By Melanie Merritt, Maria Eduarda Maldaner, and Ana Maria Rocha de Almeida and Reviewed by Songo Info

---

22.4: How many species are there?

To date, taxonomists have described about 2.2 million species that share this planet with us (http://www.catalogueoflife.org/annual-checklist/2019/info/about). While this total may seem impressive, available evidence suggests that this estimate vastly underestimates the true extent of Earth's biodiversity. In fact, even now, after all the exploration in years gone by, several thousand new species are being described each year. Many new discoveries are made by skilled researchers recognizing new species by being able to discern variation in morphological characters; that includes the discoveries of a new small forest antelope from West Africa (Colyn et al., 2010) and a new species of shark off Mozambique (Ebert & Cailliet, 2011). New genetic technologies have highlighted that there are many thousands of species yet to be described. Both traditional and genetic techniques rely heavily on the availability of specimens in Natural History Museums collections to help identify and describe new species (Sforzi et al., 2018). A lack of taxonomists and natural history collections in many of the world's most biodiverse countries means there is a still a great deal of work to do (Paknia et al., 2015).

The most exciting and newsworthy discoveries of new species generally involve higher-level taxa, especially living fossils. For example, in 1938, biologists across the world were stunned by the report of a strange fish caught in the Indian Ocean off South Africa. This fish, subsequently named coelacanth *Latimeria chalumnae*, belongs to a group of marine fishes that were common in ancient seas but were thought to have gone extinct 65 million years ago. Coelacanths are of interest to evolutionary biologists because they show certain features of muscles and bones in their fins that are comparable to the limbs of the first vertebrates that crawled onto land. Following the initial discovery, coelacanths have been found along Africa's Indian Ocean coast from South Africa to the Comoros and through to Kenya. Unfortunately, the entire coelacanth population, estimated at fewer than 500 individuals, is currently highly threatened because of ongoing fishing pressures (Musick, 2000).

Although field surveys have proven to be of great importance for discovering new species and populations, perhaps the greatest taxonomic progress has come from advances in genetic analyses which help to separate cryptic species previously lumped under more widespread species. For example, advances in genetic research recently highlighted that the African clawed frog *Xenopus laevis*—a popular model organism in biomedical research—consists of seven distinct species (Evans et al., 2015). Similarly, using new genetic methods, scientists recently confirmed that the slender-snouted crocodile *Mecistops cataphractus* consists of two different species, one endemic to West Africa and the other to Central Africa (Shirley et al., 2018).

> Estimates suggest there are somewhere between 1–6 billion distinct species on Earth. The most diverse group of species is bacteria.

The presence of so many undiscovered species and communities makes precise estimates of species diversity incredibly difficult, especially in Africa where so many areas remain scientifically unexplored. Our most recent estimates, combining genetic analysis of well-known groups with mathematical patterns, suggests there are between 1–6 billion distinct species on Earth (Table 22.4.1) of which there are only about 163 million animals and 340 thousand plants (Larsen et al., 2017)—this is obviously much greater than the current catalog of almost 2 million species!

Table 22.4.1: Estimated living biomass and number of species for each kingdom of life, following the seven-kingdom system (Ruggiero et al., 2015). Note how plants weigh the most, but bacteria have the most species.

Kingdom	Weight (Gt)[a]	Number of species (in million)	% of all species[b]	Number of described species[c]	% of described species
Animals	2	163	7	1,205,336	< 1
Fungi	12	165	7	135,110	< 0.1
Plants	450	0.382c	< 0.5	364,009	95

Kingdom	Weight (Gt)[a]	Number of species (in million)	% of all species[b]	Number described species[c]	% of described species
Chromista	Unknown	0.025c	< 0.5	23,428	94
Protozoans	4	163	7	2,686	0.1
Archaea	7	0.0005	< 0.5	377	75
Bacteria	70	1,746	78	9,982	0.1

a. As gigatonnes of carbon, from Bar-On et al., 2018

b. From Larsen et al. (2017)’s Table 1, Scenario 1

c. From http://www.catalogueoflife.org

✓ Rarefaction Curves 22.4.1

In ecology, rarefaction is a technique to assess species richness from the results of sampling. When sampling various species in a community, the larger the number of individuals sampled, the greater number of species that will be found. Rarefaction allows the calculation of species richness for a given number of individual samples, based on the construction of so-called rarefaction curves. This curve is a plot of the number of species as a function of the number of samples. Rarefaction curves generally grow rapidly at first, as the most common species are found, but the curves plateau as only the rarest species remain to be sampled.

Rarefaction curves are necessary for estimating species richness. Raw species richness counts, which are used to create accumulation curves, can only be compared when the species richness has reached a clear asymptote. Rarefaction curves also help to tell us what we *don’t know*. If a curve hasn’t yet reached its asymptote, there are additional species in that habitat still to discover.

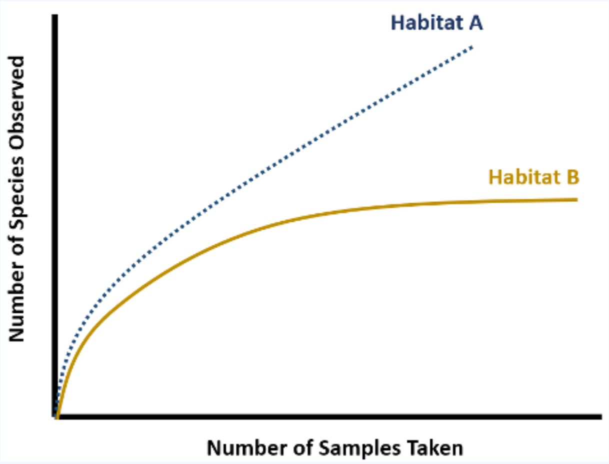


Figure 22.4.1 : A simplified example of a rarefaction curve. In both habitats, the number of species observed (species richness) increases with the number of samples taken. In Habitat B, the curve eventually saturates (reaches an asymptote), suggesting that the actual species richness of the habitat has been reached. Habitat A, however, has not yet reached its asymptote, so additional sampling would reveal additional new species in this habitat.

Case Study: The Deep Sea of the Mediterranean Basin

From: Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C. and Olu, K., 2010. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. PloS one, 5(8), p.e11832.

Deep-sea ecosystems represent the largest biome of the global biosphere, but knowledge of their biodiversity is still scant. The Mediterranean basin has been proposed as a hotspot of terrestrial and coastal marine biodiversity, but has been supposed to be impoverished of deep-sea species richness. Danovaro et al. (2010) summarized all available information on benthic biodiversity (Prokaryotes, Foraminifera, Meiofauna, Macrofauna, and Megafauna) in different deep-sea ecosystems of the Mediterranean Sea (200 to more than 4,000 m depth), including open slopes, deep basins, canyons, cold seeps, seamounts, deep-water corals and deep-hypersaline anoxic basins and analyzed overall longitudinal and bathymetric patterns.

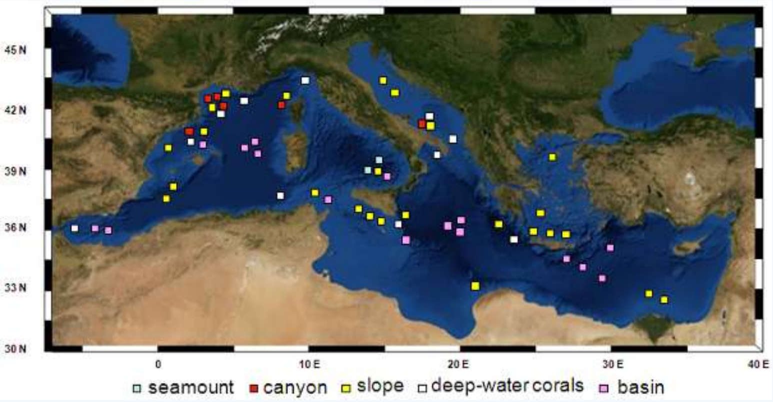


Figure 22.4.2: Investigated areas in the Mediterranean basin. Areas include slopes, seamounts, canyons, deep-water corals, and basin.

Danovaro et al. (2010) found that all of the biodiversity components, except Bacteria and Archaea, displayed a decreasing pattern with increasing water depth, but to a different extent for each component. Unlike patterns observed for faunal abundance, highest negative values of the slopes of the biodiversity patterns were observed for Meiofauna, followed by Macrofauna and Megafauna. Comparison of the biodiversity associated with open slopes, deep basins, canyons, and deep-water corals showed that the deep basins were the least diverse. Rarefaction curves allowed for estimation of the expected number of species for each benthic component in different bathymetric ranges. Species were unique across ecosystems, so each ecosystem contributes significantly to overall biodiversity.

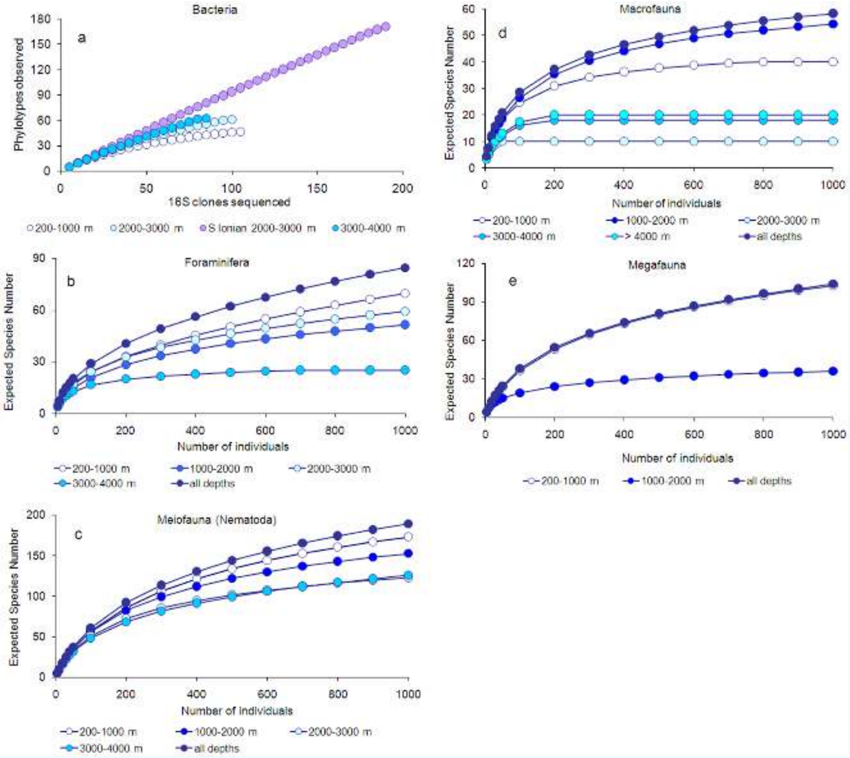


Figure 22.4.3: Rarefaction curves for the different components of the deep biota.

Danovaro et al. (2010) estimated that the overall deep-sea Mediterranean biodiversity (excluding prokaryotes) reaches approximately 2,805 species, of which about 66% is still undiscovered. Among the biotic components investigated (Prokaryotes excluded), most of the unknown species are within the phylum Nematoda, followed by Foraminifera, but an important fraction of macrofaunal and megafaunal species also remains unknown. The data in this study provide new insights into the patterns of biodiversity in the deep-sea Mediterranean and new clues for future investigations aimed at identifying the factors controlling and threatening deep-sea biodiversity.

References

Bar-On, Y.M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, *25*, pp. 6505–11. https://doi.org/10.1073/pnas.1711842115

Colyn, M., Hulselmans, J., Sonet, G., et al. (2010). Discovery of a new duiker species (Bovidae: Cephalophinae) from the Dahomey Gap, West Africa. *Zootaxa*, *2637*, pp. 1–30. http://doi. org/10.11646/zootaxa.2637.1.1

Costello, M.J., Wilson, S., & Houlding, B. (2012). Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, *61*, pp. 871–83. http://doi.org/10.1093/sysbio/syr080

Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C., & Olu, K. (2010). Deep-sea biodiversity in the Mediterranean Sea: The known, the unknown, and the unknowable. *PloS one*, *5*(8), p.e11832.

Ebert, D.A., & Cailliet, G.M. (2011). Pristiophorus nancyae, a new species of sawshark (Chondrichthyes: Pristiophoridae) from southern Africa. *Bulletin of Marine Science*, *87*, pp. 501– 12. https://doi.org/10.5343/bms.2010.1108

Paknia, O, Rajaei H., & Koch, A. (2015). Lack of well-maintained natural history collections and taxonomists in megadiverse developing countries hampers global biodiversity exploration. *Organisms Diversity & Evolution*, *15*, pp. 619-629. http://doi.org/10.1007/s13127-015-0202-1

Larsen, B.B., E.C. Miller, M.K. Rhodes, et al. (2017). Inordinate fondness multiplied and redistributed: The number of species on Earth and the new pie of life. *Quarterly Review of Biology, 92*, pp. 229–65. https://doi.org/10.1086/693564

Musick, J.A. (2000). Latimeria chalumnae. *The IUCN Red List of Threatened Species*, e.T11375A3274618. http://doi.org/10.2305/IUCN.UK.2000....375A3274618.en

Ruggiero, M.A., Gordon, D.P., Orrell, T.M., et al. (2015). A higher-level classification of all living organisms. *PLoS ONE 10*: e0119248. http://doi.org/10.1371/journal.pone.0119248

Sforzi, A., Tweddle, J., Vogel, J., Lois, G., Wägele, W., Lakeman-Fraser, P., Makuch, Z., & Vohland, K. (2018). In Hecker, S., Haklay, M., Bowser, A., Makuch, Z., Vogel, J. & Bonn, A. (Eds.), *Citizen science: Innovation in open science, society and policy*. UCL Press, London. https://doi.org/10.14324 /111.9781787352339

Shirley, M.H., Carr, A.N., Nestler, J.H., et al. (2018). Systematic revision of the living African slender-snouted crocodiles (Mecistops Gray, 1844). *Zootaxa, 4504*, pp. 151–93. http://doi. org/10.11646/zootaxa.4504.2.1

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) with material from the following open-access sources:

- Conservation Biology of Sub-Saharan Africa by John W. Wilson and Richard B. Primack
- Rarefaction (ecology) by Wikipedia, the Free Encyclopedia
- Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C. and Olu, K., 2010. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. PloS one, 5(8), p.e11832.

22.5: Measuring Biodiversity using DNA

Learning Objectives

- Explain how DNA barcoding aids in measuring biodiversity

Measuring Biodiversity using DNA

The technologies of molecular genetics, data processing, and data storage are maturing to the point where cataloging the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of the rapid evolution in a mitochondrial gene present in eukaryotes, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes.

DNA barcoding is a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species. It differs from molecular phylogeny in that the main goal is not to determine patterns of relationship, but to identify an unknown sample in terms of a preexisting classification. The most commonly-used barcode region for animals, at least, is a segment of approximately 600 base pairs of the mitochondrial gene cytochrome oxidase I (COI).

Applications include, for example, identifying plant leaves (even when flowers or fruit are not available), identifying insect larvae (which may have fewer diagnostic characters than adults and are frequently less well-known), identifying the diet of an animal (based on its stomach contents or feces), and identifying products in commerce (for example, herbal supplements or wood).

Rapid, mass-sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid-2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN (International Union for Conservation of Nature) which maintains the Red List: an online listing of endangered species categorized by taxonomy, type of threat, and other criteria. The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

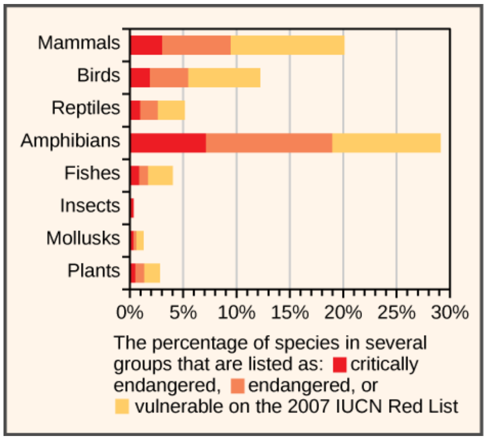


Figure 22.5.1: IUCN Red List: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007. The Red List is an online listing of endangered species categorized by taxonomy, type of threat, and other criteria.

Key Points

- DNA barcoding is a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species.

- Barcoding allows us to classify organisms that would otherwise be difficult to identify, such as in situations where only part of an organism is available, or is too immature to identify by conventional methods.
- At the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known; however, most species will be extinct before this time.
- Even with barcoding, it is difficult to know which species are threatened and to what degree they are threatened, a task carried out by the non-profit IUCN (International Union for Conservation of Nature).

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) with material from the following open-access sources:

- **47.4A: Measuring Biodiversity** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

- **47.4A: Measuring Biodiversity** by Boundless is licensed CC BY-SA 4.0.

CHAPTER OVERVIEW

23: Conservation Biology

Learning Objectives

- Understand and explain the scientific process as related to conservation biology
- Be able to put the current biodiversity crisis in a historical perspective
- Identify and understand the main threats to biodiversity
- Show an understanding of the importance of biodiversity to human life
- Explain how biodiversity loss can be stopped, or slowed

Summary

Biodiversity is declining rapidly at a global scale, leading to a human-caused sixth mass extinction. Conservation biology aims to document earth's biological diversity, to understand how humans impact this diversity, and to explore potential solutions to biodiversity decline. The major current threats to biodiversity include habitat loss, overexploitation, invasive species, pollution, and climate change - habitat loss is the most important, particularly in terrestrial habitats, and has lead to around 50% of all biodiversity loss. Preserving biodiversity has numerous benefits to humans through the protection of ecosystem services.

23.1: The Science of Conservation Biology

Figure 23.1.1: East Africa’s great migration is one of the most famous wildlife spectacles on Earth. Each year, tens of thousands of tourists from around the world flock to the region to see the 1.7 million common wildebeest (*Connochaetes taurinus*, LC) and hundreds of thousands of other plains mammals make their way from Tanzania’s Ngorongoro Conservation Area, through the Serengeti Plains, to Kenya’s Maasai Mara National Reserve. "Wildebeest Migration in Serengeti National Park, Tanzania" by Daniel Rosengren is licensed under CC BY 4.0.

Popular interest in protecting biological diversity—which describes the amazing range of species, genetic diversity within each species, and the multitude of Earth’s complex biological communities with their associated ecosystem processes—has intensified during the past few decades. During this time, scientists and the public have recognized that biological diversity (often shortened to biodiversity) is being lost at increasing rates. Across the world, human activities are destroying ecological communities that have developed over millions of years. Over the next several decades, thousands of species and millions of populations will likely go extinct.

The fundamental driver of all the biodiversity losses we are currently witnessing is a rapidly expanding human population coupled with increased consumptive needs. In 1850, after roughly 300,000 years of *Homo sapiens* on the planet, there were around 1 billion people on Earth. By 1987, not even 140 years later, the world’s human population had surpassed 5 billion. By 2017, there were 7.5 billion humans globally, of which over 1 billion lived in Sub-Saharan Africa (World Bank, 2019). With this many people, the human population grows by tens of millions of people each year, even with modest population growth Figure 23.1.2. To make matters worse, Sub-Saharan Africa has the fastest population growth rate in the world, with a projected human population estimate of over 4 billion people by the year 2100—a number that is well beyond the ecological capacity of the region to support.

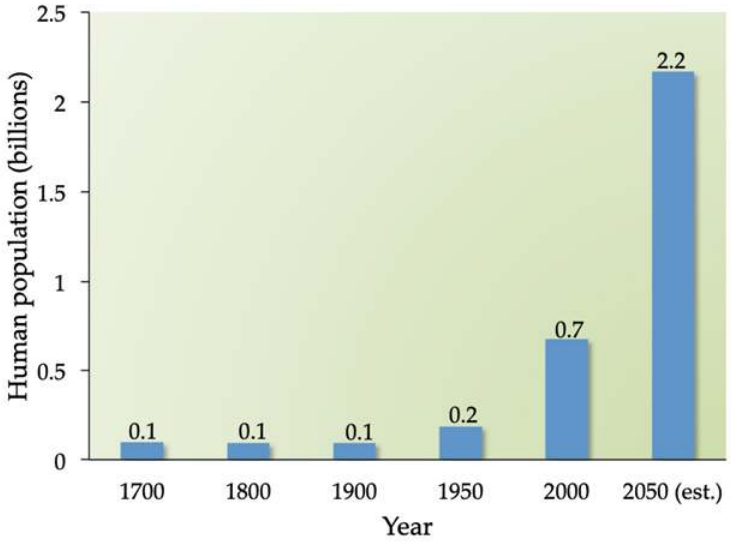


Figure 23.1.2: Sub-Saharan Africa's human population crossed the 1 billion mark in 2015. At the current annual population growth rate of 2.7%, more than 28 million people will be added to the region in 2019. This number will escalate each subsequent year as increases are compounded. *Sources: Biraben, 2003; World Bank, 2019, CC BY 4.0.*

To survive and prosper, people use natural resources. They harvest and use oil, water, and wildlife products, and convert natural ecosystems for agriculture, cities, roads, and industrial activities. This consumption, which reduces natural habitat and the associated wildlife populations, is intensifying because of the demands of a rapidly increasing human population. Consumption of resources also increases as countries develop and industrialize: the average citizen of the USA uses five times more resources than the average global citizen, 11 times more than the average Chinese citizen, and 32 times more than the average Kenyan citizen (Worldwatch Institute, 2015). This growth in the number of humans, together with their ever-more-intensive use of natural resources, is the fundamental driver behind most current species extinctions.

For conservation biologists and other nature lovers, the widespread extinction of species and destruction of natural ecosystems are incredibly discouraging.

Conservation Biology as a Discipline

As a distinct scientific field, conservation biology is an integrated, multidisciplinary subject that developed in response to the challenge of preserving populations, species, ecosystems, and biological interactions. The main aim of conservation biology is to ensure the long-term preservation of biodiversity. To achieve its aim, conservation biology has set three goals:

- To document Earth's biological diversity.
- To investigate how humans influence species, evolution, and ecosystem processes.
- To investigate practical approaches to protect and restore biological communities, maintain genetic diversity, and prevent the extinction of species.

The first two goals describe typical scientific research investigating objective facts. The third goal, however, is a part of what makes conservation biology a normative discipline; that is, conservation biology incorporates human values, not just facts, to understand and achieve its value-laden goals (Lindenmayer & Hunter, 2010). In this sense, conservation biology is related to environmentalism, in which people aim to protect the natural environment for its own sake. However, conservation biology is at its core a scientific discipline; it is founded on scientific principles. This is not to say you must be a scientist to practice conservation biology; there are many people who are not scientists who apply the principles of conservation biology in their professional and personal lives.

The emergence of conservation biology as a distinct scientific field in the 1970s has given rise to the formation of various formal societies representing the field in a united voice. Most notable among these is the Society for Conservation Biology (SCB, Figure 23.1.3), which is a non-profit international professional organization with a mission to advance "the science and practice of conserving the Earth's biological diversity". To facilitate opportunities where like-minded people can share ideas locally, the SCB has regional branches, including an active Africa Section (http://conbio.org/groups/sections/africa) which hosts regular conferences. In addition to the SCB, a great number of other local, national, and regional conservation organizations also exist and act as mouthpieces for grassroots movements and as custodians of nature. Many of these groups focus on specific animals or local protected areas. Others organically adapt their missions and visions in response to a specific need or threat. For example, established in 1913 as an exchange forum between collectors of rare plants, the Botanical Society of South Africa now actively works toward protecting those rare plants in their natural habitats.

Figure 23.1.3: The logo of the Society for Conservation Biology (SCB) has several layers of symbolism. Enclosed in the circle of life are ocean waves, representing change. The bird symbolises beauty, and the leaves (the bird's wings) remind us of nature's productivity. Image courtesy of SCB, all rights reserved.

In recent years, conservation practice has evolved from just a plan to save the environment to a vision that includes sustainable development and social justice.

Conservation biology also has a history of adapting to new challenges. The very first conservation activities, in Africa and beyond, were geared towards securing the rights to valuable natural resources for people in powerful positions, such as kings and tribal chiefs, enforced through a strictly adherence to cultural norms and customary laws. But as a growing human population expanded its influence on the environment, and wildlife started to decline, earliest conservation models gradually shifted towards fortress conservation approaches (Wilshusen et al., 2002) which aimed to shield wildlife from people by setting aside protected areas where human activities were strictly controlled.

Today, however, as human populations are exploding, and consumption is increasing, even protected areas are increasingly unable to withstand the multitude of threats to biodiversity that ignore property boundaries and political borders. In response, fortress conservation approaches are beginning to make way for large-scale integrated activities that highlight the social and economic benefits of biodiversity conservation. To do this, new alliances are being formed and new agendas are being established, such as those that directly link human health with environmental health (Box 23.1.1). These integrated conservation philosophies that pursue strategies that benefit both humans and biodiversity show much promise because they focus on fundamental extinction drivers, and advocate for more inclusive sustainable development. In this way, the practice of conservation has evolved from just a plan to save the environment to a vision that accomplishes its goals through sustainable development and social justice.

Yet, as we consider how to best invest limited conservation resources, some difficult questions arise. With seemingly more work to be done than can be accomplished, should we let some species go extinct (Bottrill et al., 2008)? Which species? Who decides? How can we even dare to think that we can play god? Such questions predictably bring about strongly opinionated and emotional debate (Soulé, 2013 vs. Marvier, 2014; Tallis & Lubchenco, 2014). Given the successful track record of fortress conservation initiatives in preventing extinctions despite limited budgets (Young et al., 2014), as well as the promising progress of more complex people-centred initiatives (Pooley et al., 2014), it seems clear that conservation relies on some balance between these two conservation philosophies (Sodhi et al., 2011). Conservation biologists of tomorrow will be able to fine-tune the balance between these strategies by closely inspecting the successes and failures of our actions today.

Box 23.1.1 Conservation Through Public Health: A Case Study

Gladys Kalema-Zikusoka

Conservation Through Public Health,

Kampala, Uganda.

http://www.ctph.org

Conservation Through Public Health (CTPH) is a grassroots non-governmental organization (NGO) and non-profit that promotes biodiversity conservation by enabling people, wildlife, and livestock to coexist. The organization was founded in 2003 after fatal scabies skin disease outbreaks in mountain gorillas (*Gorilla beringei beringei*, EN) were traced to people living around Bwindi Impenetrable National Park, Uganda, who had limited access to basic health services (Kalema-Zikusoka et al., 2002). Since then, CTPH has contributed to conservation and sustainable development in Africa by improving human and animal health and welfare in and around protected areas.

One of the main goals of CTPH is to reduce disease transfer between humans and gorillas. We accomplish this through an integrated population, health, and environment (PHE) program that was established in 2007 with funding from the US Agency for International Development (USAID). As a first step, piloted around Bwindi, CTPH held consultative meetings with local leaders, during which at least one Village Health and Conservation Team (VHCT) volunteer was selected from each village and two from each parish (consisting of 11 villages) to oversee distribution of family planning supplies. This initiative rapidly expanded into a sustainable social service delivery network that promotes family planning, hygiene, and sanitation. The network resulted in a 20% to 60% (national average is 30%) increase in new users to modern family planning, and a 10% to 60% increase in adoption of hand washing facilities at homes visited by VHCTs. VHCT volunteers also refer people suffering from infectious diseases and malnutrition to local health centres and promote more sustainable alternative livelihoods. Another group of community volunteers, the "Human and Gorilla Conflict Resolution" (HUGO) team, in turn collect gorilla faecal samples left on communal land to monitor their health Figure 23.1.4, and visually monitor gorillas for clinical signs of disease inside and outside protected areas (Gaffikin & Kalema-Zikusoka, 2010). In the process, we have seen reduced disease incidences in the gorillas, reduced conflict between people and gorillas, and improved attitudes toward conservation. One unintended outcome has been increased gender equality: men are now more involved in family planning, and women are more involved in natural resource management.

Figure 23.1.4: A park ranger from the Uganda Wildlife Authority teaching HUGO community volunteers how to collect faecal samples from gorilla night nests during a CTPH training workshop. Photograph by CTPH, CC BY 4.0.

Our experience in initiating and managing PHE programs for the past 10 years has taught us several lessons. One of the most important lessons to ensure project sustainability is to regularly engage with local leaders and the government. The Uganda Wildlife Authority, Uganda's Ministry of Health, and local health centres all attend CTPH meetings with VHCTs. Attendance by and representation of these groups not only informs them of our activities, but also provides a platform to inform or train the VHCTs in what they would like them to disseminate to the local communities.

We have also learnt that PHE-implementing partners and projects need to be well-suited to each other and each site; this remains true even though health needs are often the same, regardless of the location. For example, at Mount Elgon National Park in Uganda, we found that training VHCTs in reducing conflict with park management played a key role in changing community attitudes toward conservation. In contrast, at Virunga National Park, Democratic Republic of the Congo (DRC), we found that VHCTs needed to work more closely with local health centres to prevent disease transmission between people and gorillas, and to promote family planning in a largely Catholic country.

> Lastly, we found that establishing income-generating projects for groups rather than individuals was key to sustaining VHCT networks and program goals beyond donor funding cycles where we have had no volunteer dropouts in the first 10 years of initiating the PHE program. These key components were accomplished by initiating livestock group enterprises and by encouraging VHCT volunteers to invest generated income into Village Saving and Loan Associations (see http://www.care.org/vsla).

The Role of Conservation Biologists

While there are a few extinctions that have only one cause, more generally, extinctions occur because several factors acted simultaneously and/or sequentially. Blaming a certain industry or specific group of people for an extinction (or other biodiversity loss) is thus simplistic, ineffective, and often counter-productive. Though challenging, a better approach would be to better understand how local, national, and international links led to those losses, and to find viable alternatives to prevent it from happening again. To succeed in this challenge, conservation biologists should strongly consider taking on one or more of several roles:

- Conservation biologists should be curious. The world around us is full of natural wonders waiting to be discovered. These discoveries underpin conservation action, by allowing us to define all the different components of biodiversity, enabling us to better understand the needs of different species, and providing us with opportunities to celebrate our conservation successes.
- Conservation biologists must be good listeners. Sometimes, the only difference between attracting a new ally and making an enemy, or between developing a landscape and saving a species from extinction, is the way we communicate. Conservationists must be careful and respectful listeners, especially to opposing perspectives. Careful listening is particularly important in rural areas, where villagers often have practical concerns related to their daily contact with wildlife, such as staying safe and preventing crop damage and livestock loss. Quite often, those villagers may also have unique insights into wildlife ecology that could prove valuable in local conservation measures.
- Conservation biologists must be law-abiding citizens. Activities that involve wildlife and ecosystems are regulated by laws and regulations. These laws are important because ethical boundaries differ from person to person—activities acceptable to one group of people may be considered harmful by another. As conservation biologists, abiding by environmental laws is especially important if we want others to take those laws seriously.

  Laws are important because ethical boundaries differ from person to person—activities acceptable to one person may be immensely harmful to another.

- Conservation biologists should become effective communicators. They should be able to discuss the problems facing biodiversity in depth, as well as the consequences of losing biodiversity, to as broad a range of people as possible. Groups like hunters, community leaders and organizers, and church leaders may be interested in participating in conservation efforts once they recognize that their activities, health, and emotional well-being depend on conservation action.
- Conservation biologists could become politically active leaders, so that they can influence public opinion and policy. As a starting point, those interested in this role can join a conservation organization to learn more about broader issues. They could also use their personal networks to form alliances with lawyers, citizen groups, and politicians.
- Conservation biologists could become pro-active land managers. Those taking on this task must be willing to walk on the land and go out on the water to find out what is really happening. They should also talk with local people to communicate their knowledge to others in ways that are clear and easily understood.
- Above all, a conservation biologist must be honest. To encourage effective action, both from the public and through policy, conservationists must present arguments backed by reliable evidence. To do otherwise, conservation biologists could lose credibility, which would very likely delay or even compromise conservation efforts.

It is worth taking a moment to distinguish between two important pillars of conservation action, namely conservation advocacy and conservation science. Conservation advocacy describes the roles that conservation biologists adopt to guide social, political, and economical systems towards a personally-preferred outcome—adopting environmentally-friendly practices; incorporating these activities makes conservation biology a normative discipline. Conservation science, in contrast, describes activities that conservation biologists undertake to generate knowledge, like objectively describing biodiversity and measuring biodiversity's response to stressors and safeguards. While conservation advocacy and conservation science often support and inform each other as to the next steps required for "doing conservation", it is important to distinguish between these two pillars to ensure that policymakers and other stakeholders in the environment understand when we advocate for personal preferences and when we offer objective findings (Rykiel, 2001; Lackey, 2007; Nelson & Vucetich, 2009). The next section will further expand on the importance of science in conservation biology.

The Importance of Scientific Methods

The field of conservation biology applies scientific methods to achieve its goals. Like the medical sciences, which apply principles from physiology, anatomy, and genetics to problems of human health, conservation biologists solve biodiversity problems using principles from fields, such as mathematics, veterinary medicine, social sciences, and several natural sciences (Figure 23.1.5). Conservation biology differs from these and other component disciplines in that its primary goal is the long-term preservation of biodiversity. Unlike many other scientific fields, conservation biology can also be described as a crisis discipline (Soulé, 1985; Kareiva & Marvier, 2012). That is, conservation biologists are often required to take creative steps to respond to imminent threats, typically without complete knowledge of the systems requiring attention. Conservation scientists must also articulate long-term visions for conservation beyond solving immediate problems.

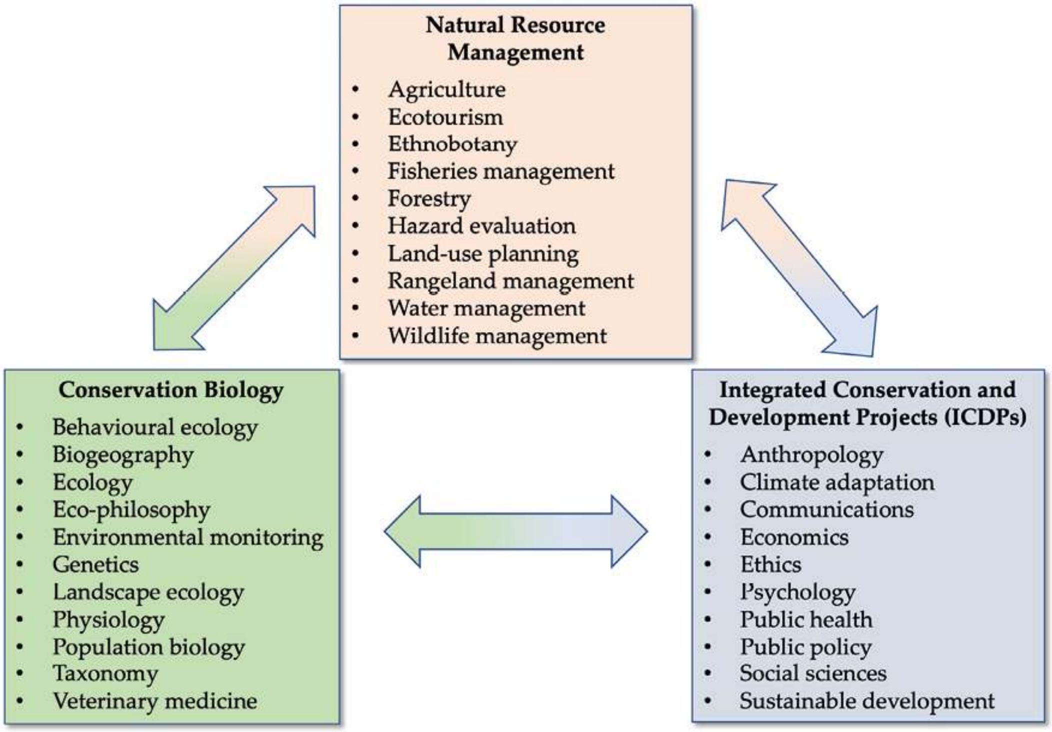


Figure 23.1.5: Conservation biology draws from many other sciences to protect biodiversity. It is closely related to natural resource management, which aims to manage biodiversity primarily for the benefit of humans. Integrated conservation and development projects (ICDP) are projects that manage nature for the benefit of both humans and biodiversity. After Kareiva and Marvier, 2012; Temple, 1991, CC BY 4.0.

To be effective, conservation biologists must demonstrate the relevance of their findings to a range of stakeholders. To be successful in this task, the importance of sound scientific principles cannot be over-emphasized. Nature is a complex network of many interdependent connections and feedback loops. Science is underpinned by principles that provide conservationists the necessary quantitative and qualitative tools to better measure and control for all these different aspects of biodiversity. Such measurements allow us to gain a better understanding of complex natural systems, and the consequences of human activities. Reliable, unbiased data obtained from sound and transparent scientific methods also facilitate policymaking that is too often based on value judgments by non-experts who must balance many needs and different sources of information (Ntshotsho et al., 2015).

One of the cornerstones of modern science is to identify a hypothesis (a proposed explanation for a specific observation) to evaluate. The best hypotheses, often expressed as goals or objectives, are usually those that are SMART:

Specific: not overly general

Measurable: has both units and a method of measurement
Attainable: realistic to achieve
Relevant: related to what needs to be accomplished
Time-bound: achievable within a specific timeframe

Identifying SMART goals and objectives is an essential aspect of conservation biology. Without such benchmarks, practitioners cannot know whether their tasks were successful, or when management actions should be adjusted to achieve success. While this may seem obvious, many previous conservation projects have failed because biologists neglected to set SMART goals and objectives (Tear et al., 2005). While lofty, "We're going to save all species" is not a SMART conservation goal because it is overly general, hard to measure, unrealistic, and not time-bound. In contrast, "We want to protect 25% of our country's wetlands within the next 10 years" is a SMART goal because it sets a very clear and measurable objective. In general, it is wise to set smaller short-term (e.g. quarterly), and medium-term (e.g. annual) goals as one works towards long-term (e.g. 5–10 years) objectives; this allows one to constantly assess progress, which in turn provides opportunities for celebrations and strategic adjustments as and when needed.

Conservation biology's ethical principles

Conservation biology rests on a set of underlying ethical principles that is generally agreed upon (Soulé, 1985) and can be summarized as follows:

- The diversity of species and biological communities should be preserved: Most people appreciate biodiversity. Hundreds of millions of people visit national parks, game reserves, zoos, botanical gardens, and aquaria each year. They spend money and take actions to protect these places and species. People also recognize that biodiversity has economic value, whether through tourism, consumption, or other services.
- The untimely extinction of populations and species should be prevented: Throughout history, species have occasionally died off as a result of natural, non-human causes. The loss of a local population was generally temporary until a new population established itself through dispersal. However, human activities have increased the rate at which species are going extinct by more than a hundredfold. Meanwhile, there is no similar increase in the rate at which new populations and species are being created.
- Ecological complexity should be maintained: In complex natural environments, biodiversity expresses many of its most valuable features and interactions. Although the biodiversity of species may be partially preserved in captivity, maintaining ecological complexity requires that natural areas be preserved.
- Evolution should continue: Evolution creates new species, increases biodiversity over time, and facilitates adaptation to changing environmental conditions. People can help preserve these evolutionary processes by maintaining genetic diversity in wild populations and allowing populations to exchange genetic material. In captivity, many natural evolutionary processes do not occur, which can hamper survival when species are reintroduced in the wild.
- Biodiversity has intrinsic value: The value of species, communities, and ecosystems does not depend on their utility to people. They are intrinsically valuable on their own, with unique evolutionary histories and ecological roles. There are certain iconic species that people simply want to have around, but other, lesser-known species or species seen as problematic to people are not less valuable.

These principles are not absolute, nor are conservation biologists required to agree with them—they are actively discussed and debated. But many individuals and organizations agree with two, three, or all the principles, and support conservation efforts.

✓ Box 23.1.2 Biodiversity: Can Humanity be Saved?

Nkengifor Nkeshia Valery, Regina International Cameroon, Member of Union Farms of Africa, Yaoundé, Cameroon.

What happened over the past 200 years that we have arrived where we are? How did we get to this modern paradox? A society where we cherish comfort at the cost of the ever-increasing destruction of our planet. Never in the history of humanity has the environment been degraded to the point that even the air we breathe has become cancerous. Animals are exploited by industries at an alarming rate and those remaining are killed to enrich a privileged few. And all this evil happens with our

> complicity as indirect consumers. Our inheritance from God, the source of all our nourishment, does not belong to us. Yet it has been bought and exploited by multinational corporations and financial markets that hinder us from cultivating sustainably. We are pushed to feed ourselves and our crops with chemical products that are dangerous to our long-term health. We are also experiencing the start of the sixth mass extinction episode of biodiversity (Ceballos et al., 2017). As a result, the natural world has declared World War III against humanity. This is a war fought not by nation against nation, but that the environment has declared against the whole human race.
>
> This war condemns us to live in an illusion of freedom; we are, in fact, destroyed at an increasing rate by different dangerous diseases and rendered slaves of the polluted environments that we blindly accept. The question we need to ask is not whether we should act to save our planet, but what future and meaning we are going to give the word “HUMANITY”. We are all actors in a civilization that we are constructing; to quote the Indian leader Mahatma Gandhi: “If we could change ourselves, the tendencies in the world would also change. As a man changes his own nature, so does the attitude of the world change towards him. […] We need not wait to see what others do”. Let us pause and ask ourselves what we want the future to say of us. Are we a destructive generation, or a generation that is ready to sustainably preserve its biodiversity? It is a question every reader needs to ponder. The future is judging no one and blaming no one, but it needs us to change our habits towards protecting the world’s biodiversity.
>
> To change our attitude and make the world a better place, I drafted the following poem with passion to see my words become action for every lover of biodiversity
>
> **WORLD CHANGERS**
>
> *We are a people of peace called forth out of humanity into restoring life to our natural habitat. We are governed and guided by a sense of sustainability. Conservation and protection is our priority in all things at all times we are led and driven by the spirit of an environment free of pollution we are called to effect and affect every life that we come in contact with towards the sustainable development of the environment.*
>
> *We are called by humanity to be world changers we refuse to conform with the thinking pattern of the world system because we are world changers.*

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) with material from the following open-access sources:

- © 2019 J.W. Wilson and R.B. Primack, CC BY 4.0 https://doi.org/10.11647/OBP.0177.01
- **13.1: What is Conservation Biology?** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.1: Conservation Biology is Still Evolving** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.2: The Role of Conservation Biologists** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.3: The Value of Scientific Methods** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.4: Environmental Ethics** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.

- **13.1: What is Conservation Biology?** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.1: Conservation Biology is Still Evolving** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.2: The Role of Conservation Biologists** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **1.3: The Value of Scientific Methods** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.

23.2: Biodiversity Loss over time

Human activity is the driving force behind the current biodiversity crisis, which is causing great species loss in a short time period.

Learning Objectives

- Explain the biodiversity crisis
- Describe how biodiversity has changed through geological time as a result of mass extinctions
- Describe the biodiversity loss associated with the Pleistocene extinction
- Describe the biodiversity loss during the Holocene extinction

The Biodiversity Crisis

Traditionally, ecologists have measured biodiversity, a general term for the variety of species present in the biosphere, by taking into account both the number of species and their commonness. Biodiversity can be estimated at a number of levels of the organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems, yet they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. The five previous extinctions on this scale were caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

✓ Box 23.2.1 Chiclids in Lake Victoria

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an adaptive radiation. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely-related species; typically, the species “radiate” into different habitats and niches. The Galápagos finches are an example of modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but was not a problem until the 1980s when its population began to surge by consuming cichlids, driving species after species to the point of extinction (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria. These factors included not only the Nile perch, but also the declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even cataloged all of the species present, so many were lost that they were never named. The diversity is now a shadow of what it once was.

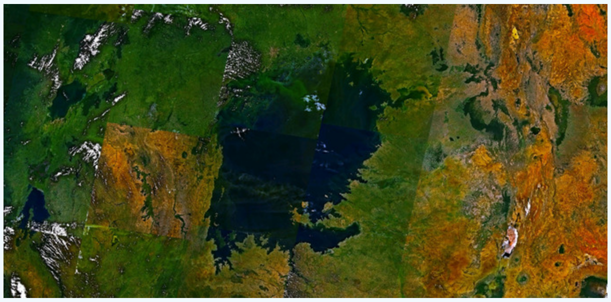


Figure 23.2.1: Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss.

Biodiversity Change through Geological Time

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are ongoing: speciation and extinction. Both are natural "birth" and "death" processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the number of species will decrease when extinction rates begin to overtake speciation rates. Throughout earth's history, these two processes have fluctuated, sometimes leading to dramatic changes in the number of species on earth.

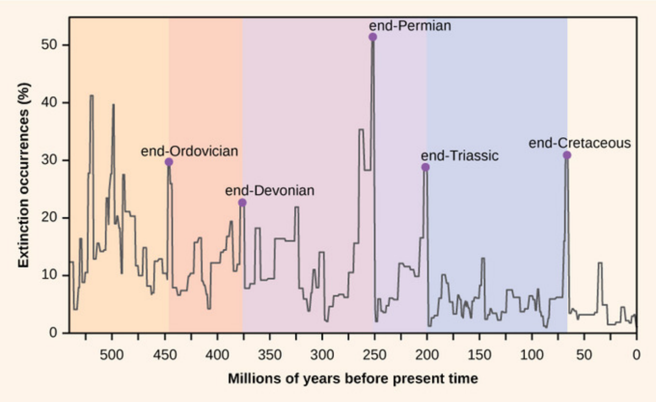
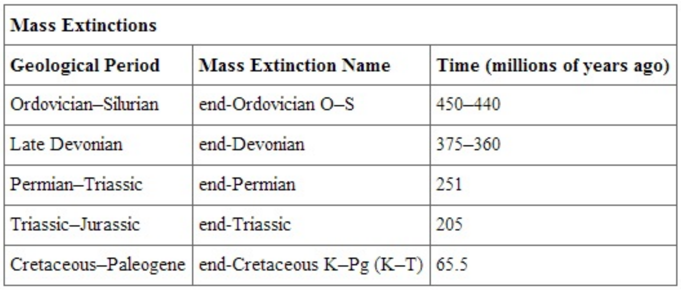


Figure 23.2.2: Extinction occurrences, as reflected in the fossil record, have fluctuated throughout earth's history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic losses in biodiversity known as mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. An argument can be made that the five mass extinctions are only the five most extreme events in a continuous series of large extinction events throughout the Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial.

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species.



Mass Extinctions		
Geological Period	**Mass Extinction Name**	**Time (millions of years ago)**
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

Figure 23.2.3: The transitions between the five main mass extinctions can be seen in the rock strata. The table shows the time that elapsed between each period.

The Ordovician-Silurian extinction event is the first-recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause was a period of glaciation followed by warming. These two extinction events, cooling and warming, were separated by about 1 million years; the climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst caused by a nearby supernova is a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the earth's ozone layer, causing intense ultraviolet radiation from the sun. It may account for climate changes observed at the time.

The late Devonian extinction may have occurred over a relatively long period of time. Its causes are poorly-understood and it appears to have have affected only marine species.

The end-Permian extinction was the largest in the history of life. Estimates predict that 96 percent of all marine species and 70 percent of all terrestrial species were lost.The causes for this mass extinction are not clear, but the leading suspect is extended and widespread volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered earth's biodiversity composition and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear. Hypotheses of climate change, asteroid impact, and volcanic eruptions have been argued. The extinction event occurred just before the breakup of the supercontinent Pangaea; although, recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event, about 65 million years ago, that the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds). Indeed, every land animal that weighed more then 25 kg became extinct. The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite or asteroid off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of iridium (which rains down from space in meteors at a fairly constant rate, but is otherwise absent on earth's surface) at the rock stratum that marks the boundary between the Cretaceous and Paleogene periods. The Cretaceous-Paleogene (K-Pg) boundary marked the disappearance of the dinosaurs in fossils, as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid), rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more credible. Now, an abundance of geological evidence supports the hypothesis. Recovery times for biodiversity after the end-Cretaceous extinction were shorter, in geological time, than for the end-Permian extinction: on the order of 10 million years.

Figure 23.2.4: In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In the photo, the iridium layer is the light band.

The Pleistocene Extinction

The Pleistocene Extinction is one of the lesser extinctions and a relatively-recent one. It is well known that the North American, and to some degree Eurasian, megafauna disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively-restricted time period between 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (last dated about 4,000 years ago in an isolated population), mastodons, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, to name just a few. The possibility that the rapid extinction of these large animals was caused by over-hunting was first suggested in the 1900s; research into this hypothesis continues today. It seems probable that over-hunting was a factor in extinctions in many regions of the world.

Figure 23.2.5: Giant ground sloths, relatives of the living South American tree sloths, lived across much of North America. The giant sloths disappeared, along with the mammoths, mastodons, and many other large animals, at the end of the Pleistocene Epoch.

In general, the timing of the Pleistocene extinctions correlated with the arrival of humans and not with climate -change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, 10,000 to 20,000 years after the arrival of humans in the area. A marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000 to 12,000 years ago, several thousand years after the first evidence of humans in North America. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred with the coincidence of human arrivals. Not all of the islands had large animals, but when there were large animals, they were lost. Madagascar was colonized about 2,000 years ago; the large mammals (prosimians) that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of humans. Humans arrived in Eurasia hundreds of thousands to over one million years ago, after the origin of the species in Africa. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, human hunting was an additional factor in the extinctions.

Present-Time Extinctions

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and is mostly due to the activities of *Homo sapiens*. Since the beginning of the Holocene period, there have been numerous recent extinctions of individual species that are recorded in human writings. Most of these coincide with the expansion of the European colonies in the 1500s.

One of the earlier and popularly-known examples of extinction in this period is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean, but became extinct around 1662. It was hunted for its meat by sailors as it was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs, brought to the island by European ships, also killed dodo young and eggs.

Another example, Steller’s sea cows, became extinct in 1768.The sea cow, first discovered by Europeans in 1741, was hunted for meat and oil. The last of the species was killed in 1768, which amounts to 27 years between the species’ first contact with Europeans and its extinction. In addition, the last living passenger pigeon died in a zoo in Cincinnati, Ohio in 1914. This species was hunted and suffered from habitat loss through the clearing of forests for farmland. Furthermore, in 1918, the last living Carolina parakeet died in captivity. This species, once common in the eastern United States, was a victim of habitat loss and hunting as well. Adding to the extinction list, the Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to overfishing. The Caribbean monk seal, found in the Caribbean Sea, was driven to extinction through hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years. The International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 extinct species of vertebrates after 1500 AD, 86 of which were made extinct by over-hunting or overfishing.

Estimates of Present-Time Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without observation since there are many organisms that are of less interest to humans and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year.

One contemporary extinction rate estimate uses the extinctions in the written record since the year 1500. For birds alone, this method yields an estimate of 26 E/MSY. However, this value may be underestimated for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Secondly, the number of recently-extinct species is increasing because extinct species now are being described from skeletal remains. Lastly, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate closer to 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY. A second approach to estimating present-day extinction rates is to correlate species loss with habitat loss by measuring forest-area loss and understanding species-area relationships. The species-area relationship is the rate at which new species are seen when the area surveyed is increased. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other habitats as well. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss, suggesting that there is a delay in extinction. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species-area relationship leads to an overestimate of extinction rates. A better relationship to use may be the endemics-area relationship. Using this method would bring estimates down to around 500 E/MSY in the coming century. Note that this value is still 500 times the background rate.

Contributors and Attributions

Written and curated by A. Wilson and N. Gownaris (Gettysburg College) with material from the following open-access sources:

- **47.1A: Loss of Biodiversity** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **47.1C: Biodiversity Change through Geological Time** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **47.1D: The Pleistocene Extinction** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **47.1E: Present-Time Extinctions** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

- **47.1A: Loss of Biodiversity** by Boundless is licensed CC BY-SA 4.0.
- **47.1C: Biodiversity Change through Geological Time** by Boundless is licensed CC BY-SA 4.0.
- **47.1D: The Pleistocene Extinction** by Boundless is licensed CC BY-SA 4.0.
- **47.1E: Present-Time Extinctions** by Boundless is licensed CC BY-SA 4.0.

23.3: Threats to Biodiversity

Learning Objectives

- Describe the effects of habitat loss to biodiversity and concept of sustainability
- Explain why overharvesting is a threat to biodiversity
- Describe the impact of exotic and invasive species on native species
- Summarize the impact of pollution on species diversity
- Evaluate climate change and its impact on biodiversity

According to the 2020 Living Planet Report (https://livingplanet.panda.org/en-us/), there are five key drivers of biodiversity loss:

1. Habitat Loss (Changes in land and sea use, including habitat loss and degradation)
2. Species Overexploitation
3. Invasive species and disease
4. Pollution
5. Climate change

Of these, habitat loss is the most important, accounting for around half of all biodiversity loss (but see Box 23.3.1). The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are **habitat loss**, **overharvesting**, and introduction of **exotic species**. The first two of these are a direct result of **human population growth** and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic **climate change**, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs. Environmental issues, such as toxic **pollution**, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

It should be noted that biodiversity doesn't just mean the loss of species, it also means a loss of the number of individuals of each species. In an analysis of the abundance of almost 21,000 populations, across 4,392 species of mammals, birds, fish, reptiles and amphibians, the Living Planet Index shows an average 68% decline in monitored populations between 1970 and 2016. Or put another way, on average less than one-third of the populations of these species found in 1970 remain. Further, many of these species were probably already present in much-depleted numbers in 1970, because human-driven biodiversity loss has been happening for thousands of years.

✓ Box 23.3.1 The Largest Threat to Wildlife

The IUCN Red List tracks the extinction status of thousands of species across the world, and assesses the threats to each. In a study published in *Nature*, Sean Maxwell and colleagues documented the threats to 8,688 near-threatened and threatened species that have been fully-assessed. This means this study will capture the threats of some taxonomic groups better than others. We know much more about the world's mammals, birds, reptiles and amphibians, than we do about its fungi and insects. All bird and mammal species have been assessed but only 0.1% of fungi species have. But most of the key drivers of extinction risk for these studied groups are similar to the lesser-studied ones: for example, insects are highly threatened by agriculture and habitat loss.

The headline message is that the largest threats to wildlife is overexploitation (Figure 23.3.2) – the harvesting of animals for meat, products such as horns and medicines, logging, and fishing – and agriculture. These have been the largest threats to biodiversity for millennia, and this still holds true today.

In the chart we see the number of species that are threatened by each group of threats. You will notice that these sum to much greater than the 8,688 threatened species that the authors studied. This is because more than 80% of the species were affected by more than one major threat. Species that are under threat from human poaching might also be under threat from deforestation and loss of their habitats.

Overexploitation is the biggest threat. Nearly three-quarters (72%) of the studied species – that's 6,241 of them – were under pressure from hunting, fishing or logging of forests. Agriculture – which includes arable farming, livestock, timber plantations and aquaculture – was also a massive threat. Nearly two-thirds (62%) of species were affected. In this analysis, **Habitat Loss**

is included in several categories, for example as part of **Overexploitation** (logging), **Agriculture** (conversion of land to crop farming or livestock farming), **Urban Development** (e.g housing), and **Landscape Modification**.

These threats are not only the biggest pressures on all species that are near-threatened or threatened, we also see that they dominate for the species closest to extinction – the endangered and critically endangered ones.

Figure 23.3.1 : The numbers of species threatened with extinction by specific driver of biodiversity loss.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra’s forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 23.3.2). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe.

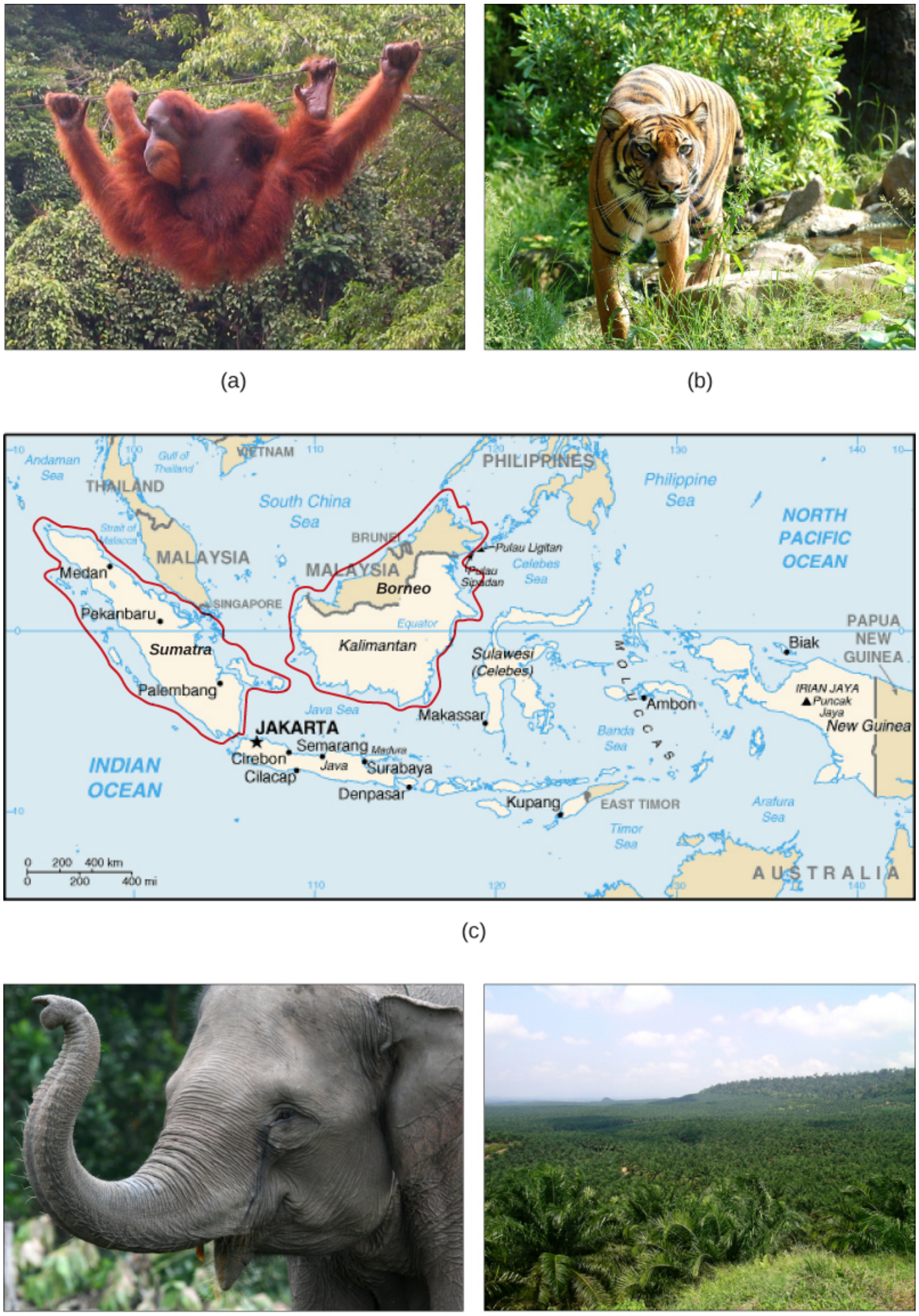


Figure 23.3.2: (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

According to Global Forest Watch, 9.7% of tree cover was lost globally from 2002 to 2019, and 9% of that occurred in Indonesia and Malaysia (where Sumatra and Borneo are located). Figure 23.3.3 shows the average annual change in forest area around the world from 1990 to 2015. In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism (species unique to those areas).

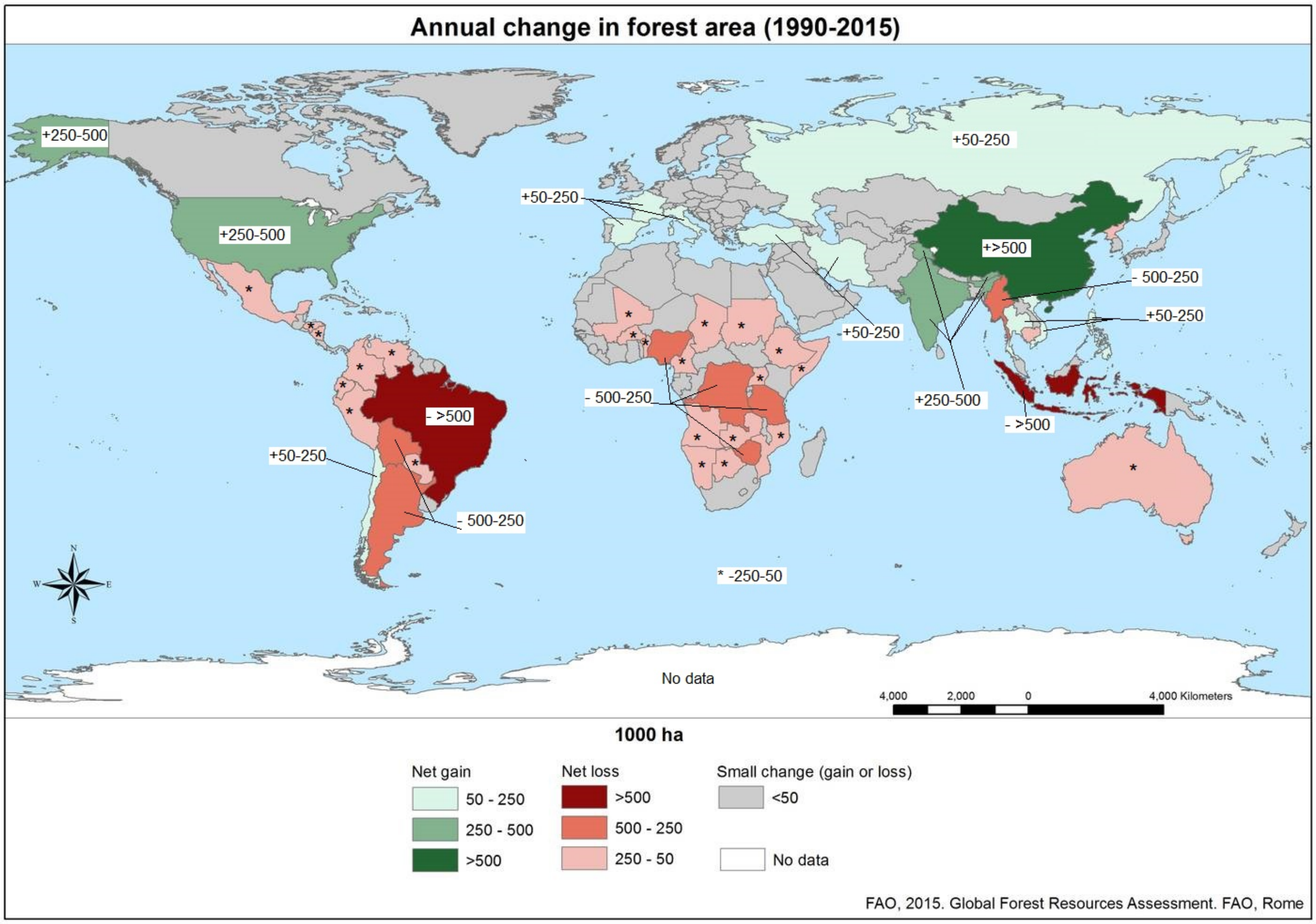


Figure 23.3.3: Average annual change in forest area globally from 2005 to 2015. China is dark green, indicating that have gained more than 500 "kilohectares" (kha) of forest. Medium green indicates countries that have gained 250-500 kha, including the the United States, India, Ghutan, and Bangladesh. Light green indicates countries that have gained 50-250 khA, including Chile, Spain, France, Italy, Turkey, Iran, Russia, Vietnam, and Thailand. Indonesia and Brazil lost more than 500 kha of forest (marked with dark red). Countries that lost 500-250 kha are marked with medium red, including Bolivia, Argentina, Nigeria, Democratic Republic of the Congo, Tanzania, Zimbabwe, and Myanmar. Countries that lost 250-50 kha are marked with light red and an asterisk (*). These include Mexico, Honduras, Nicaragua, Venezuela, Colombia, Ecuador, Peru, Paraguay, Mali, Burkina Faso, Benin, Cameroon, Chad, Sudan, Ethiopia, Somalia, Uganda, Angola, Namibia, Botswana, Zimbabwe, Mozambique, Cambodia, North Korea, and Australia. No data has been collected for Antarctica. All other regions have had lost or gained less than 50 kha in forest area. Image by FAO, 2015. Global Forest Resources Assessment. FAO. Rome (Open Access Policy).

Everyday Connection: Preventing Habitat Destruction with Wise Wood Choices

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that up to 10% of the imported timber stream in the United States, which is the world's largest consumer of wood products, is illegally logged. A 2012 United Nations and Interpol report estimated that the illegal timber trade is worth $30-100 billion each year. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

Figure 23.3.4: The sawmill in Uaxactun, Guatamala is Forest Stewardship Council (FSC) certified and provides good income from a sustainable resource for not only the saw operators but also many others who help keep the operation running. Image by Jason Houston for USAID (public domain).

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products; therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest (Figure 23.3.4). Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. There are certifications other than the FSC, but these are run by timber companies creating a conflict of interest. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal woods, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being sustainably maintained all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Worldwide, for example, the conversion of land to agriculture and cultivation have led to significant losses in grassland ecosystems. In North America, nearly 70% of the tallgrass prairie ecosystem (which once covered 142 million acres) has been converted to agriculture, and losses from other causes, such as urban development, have brought the total to about 90%. Current estimates indicate that agricultural activity and cultivation systems now cover nearly 25% of the Earth's surface.

Rivers and streams are important ecosystems and are frequently the target of habitat modification through building and from damming or water removal. Damming of rivers affects flows and access to all parts of a river. Altering a flow regime can reduce or eliminate populations that are adapted to seasonal changes in flow. For example, an estimated 91 percent of river lengths in the United States have been have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. The category "wetlands" includes many types of ecosystems, but current estimates indicate that about 50% of the world's wetland habitat has been lost. The former extent of wetland habitats worldwide (fresh, brackish and salt) is difficult to determine but certainly exceeded a billion acres.

Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats are at greater risk of population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost. This is of particular concern because amphibians have been declining in numbers and going extinct more rapidly than many other groups for a variety of possible reasons.

Link to Learning

Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select “Visit the online mapper.”

Habitat fragmentation occurs when the living space of a species is divided into discontinuous patches. For example, a mountain highway could divide a forest habitat into separate patches. This is especially problematic for consumers at the top of the food chain, which require large ranges to find adequate prey. Additionally, habitat fragmentation separates individuals from potential mates. **Wildlife corridors** mitigate the damage of habitat fragmentation by connecting patches with suitable habitat. For example, the bridge over a highway could allow animals to move between habitat patches (Figure 23.3.5). Riparian areas, areas of land adjacent to bodies of water, such as streams, can serve as natural wildlife corridors when left intact.

Figure 23.3.5: This overpass on the Trans-Canada Highway between Banff and Lake Louise, Alberta, serves as a wildlife corridor. "Wildlife overpass Trans-Canada Hwy between Banff and Lake Louise Alberta" by WikiPedant is licensed under CC BY-SA 4.0.

✓ Box 23.3.2 Sustainability

Sustainability is a concept that describes how biological systems remain diverse and productive over time. Long-lived and healthy wetlands and forests are examples of sustainable biological systems. For humans, sustainability is the potential for long-term maintenance of well-being, which has ecological, economic, political, and cultural dimensions. Sustainability requires the reconciliation of environmental, social, and economic demands, which are also referred to as the “three pillars” of sustainability.

Healthy ecosystems and environments are necessary for the survival and flourishing of humans and other organisms, and there are a number of ways to reduce humans’ negative impact on the environment. One approach is environmental management, which is based largely on information gained from earth science, environmental science, and conservation biology. A second approach is management of human consumption of resources, which is based largely on information gained from economics. A third, more recent, approach adds cultural and political concerns into the sustainability matrix.

Loss of biodiversity stems largely from the habitat loss and fragmentation produced by human appropriation of land for development, forestry and agriculture as natural capital is progressively converted to human-made capital. At the local human scale, sustainability benefits accrue from the creation of green cities and sustainable parks and gardens. Similarly, environmental problems associated with industrial agriculture and agribusiness are now being addressed through such movements as sustainable agriculture, organic farming, and more-sustainable business practices.

Figure $23.3.6$: Since the Neolithic Revolution, nearly half of the world’s forests have been destroyed for human use. Sustainable practices, which preserve environments for long-term maintenance and well-being, can help preserve habitats and ecosystems for greater biodiversity.

Species Overexploitation

Overharvesting, also called overexploitation, refers to harvesting a renewable resource to the point of diminishing returns. Ecologists use the term to describe populations that are harvested at a rate that is unsustainable, given their natural rates of mortality and capacities for reproduction. The term applies to natural resources such as wild medicinal plants, grazing pastures, game animals, fish stocks, forests, and water aquifers. Sustained overharvesting can lead to the destruction of the resource, and is one of the five main activities – along with pollution, introduced species, habitat fragmentation, and habitat destruction – that threaten global biodiversity today.

All living organisms require resources to survive. Overharvesting these resources for extended periods of time can deplete natural resources to the point where they are unable to recover within a short time frame. Humans have always harvested food and other resources they have needed to survive; however, human populations, historically, were small and methods of collection limited to small quantities. Exponential increase in human population, expanding markets, and increasing demand, combined with improved access and techniques for capture, are causing the exploitation of many species beyond sustainable levels.

As mentioned above, sustained overharvesting is one of the primary threats to biodiversity. Overharvesting can lead to resource destruction, including extinction at the population level and even extinction of whole species. Depleting the numbers or amount of certain resources can also change their quality; for example, the overharvesting of footstool palm (a wild palm tree found in Southeast Asia, the leaves of which are used for thatching and food wrapping) has resulted in its leaf size becoming smaller.

Overharvesting not only threatens the resource being harvested, but can directly impact humans as well--for example by decreasing the biodiversity necessary for medicinal resources. A significant proportion of drugs and medicines are natural products which are derived, directly or indirectly, from biological sources. However, unregulated and inappropriate harvesting could potentially lead to overexploitation, ecosystem degradation, and loss of biodiversity; further, it can negatively impact the rights of the communities and states from which the resources are taken.

Overexploitation of species can also result in **cascade effects**, particularly if a habitat loses its apex predator. Because of the loss of the top predator, a dramatic increase in their prey species can occur. In turn, the unchecked prey can then overexploit their own food resources until population numbers dwindle, possibly to the point of extinction.

There are many examples of regulated fisheries (including hunting of marine mammals and harvesting of crustaceans and other species) monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. Bluefin tuna are in danger of extinction. The once-abundant

Mediterranean swordfish fishery have been depleted to commercial and biological exhaustion. Figure $23.3.7$ illustrates the extent of overfishing in the U.S. Despite considerable effort, few fisheries are managed sustainability.

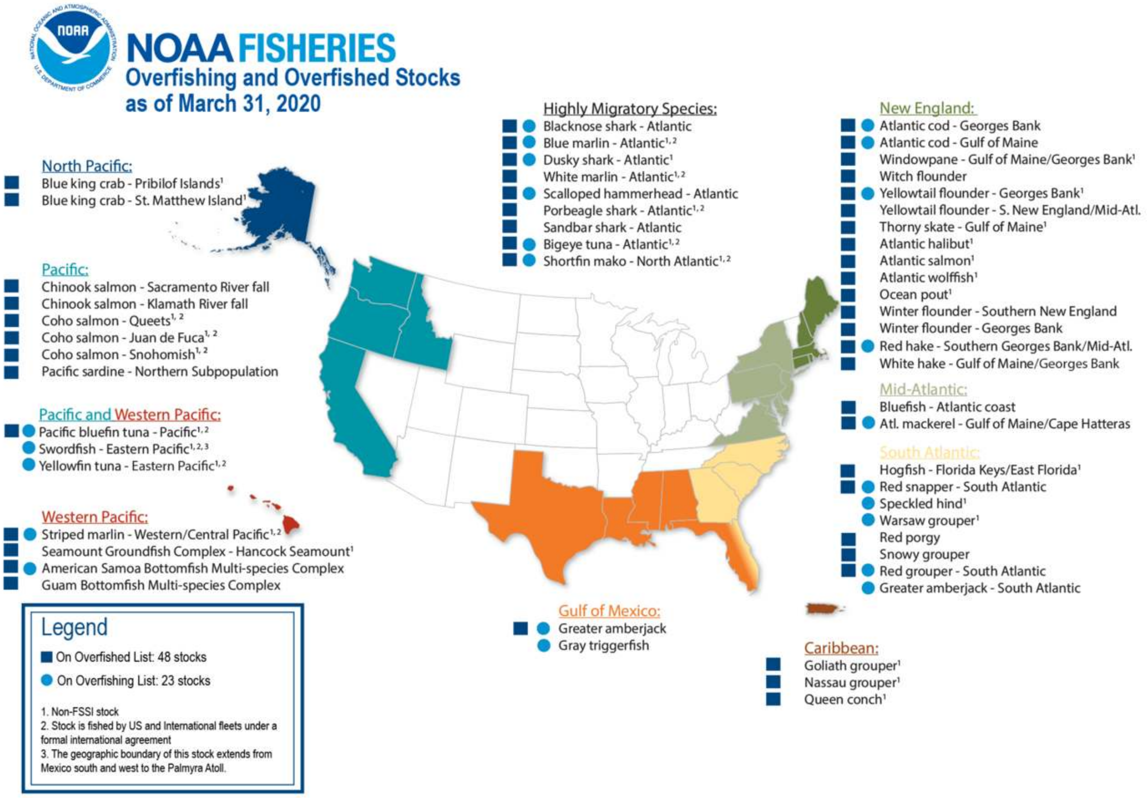


Figure $23.3.7$: Map of overfishing and overfished stocks in the U.S. by region. Stocks on the overfishing list are being harvested too quickly, and those on the overfished list have population sizes that are too low. For example, stocks of Chinook salmon, Coho salmon, and Pacific sardines are overfished in the Pacific. Some species, including stocks of Pacific bluefin tuna and Atlantic cod, are on both the overfishing and overfished lists. Image by NOAA (public domain).

The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common resource, available to anyone willing to fish, even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the **tragedy of the commons**, in which fishers have little motivation to exercise restraint in harvesting a fishery when they do not own the fishery. The general outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will drive toward fishing the population to extinction.

✓ Box 23.3.3 Tragedy of the Commons

Overharvesting is a serious threat to many species, especially aquatic ones. Common resources – or resources that are shared, such as fisheries – are subject to an economic pressure known as "the tragedy of the commons," in which essentially no harvester has a motivation to exercise restraint in harvesting from a certain area, because that area is not owned by that harvester. The natural outcome of harvesting common resources is their overexploitation.

For example, most fisheries are managed as a common resource even when the fishing territory lies within a country's territorial waters; because of this, fishers have very little motivation to limit their harvesting, and in fact technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases (for example, whales) economic forces will always drive toward fishing the population to extinction.

Figure 23.3.8: Overharvesting fisheries is an especially salient problem because of a situation termed the tragedy of the commons. In this situation, fishers have no real incentive to practice restraint when harvesting fish because they do not own the fisheries.

Early efforts to control overfishing used several kinds of regulations on quotas, fishing effort, and gear. Some forms of fishery management limit the number of fish that can be caught in an entire fishery. Under a total allowable catch (TAC) system, fishers can fish when and how they want, but once the quota for the fishery has been met, fishing must stop until the next season. Unfortunately, TAC policies do not solve the underlying problem that fishermen compete for the fish, and often yield perverse incentives and undesirable outcomes such as overcapitalization of the industry (Beddington, Agnew, & Clark, 2007) and races between fishing boat crews to catch fish before the quota is reached. In the well-known case of the Alaskan halibut fishery, the race became so extreme that the fishing season was reduced to a single 24-hour mad dash; given that fish are perishable, this temporal clumping of the catch is not a desirable outcome. Resource economists developed the idea of a tradable permit scheme to help manage fisheries. Individual tradable quota (ITQ) schemes are cap-and-trade policies for fish, where total catch is limited but fishers in the fishery are given permits that guarantee them a right to a share of that catch. Players in the fishery can sell their quota shares to each other (helping the catch to flow voluntarily to the most efficient boats in the industry) and there is no incentive for captains to buy excessively large boats or fish too rapidly to beat the other boats to the catch. ITQ policies have rationalized the

Alaskan halibut fishery completely: the fish stock is thriving, overcapitalization is gone, and the fish catch is spread out over time (Levy, 2010). ITQs have also been implemented in the fisheries of New Zealand, yielding large improvements in the biological status of the stocks (Annala, 1996).

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. But there are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. Also, there are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

A related consequence of fishing practices is "**bycatch**," animals that fishers sometimes catch and discard because they do not want them, cannot sell them, or are not allowed to keep them. Bycatch can be fish, but also includes other animals such as dolphins, whales, sea turtles, and seabirds that become hooked or entangled in fishing gear. Fishing boats are forbidden in some places from using conventional longlines because that gear yields high levels of bycatch and kills endangered leatherback turtles.

Overfishing can result in a radical restructuring of the marine ecosystem in which a dominant species is so overexploited that it no longer serves its ecological function. For example, overfishing a tertiary consumer could causes populations of secondary consumers to increase. Secondary consumers would then feed on primary consumes (like zooplankton), decreasing their population size. With fewer zooplankton, populations of primary producers (**phytoplankton**, or photosynthetic microorganisms) would be unregulated.

Sustainable seafood is a movement that has gained momentum as more people become aware of overfishing and environmentally-destructive fishing methods. Sustainable seafood is seafood from either fished or farmed sources that can maintain or increase production in the future without jeopardizing the ecosystems from which it was acquired. In general, slow-growing fish that reproduce late in life, such as orange roughy, are vulnerable to overfishing and are considered unsustainable seafood. Seafood species that grow quickly and breed young, such as anchovies and sardines, are much more resistant to overfishing and are therefore labeled “sustainable” and promoted as good alternatives. You can find more information about sustainable seafood from Seafood Watch, the WWF Seafood Guide, or the EDF Seafood Selector.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world’s marine fish species—about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels.

Terrestrial animals may be overexploited as sources of food, garments, jewelry, medicine, or pets. For example, the poaching of elephants for their valuable ivory and rhinos for their horns, which are used in traditional medicine, is a major threat to these species. There are also concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutans. Harvesting of pangolins for their scales and meat, and as curiosities, has led to a drastic decline in population size (Figure 23.3.9).

Figure 23.3.9: Pangolins are threatened by overexploitation. "Manis temminckii" by David Brossard is licensed under CC-BY 2.0.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly. However, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many monkeys and the great apes living in the Congo basin.

Some plant and fungal species are also overexploited, particularly if they are slow-growing. For example, stocks of wild ginseng, which is valued for its health benefits, are dwindling. Peyote cactus, which causes hallucinations and is used in sacred ceremonies, is also declining. Yarsagumba, dead moth larvae that were infected by fungal parasites (caterpillar fungus, *Ophiocordyceps sinensis*), is overexploited because it is highly valued in traditional medicine and used as an aphrodisiac (Figure $23.3.10$).

Figure $23.3.10$: Yarsagumba is a combination of moth larvae and the fungus that infected and killed it. "Yarsagumba" by Punya is licensed under CC BY-SA 4.0.

Exotic Species

Non-native (exotic) refers to species occurring outside of their historic distribution. Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, have characteristics that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. When this happens, the exotic species also becomes an invasive species. I Invasive species can cause ecological and economic damage. They threaten other species through competition for resources, predation, or disease. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. In the United States, invasive species like the purple loosestrife (*Lythrum salicaria*) and the zebra mussel (*Dreissena polymorpha*) have drastically altered the ecosystems they invaded. Some well-known invasive animals include the emerald ash borer (*Agrilus planipennis*) and the European starling (*Sturnus vulgaris*; Figure $23.3.11$). Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

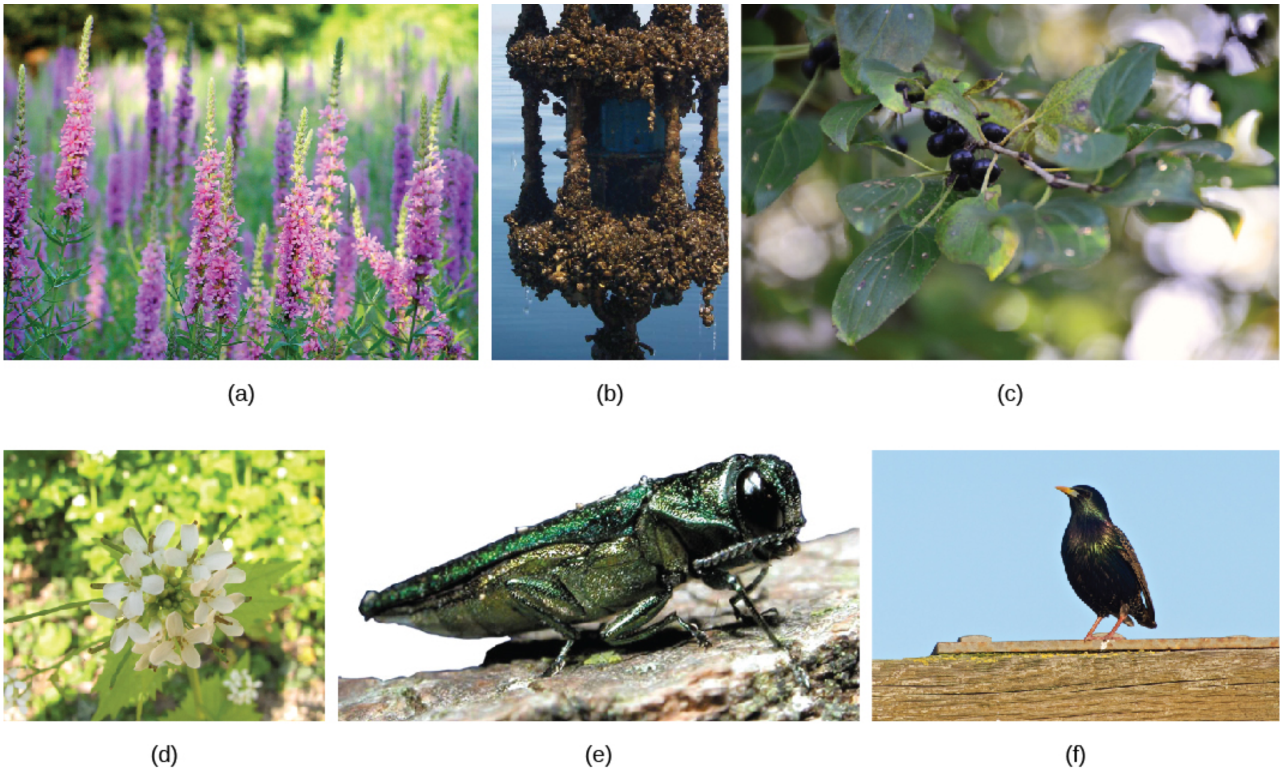


Figure 23.3.11: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata)*, and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

Link to Learning

Explore an interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft (Figure 23.3.12) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

Figure 23.3.12: The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950 (credit: NPS).

Many introductions of aquatic species, both marine and freshwater, have occurred when ships have dumped ballast water taken on at a port of origin into waters at a destination port. Water from the port of origin is pumped into tanks on a ship empty of cargo to increase stability. The water is drawn from the ocean or estuary of the port and typically contains living organisms such as plant parts, microorganisms, eggs, larvae, or aquatic animals. The water is then pumped out before the ship takes on cargo at the destination port, which may be on a different continent. The zebra mussel was introduced to the Great Lakes from Europe prior to 1988 in ship ballast. The zebra mussels in the Great Lakes have cost the industry millions of dollars in clean up costs to maintain water intakes and other facilities. The mussels have also altered the ecology of the lakes dramatically. They threaten native mollusk populations, but have also benefited some species, such as smallmouth bass. The mussels are filter feeders and have dramatically improved water clarity, which in turn has allowed aquatic plants to grow along shorelines, providing shelter for young fish where it did not exist before. The European green crab, *Carcinus maenas*, was introduced to San Francisco Bay in the late 1990s, likely in ship ballast water, and has spread north along the coast to Washington. The crabs have been found to dramatically reduce the abundance of native clams and crabs with resulting increases in the prey of native crabs.

One of the many recent proliferations of an invasive species concerns the Asian carp in the United States. Asian carp were introduced to the United States in the 1970s by fisheries (commercial catfish ponds) and by sewage treatment facilities that used the fish's excellent filter feeding abilities to clean their ponds of excess plankton. Some of the fish escaped, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers. Voracious feeders and rapid reproducers, Asian carp may outcompete native species for food and could lead to their extinction. One species, the grass carp, feeds on phytoplankton and aquatic plants. It competes with **native** species (those that historically occurred in the area and are adapted to the local ecosystem) for these resources and alters habitats for other fish by removing aquatic plants. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not desired in the United States. The Great Lakes and their prized salmon and lake trout fisheries are being threatened by Asian carp. The carp are not yet present in the Great Lakes, and attempts are being made to prevent its access to the lakes through the Chicago Ship and Sanitary Canal, which is the only connection between the Mississippi River and Great Lakes basins. To prevent the Asian carp from leaving the canal, a series of electric barriers have been used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem. In general, governments have been ineffective in preventing or slowing the introduction of invasive species.

Invading exotic species can also be disease organisms. It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure 23.3.13). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytrium dendrobatidis* and can act as a reservoir for the disease.

Figure $23.3.13$: This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease (credit: Brian Gratwicke).

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State (Figure $23.3.14$). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.

Figure 23.3.14: This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome (credit: Marvin Moriarty, USFWS).

Biological Control of Invasive Species

One reason why invasive species proliferate dramatically outside of their native range is due to **release from predators**. This means that parasites, predators, or herbivores that usually regulate their populations are not present, allowing them to outcompete or overpredate native species, which are still regulated. Based on this principle, organisms that regulate the invasive species populations have been introduced to the newly colonized areas in some cases. The release of organisms (or viruses) to limit population size is called **biological control**. As described in the examples below, biological control of invasive species has had varying success, exacerbating the problem in some cases and solving it in others.

Introduced into Australia, this Prickly-pear Cactus (*Opuntia*) soon spread over millions of hectares of range land driving out forage plants. In 1924, the cactus moth, *Cactoblastis cactorum*, was introduced (from Argentina) into Australia. The caterpillars of the moth are voracious feeders on prickly-pear cactus, and within a few years, the caterpillars had reclaimed the range land without harming a single native species. However, its introduction into the Caribbean in 1957 did not produce such happy results. By 1989, the cactus moth had reached Florida, and now threatens five species of native cacti there.

The leaf beetle (*Galerucella calmariensis*) has been introduced to suppress purple loosestrife, a noxious weed (Figure 23.3.15). A combination of four biological controls, including the leaf beetle were released in Minnesota since 1992. While it has not eradicated populations of this invasive species, biological control largely removed leaves from 20% of the purple loosestrive populations where it was released, which could reduce competition for native species. The biological controls established populations in most locations where they were released and even spread to new patches of purple loosestrife.

Figure $23.3.15$: Young larvae of the leaf-beetle feed in and on the developing buds of plants, often destroying them. This may stunt plant growth and delay or prevent flowering. Adults (shown) and older larvae feed on leaves and cause severe defoliation. Leaf-beetles can be used to as a biocontrol for invasive plants such as purple loosestrife.

In 1946 two species of *Chrysolina* beetles were introduced into California to control the Klamath weed (St. Johnswort) that was ruining millions of acres of range land in California and the Pacific Northwest. Before their release, the beetles were carefully tested to make certain that they would not turn to valuable plants once they had eaten all the Klamath weed they could find. The beetles succeeded beautifully, restoring about 99% of the endangered range land and earning them a commemorative plaque at the Agricultural Center Building in Eureka, California.

In 1859, the European rabbit was introduced into Australia for sport. With no important predator there, it multiplied explosively (Figure $23.3.16$). The raising of sheep (another imported species) suffered badly as the rabbits competed with them for forage. In 1950, the **myxoma virus** was brought from Brazil and released. The epidemic that followed killed off millions of rabbits (more than 99% of the population). Green grass returned, and sheep raising once again became profitable. Rabbit populations gradually increased, however, because the rabbits evolved to be more resistant to the virus, and the myxoma virus evolved to cause less damage. (Parasites, like viruses, benefit from multiplying inside the host and spreading to other individuals. If they kill their hosts too soon, they typically limit opportunities to multiply and spread.) More recently, the rabbit hemorrhagic disease virus has been used as biological control.

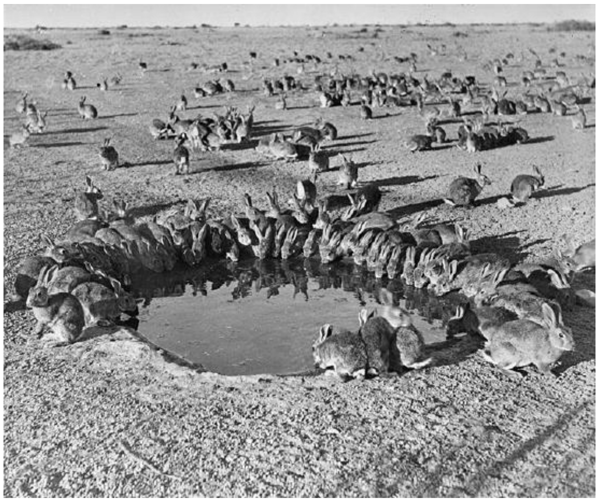


Figure $23.3.16$: These rabbits in Australia removed all forage plants, which ordinarily supply them with water as well as food. They thus had to drink from a pool. Image by National Archives of Australia (public domain).

To summarize the lessons learned from biological control successes and failures, only candidates that have a very narrow target preference (eat only a sharply-limited range of hosts) should be chosen. Each candidate should be carefully tested to be sure that once it has cleaned up the intended target, it does not turn to desirable species. Biological controls must not be used against native species. Finally, introduction of non-native species into the environment should be avoided because they could themselves be invasive.

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Anthropogenic warming of the planet has been observed and is hypothesized to continue due to past and continuing emission of greenhouse gases, primarily carbon dioxide and methane, into the atmosphere caused by the burning of fossil fuels and deforestation. These gases decrease the degree to which Earth is able to radiate heat energy created by the sunlight that enters the atmosphere. The changes in climate and energy balance caused by increasing greenhouse gases are complex and our understanding of them depends on predictions generated from detailed computer models. Scientists generally agree the present warming trend is caused by humans and some of the likely effects include dramatic and dangerous climate changes in the coming decades.

However, there is still a lack of understanding about outcomes for specific species related to climate change. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. Range shifts are already being observed: for example, on average, European bird species ranges have moved 91 km (56.5 mi) northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, amphibians, and mammals.

The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears (Figure $23.3.17$). Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring.

Figure 23.3.17: Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice and glacier coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models (Figure 23.3.18).

Figure 23.3.18: The effect of global warming can be seen in the continuing retreat of Grinnell Glacier. The mean annual temperature in Glacier National Park has increased 1.33°C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems (credit: USGS, GNP Archives).

Finally, global warming will raise ocean levels due to meltwater from glaciers and the greater volume occupied by warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will be altered. This could result in an overabundance of salt water and a shortage of fresh water.

Pollution

Figure 23.3.19: This photograph shows an example of a polluted sky, partially created by this smokestack's emissions. "Air Pollution" by Janak Bhatta is licensed under CC BY-SA 4.0.

Pollution is the introduction of contaminants into the natural environment that cause adverse change.[1] The United Nations considers pollution to be the "presence of substances and heat in environmental media (air, water, land) whose nature, location, or quantity produces undesirable environmental effects."[14] Pollution can take the form of any substance (solid, liquid, or gas) or energy (such as radioactivity, heat, sound, or light). Pollutants, the components of pollution, can be either foreign substances/energies or naturally occurring contaminants. Although environmental pollution can be caused by natural events, the word pollution generally implies that the contaminants have an anthropogenic source – that is, a source created by human activities, such as manufacturing, extractive industries, poor waste management, transportation or agriculture. Pollution is often classed as point source (coming from a highly concentrated specific site, such as a factory or mine) or nonpoint source pollution (coming from a widespread distributed sources, such as microplastics or agricultural runoff). Many sources of pollution were unregulated parts of industrialization during the 19th and 20th centuries until the emergence of environmental regulation and pollution policy in the later half of the 20th century. Sites where historically polluting industries released persistent pollutants may have legacy pollution long after the source of the pollution is stopped. Major forms of pollution include air pollution, light pollution, litter, noise pollution, plastic pollution, soil contamination, radioactive contamination, thermal pollution, visual pollution, and water pollution.

Pollution has been found to be present widely in the environment and has widespread negative impacts on the environment and human society. A pollutant may cause long- or short-term damage by changing the growth rate of plant or animal species, or by interfering with resources used by humans, human health or wellbeing, or property values. Some pollutants are biodegradable and therefore will not persist in the environment in the long term. However, the degradation products of some pollutants are themselves polluting such as the products DDE and DDD produced from the degradation of DDT. A 2022 study published in *Environmental Science & Technology* found that levels of anthropogenic chemical pollution have exceeded planetary boundaries and now threaten entire ecosystems around the world.[7][8]

Pollution can directly affect a species by making the environment unsuitable for its survival (this is what happens, for example, in the case of an oil spill). Sometimes pollution does not directly cause the death of an organism, but can make it more susceptible to disease or predation. It can also affect a species indirectly, by affecting food availability or reproductive performance, thus reducing population numbers over time.

There are a number of effects of pollution that can impact biodiversity:

- Biomagnification describes situations where toxins (such as heavy metals) may pass through trophic levels, becoming exponentially more concentrated in the process. So organisms from higher trophic levels are most likely to be impacted by pollutants.
- Carbon dioxide emissions cause ocean acidification, the ongoing decrease in the pH of the Earth's oceans as CO_2 becomes dissolved. Ocean acidification alters the balance of dissolution and precipitation of calcium carbonate which impacts organisms that use calcium carbonate for shells or skeletons.
- The emission of greenhouse gases leads to climate change which affects ecosystems in many ways including changes in temperature, precipitation, and environmental variability.
- Invasive plants can contribute debris and biomolecules (allelopathy) that can alter soil and chemical compositions of an environment, often reducing native species competitiveness.
- Nitrogen oxides are removed from the air by rain and fertilize land which can change the species composition of ecosystems.
- Smog and haze can reduce the amount of sunlight received by plants to carry out photosynthesis and leads to the production of tropospheric ozone which damages plants.
- Soil can become infertile and unsuitable for plants due to the accumulation of toxins. This will affect other organisms in the food web.
- Sulfur dioxide and nitrogen oxides can cause acid rain which lowers the pH value of soil and lakes and can lead to increases in aluminum concentration and the loss of some plant nutrients (such as calcium and magnesium) from soils.
- Organic pollution of watercourses can deplete oxygen levels by stimulating decomposition and therefore reduce species diversity.
- Noise and light generated by traffic, ships, vehicles, buildings and aircraft can affect the survivability of wildlife species and can reach undisturbed habitats. Noise and light pollution can interrupt communication among organisms of the same species or make it difficult for species to navigate and/or detect predators or prey. Disrupted communication can lead to both higher mortality from predation and decreased reproductive success.
- Noise, light, water, and air pollution can also increase stress in organisms, leading to lower fitness.

References

[1] "Pollution – Definition from the Merriam-Webster Online Dictionary". Merriam-Webster. 2010-08-13. Retrieved 2010-08-26.

[14] "pollution". glossary. UNdata. Retrieved 2022-05-01.

[7] Persson, Linn; et al. (2022). Outside the safe operating space of the planetary boundary for novel entities. Environmental Science & Technology, 56(3), pp. 1510–1521. Bibcode:2022EnST...56.1510P. doi:10.1021/acs.est.1c04158. PMC 8811958. PMID 35038861.

[8] *Carrington, Damian (January 18, 2022). Chemical pollution has passed safe limit for humanity, say scientists. The Guardian. Retrieved January 18, 2022.*

Global Forest Watch. (2020). World Resources Institute. Accessed 2020-07-29.

Illegal logging nets organized crime up to 100 billion dollars a year, INTERPOL–UNEP report reveals. (2012). Interpol. Accessed 2020-07-29.

Acheson, J.M. (1988). The lobster gangs of maine. *Lebanon, NH: University of New England Press*.

Annala, J.H. (1996). New Zealand's ITQ system: Have the first eight years been a success or a failure? *Reviews in Fish Biology and Fisheries*, *6*(1), pp. 43–62. doi: 10.1007/BF00058519

Beddington, J.R., Agnew, D.J., & Clark, C.W. (2007). Current problems in the management of marine fisheries. *Science*, *316*(5832), pp. 1713-1716. doi:10.1126/science.1137362

Costello, C., Gaines, S.D., & Lynham, J. (2008). Can catch shares prevent fisheries collapse? *Science*, *321*(5896), pp. 1678 – 1681. doi10.1126/science.1159478

Levy, S. (2010). Catch shares management. *BioScience*, *60*(10), pp. 780–785. doi:10.1525/bio.2010.60.10.3

Montaigne, F. (2007). Still waters, the global fish crisis. *National Geographic Magazine*. Retrieved from http://ngm.nationalgeographic.com/print/2007/04/global-fisheries-crisis/montaigne-text.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Hackson, J.B. C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., & Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*(5800), pp. 787 – 790. doi:10.1126/science.1132294

Contributors and Attributions

Written and curated by A. Wilson (Gettysburg College), N. Gownaris (Gettysburg College), Kyle Whittinghill (University of Vermont), and Melissa Ha with material from the following open-access sources:

- Threats to Biodiversity, Importance of Biodiversity, Community Ecology, and Sustainable Agriculture from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Threats to Biodiversity from *General Biology* by OpenStax (licensed under CC-BY) by

  Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

- Case Study: Marine Fisheries, and Biodiversity, Species Loss, and Ecosystem Function from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors. Download for free at CNX. (licensed under CC-BY)
- Understanding Bycatch. NOAA Fisheries. Accessed 28 March 2021 (public domain)
- Biological Control and Symbiosis from *Biology* by John W. Kimball (licensed under CC-BY)
- *Environmental Science* by Kamala Dorsner
- **Provided by**: National Geographic. **Located at**: **images.nationalgeographic.com...33_600x450.jpg**. **License**: ***CC BY: Attribution***
- Chilean purse seine. **Provided by**: Wikimedia. **Located at**: **http://commons.wikimedia.org/wiki/File:Chilean_purse_seine.jpg**. **License**: ***CC BY: Attribution***
- https://en.wikipedia.org/wiki/Pollution
- https://en.wikipedia.org/wiki/Biodiversity_loss

23.4: Scientist Spotlight - Scott Taylor

Boasting the characteristics of small, round, and fluffy, the chickadee is an endearingly cute bird. Or should we say- *are* cute *birds*. The word "chickadee" refers to a group of birds in the Paridae family. Of the 59 species in this family, there are 7 species of chickadee. Deferring to the name "chickadee" rather than each species' specific (and/or scientific) name is understandable. To the untrained eye, these birds are almost indistinguishable from one another. For example, *Poecile atricapillus* has a black cap and bib surrounding its white cheeks, hence the name black-capped chickadee. Unlike *P. atricapillus*, *Poecile hudsonicus* has a brown cap. Why do we care about such minute differences? Politics (and climate change).

In 1927, the Maine legislature designated the "chickadee" as the state bird. However, both black-capped *and* boreal chickadees reside in Maine. Aware of the two resident chickadee species, Nick Lund from Maine Audubon alerted local press. Representative Betty Austin then proposed a bill to specify Maine's official state bird (Pindell, 2019). In the end, the Maine Legislature decided to do nothing, but perhaps a warming climate will make the decision for them. At the University of Colorado Boulder, evolutionary biologist Dr. Scott Taylor is studying bird hybrid zones, areas where two species' ranges overlap, allowing interbreeding to occur. Because birds are sensitive to temperature, climate change is leading to shifts in species distributions, with many species moving northward. Different species shift at different rates, however, so climate change also alters species overlap and hybrid zones. One example of this is the climate-mediated northward shift of the chickadee hybrid zone in southeastern Pennsylvania. The importance of accurately identifying hybridization among species will only increase as climate change causes further shifts in species distribution (Taylor et al., 2014).

Dr. Scott Taylor says that none of his "mentors in high school, college, or as a graduate student or postdoc were visible members of the LGBTQIA+ community," and it is crucial that this problem be solved for others. By being a visible member of the community, Dr. Taylor hopes to inspire students who may be struggling to see themselves as scientists because of their under-represented identity in STEM.

"Boreal Chickadee" by Daniel Arndt is licensed under CC BY-NC-SA 2.0.

"Black-capped Chickadee" by Colin Durfee is licensed under CC BY 2.0.

References

Scientist Spotlight Inspiration from Project Biodiversity

American Ornithological Society. (2019). Researchers identify previously unknown hybrid zone between hummingbird species. <https://americanornithology.org/researchers-identify-previously-unknown-hybrid-zone-between-hummingbird-species/>. Accessed November 11, 2021.

Taylor, S.A., Larson, E.L., & Harrison, R.G. (2014). Hybrid zones: Windows on climate change. *Trends in Ecology & Evolution*, *30*(7), pp. 398-406.

Taylor, S.A., White, T.A., Honchahka, W.M., Ferretti, V., Curry, R.L., & Lovette, I. (2014). Climate-mediated movement of an avian hybrid zone. *Current Biology, 24*(6), pp. 1-6.

Pindell, J. (2019). Maine’s state-bird debate is ruffling some feathers. <https://www.bostonglobe.com/metro/2019/03/03/maine-state-bird-debate-ruffling-some-feathers/GpdBUYGIeY27IeMdhfBQgN/story.html> Accessed November 11, 2021.

23.5: Importance of Biodiversity

Healthy ecosystems contain a diversity of species, and each species plays a role in ecosystem function; therefore, species diversity as well as ecosystem diversity are essential to maintaining ecosystem services. Loss of biodiversity eventually threatens other species we do not impact directly because of their interconnectedness; as species disappear from an ecosystem other species are threatened by the changes in available resources. Biologists recognize that human populations are embedded in ecosystems and are dependent on them, just as is every other species on the planet. Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment: the ecosystem in which they existed. This cultural transition has made it difficult for humans to recognize their dependence on living things other than crops and domesticated animals on the planet. Today our technology smooths out the extremes of existence and allows many of us to live longer, more comfortable lives, but ultimately the human species cannot exist without its surrounding ecosystems. Our ecosystems provide our food. This includes living plants that grow in soil ecosystems and the animals that eat these plants (or other animals) as well as photosynthetic organisms in the oceans and the other organisms that eat them. Our ecosystems have provided and will provide many of the medications that maintain our health, which are commonly made from compounds found in living organisms. Ecosystems provide our clean water, which is held in lake and river ecosystems or passes through terrestrial ecosystems on its way into groundwater.

Figure 23.5.1: This tropical lowland rainforest in Madagascar is an example of a high biodiversity habitat. This particular location is protected within a national forest, yet only 10 percent of the original coastal lowland forest remains, and research suggests half the original biodiversity has been lost (credit: Frank Vassen).

Often called **ecological services** or **ecosystem services**, the products and processes associated with biological systems are of immense value to the well being of people. An incomplete list of these services and products includes the formation of soil and cycling of nutrients; provisioning of food, fresh water, fuel, fiber, and recreation opportunities; the regulation of climate, flooding, and disease. The value of these services is often overlooked or simply taken for granted, but one global estimate puts it somewhere between $16-64 trillion annually. From global food security, to a source of medicines, to even the oxygen in our air, we are dependent on biodiversity and the sustained integrity of ecological systems. Nature is also the basis for a significant part of aesthetic and spiritual values held by many cultures.

Human Health

Many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce secondary plant compounds which are toxins used to protect the plant from insects and other animals that eat them. Some of these compounds also work as human medicines. Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified the plants and their uses. Humans are not the only animals to use plants for medicinal reasons. The other great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure 23.5.2). Many medications were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.

Figure $23.5.2$: Catharanthus roseus, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas (credit: Forest and Kim Starr).

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medications improve people’s lives. Pharmaceutical companies are actively looking for new natural compounds that can function as medicines. It is estimated that one third of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds.

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. The chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to living in a natural environment and that built environments generate stresses that affect human health and well-being. There is considerable research into the psychologically regenerative benefits of natural landscapes that suggest the hypothesis may hold some truth.

Agricultural

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The people in this region traditionally lived in relatively isolated settlements separated by mountains. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the dramatic elevation changes, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields (Figure $23.5.3$).

Figure 23.5.3: A photo of the Mercado Modelo de Huancayo Peru showing many potato varieties on sale. Image by Thayne Tuason is licensed under CC BY 4.0.

Potatoes are only one example of agricultural diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: during the tragic Irish potato famine (1845–1852 AD), the single potato variety grown in Ireland became susceptible to a potato blight—wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world replacing traditional local varieties. The ability to create new crop varieties relies on the diversity of varieties available and the availability of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued supply of food.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because over time seed varieties are lost through accidents and there is no way to replace them. In 2008, the Svalbard Global seed Vault, located on Spitsbergen island, Norway, (Figure 23.5.4) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard should something happen to the regional seeds. The Svalbard seed vault is deep into the rock of the arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault’s systems will not compromise the climatic conditions inside the vault.

ART CONNECTION

Figure 23.5.4: The Svalbard Global Seed Vault is a storage facility for seeds of Earth’s diverse crops (credit: Mari Tefre, Svalbard Global Seed Vault).

The Svalbard seed vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Although crops are largely under our control, our ability to grow them is dependent on the biodiversity of the ecosystems in which they are grown. That biodiversity creates the conditions under which crops are able to grow through what are known as ecosystem services—valuable conditions or processes that are carried out by an ecosystem. Crops are not grown, for the most part, in built environments. They are grown in soil. Although some agricultural soils are rendered sterile using controversial pesticide treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. Replacing the work of these organisms in forming arable soil is not practically possible. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. It is estimated that honeybee pollination within the United States brings in $1.6 billion per year; other pollinators contribute up to $6.7 billion. Over 150 crops in the United States require pollination to produce. Many honeybee populations are managed by beekeepers who rent out their hives’ services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, a new phenomenon with an unclear cause. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors, but these are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species as well as beneficial insects like honeybees, and risking the health of agricultural workers and consumers. Moreover, these pesticides may migrate from the fields where they are applied and do damage to other ecosystems like streams, lakes, and even the ocean. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity (forests and fallow fields near to crop fields) on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. Another experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows that a diversity of pests is more effective at control than one single pest. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food. The world’s growing human population faces significant challenges in the increasing costs and other difficulties associated with producing food.

Wild Food Sources

In addition to growing crops and raising food animals, humans obtain food resources from wild populations, primarily wild fish populations. For about one billion people, aquatic resources provide the main source of animal protein. But since 1990, production from global fisheries has declined. Despite considerable effort, few fisheries on Earth are managed sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local human populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species and the larger species are overfished. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Psychological and Moral Value

Finally, it has been clearly shown that humans benefit psychologically from living in a biodiverse world. A chief proponent of this idea is Harvard entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to live in a natural environment and that city environments generate psychological stressors that affect human health and well-being. There is considerable research into the psychological regenerative benefits of natural landscapes that suggests the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

References

1. 1 International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. species.asu.edu/SOS.
2. Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*, pp. 51-57. doi:10.1038/nature09678

   Vie, J-C, Hilton-Taylor, C. & Stuart S.N. (Eds.). (2009). *Wildlife in a changing world: An analysis of the 2008 IUCN red List of threatened species*™. Gland, Switzerland: IUCN. Retrieved from http://data.iucn.org/dbtw-wpd/edocs/RL-2009-001.pdf.

Contributors and Attributions

Modified by Kyle Whittinghill and Melissa Ha from the following sources:

- Community Ecology and Importance of Biodiversity from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- *Environmental Science* by *Kamala Dorsner*
- Biodiversity, Species Loss, and Ecosystem Function from *Sustainability: A Comprehensive Foundation* by Tom Theis and Jonathan Tomkin, Editors. Download for free at CNX. (licensed under CC-BY)
- Preserving Biodiversity, **21.1: Importance of Biodiversity**, 47.2 The Importance of Biodiversity to Human Life, and **47.1: The Biodiversity Crisis** by OpenStax, is licensed CC BY by

  Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

  Access for free at https://openstax.org/books/biology-2e/pages/1-introduction

---

23.6: Preserving Biodiversity

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies. Today, the main efforts to preserve biodiversity involve legislative approaches to regulate human and corporate behavior, setting aside protected areas, and habitat restoration.

Changing Human Behavior

Legislation has been enacted to protect species throughout the world. The legislation includes international treaties as well as national and state laws. The **Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)** treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 35,000 “listed” species from being transported across nations’ borders, thus protecting them from being caught or killed when the purpose involves international trade. Species can be listed in one of three CITES appendices (Figure $23.6.1$). The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries’ ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

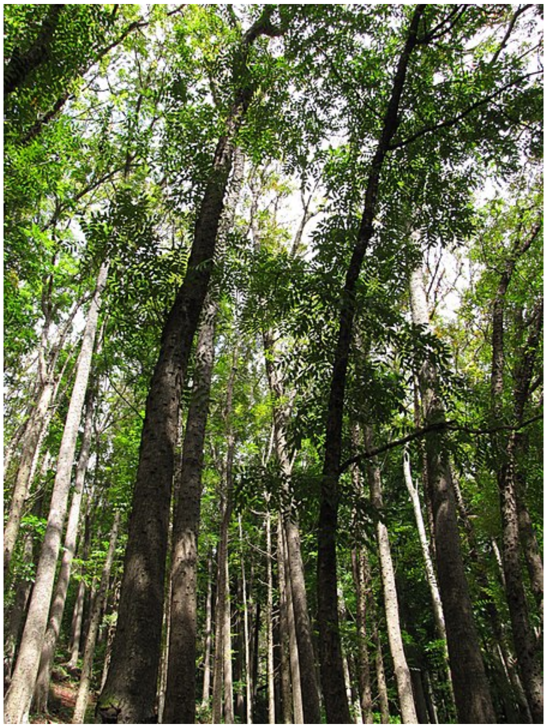


Figure $23.6.1$: Big-leaf mahogany (*Swietenia macrophylla*) timber is used to make furniture, musical instruments, boats, and other products. It listed in CITES Appendix II, meaning that it is regulated. Specifically, a permit is required to ship big-leaf mahogany timber. Image by Forest and Kim Starr (CC-BY).

Within many countries there are laws that protect endangered species and that regulate hunting and fishing. In the United States, the **Endangered Species Act** (ESA) was enacted in 1973. When an at-risk species is listed by the Act, the U.S. Fish & Wildlife Service is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed or to get an effective management plan in place once a species is listed. The ESA does not automatically protect species categorized as threatened on the IUCN Red List. Instead, the U.S. Fish and Wildlife Service (FWS), which enforces the ESA, assesses candidates for protected status as threatened or endangered (Figure $23.6.2$). Consideration of candidate species can be initiated by the FWS itself or at the request of the public. Through the Species Status Assessment Framework, the FWS compiles biological data, such as habitat and population information and current threats to the species. This biological data is used to inform decisions. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the ESA has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

Figure 23.6.2: Public Affairs Specialist for the U.S. Fish and Wildlife Service, Joanna Gilkeson, takes photos of federally endangered San Diego fairy shrimp in a vernal pool in Otay Mesa, California. Vernal pools are shallow seasonal ponds, and vernal pool species are uniquely adapted to changes in water availability. Image by Maideline Sanchez/USFWS (public domain).

The 1972 **Marine Mammals Protection Act** prohibits the "take" of marine mammals—including harassment, hunting, capturing, collecting, or killing—in U.S. waters and by U.S. citizens on the high seas. The act also makes it illegal to import marine mammals and marine mammal products into the United States without a permit. State laws can also aid in conservation. Through **California Endangered Species Act** (CESA), originally passed in 1970 and subsequently amended, the California Fish and Game Commission assesses species to be listed as threatened or endangered by the state. A listed species, or any part or product of the plant or animal, may not be imported into the state, exported out of the state, "taken" (killed), possessed, purchased, or sold without proper authorization. Note that endangered is a subcategory of threatened on the Red List, but for ESA and CESA, threatened and endangered are separate categories, with the latter representing at the greater risk of extinction.

The **Migratory Bird Treaty Act** (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers). Examples of protected species include northern cardinals, the red-tailed hawk, and the American black vulture.

Climate change is expected to be a major driver of biodiversity loss. Many governments are concerned about the effects of anthropogenic global warming, primarily on their economies and food resources. Because greenhouse gas emissions do not respect national boundaries, the effort to curb them is international. The international response to global warming has been mixed. The **Kyoto Protocol**, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two countries that were especially important in terms of their potential impact that did not ratify the Kyoto protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry, while China did so because of a concern that it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high. A renegotiated 2016 treaty, called the **Paris Agreement**, once again brought nations together to take meaningful action on climate change. But like before, some nations are reluctant to participate.

Conservation in Preserves

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity.

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts (Figure $23.6.3$). A **preserve** is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Governments or private organizations establish nature preserves. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

It is important to protect natural areas for several reasons. Some people feel a cultural or spiritual connection to the wilderness. Every year, millions of people visit recreational lands such as parks and wilderness areas to experience attractions of the great outdoors: hiking among the giant sequoias in California, traveling on a photo safari in Kenya or just picnicking at a local county park. Besides providing people with obvious health benefits and aesthetic pleasures, recreational lands also generate considerable tourist money for government and local economies. Outdoor recreation activities such as hiking and camping benefit tourist industries and manufacturers of outdoor clothes and equipment.

Figure $23.6.3$: Mequon Nature Preserve in Wisconsin. Image by Jennifer Tomaloff (CC BY-NC-SA 2.0).

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island.

Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher. As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation.

Conservation preserves can be seen as “islands” of habitat within “an ocean” of non-habitat. In general, large preserves are better because they support more species, including species with large home ranges; they have more core area of optimal habitat for individual species; they have more niches to support more species; and they attract more species because they can be found and reached more easily. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin “arms.” If preserves must be smaller, then providing **wildlife corridors** (narrow strips of protected land) between two preserves is important so that species and their genes can move between them. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin “arms.” If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Link to Learning

An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

On an international level, important wilderness lands have been designated by the United Nations through its "**Man and the Biosphere Program**." This program was established in 1973 to protect examples of major natural regions throughout the world, and provide opportunities for ecological research and education. **Biosphere reserves** are organized into three interrelated zones: the **core area**, the **buffer zone** and the **transition area**. The core area contains the landscape and ecosystems to be preserved. The buffer zone is an area where activities are controlled to protect the core area. The outer transition area contains a variety of agricultural activities, human settlements and other uses. Local communities, conservation agencies, scientists and private enterprises that have a stake in the management of the region work together to make the reserves work. Mt Kenya in Africa and the Galapagos Islands are examples of wilderness areas protected under this provision.

Types of Protected Areas in the United States

The public lands described below differ in their level of protection. For example, national parks and forests allow camping whereas wildlife refuges place more limitations on human activities. National parks and forests and wildlife refuges can contain wilderness areas.

Wilderness areas, comprise ecosystems in which human activity has not significantly affected the plant and animal populations or their environment. Natural processes predominate. According to the "Wilderness Act of 1964," wilderness areas are defined as being those areas where the nearest road is at least five miles away and where no permanent buildings stand. Activities that could disrupt native species, such as the use of motorized vehicles is prohibited. More than 100 million acres of land are now preserved as wilderness under this act. Sparsely populated Alaska contains the largest chunk of wilderness areas, over half of it. Although wilderness areas are scattered among most of the lower 48 states, the largest percentage is found in the western states. Few undesignated areas in the contiguous states remain that would qualify as wilderness. California contains significant wilderness areas, with over 4 million acres of National Forest Wilderness areas, and 1.5 million acres of mostly desert wilderness in the Mojave Desert National Preserve (Figure 23.6.4). Wilderness areas provide an essential habitat for a wide array of fish, wildlife, and plants, and are particularly important in protecting endangered species. For scientists, wilderness areas serve as natural laboratories, where studies can be performed that would not be possible in developed areas.

Figure 23.6.4: A variety of unique plant life grows at Mojave Desert National Preserve. Image by John Fowler (CC-BY 2.0).

The United States has set aside more land for public recreational use than any other country. The **National Park System** manages more than 380 parks, recreation areas, seashores, trails, monuments, memorials, battlefields, and other historic sites. It consists of more than 80 million acres nationwide (Figure 23.6.5). The largest national park is Wrangell–St. Elias National Park and Preserve in Alaska with over 13 million acres. California has eight national parks: Channel Islands, Death Valley, Joshua Tree, Lassen, Redwood, Sequoia, Kings Canyon, and Yosemite. Many national parks such as Yosemite, Yellowstone and the Grand Canyon are such popular recreation destinations that the ecosystems of those parks are being severely tested by human activities.

Figure 23.6.5: National parks, such as Grand Teton National Park in Wyoming, help conserve biodiversity (credit: Don DeBold).

Every state has also set aside significant amounts of land for recreational use. The **California State Park System** manages more than one million acres of parklands including: coastal wetlands, estuaries, scenic coastlines, lakes, mountains and desert areas. California's largest state park is Anza-Borrego Desert State Park, which is the largest state park in the United States with 600,000 acres. The stated mission of the California State Park System is "to provide for the health, inspiration and education of the people of California by helping to preserve the state's extraordinary biological diversity, protecting its most valued natural and cultural resources and creating opportunities for high-quality outdoor recreation". This is the basic goal of all recreational lands: to manage and conserve natural ecosystems, while supporting a sustainable and balanced level of human use of those areas. Unfortunately, it is a goal which is sometimes difficult to achieve due to the increasing popularity and use of recreational lands.

The **National Forest System**, managed by the U.S. Forest Service (part of the United States Department of Agriculture), consists of more than 170 forestlands and grasslands, which are available for activities such as camping, fishing, hiking and hunting. These are managed as multiple use lands, which balance the needs for recreation, grazing, timber, watershed protection, wildlife and fish, and wilderness. Some examples of national forests are the Sierra National Forest in California and the White Mountain National Forest in New Hampshire. The Coronado National Forest in Arizona is famous for "sky islands", or steep mountain ranges surrounded by low-lying areas. The dramatic increase in elevation is associated with changes in the flora and fauna (Figure 23.6.6). Explore national forests using this interactive map.

Figure $23.6.6$: The Santa Teresa Mountains of the Coronado National Forest form "sky islands." Image by Jstuby (public domain).

The U.S. Fish and Wildlife Service manage more than 500 national **wildlife refuges** (Figure $23.6.7$), which not only protect animal habitats and breeding areas but also provide recreational facilities. Find a Refuge is an interactive map for locating wildlife refuges.

Figure $23.6.7$: Bobcat at Sonny Bono National Wildlife Refuge in southern California. Image by Mark Stewart/USFWS (public domain).

Several other types of public lands complement the designated wilderness land system. These include: national forest roadless areas, national trails system, natural research areas and state and private wilderness lands. The national forest roadless areas consist of millions of acres of wild, undeveloped land without roads that exist on National Forest land outside of designated wilderness lands. The "**National Trail System**," established by Congress in 1968, includes trails in wilderness areas and other public lands. **Research Natural Areas** located throughout the country on public lands serve as outdoor laboratories to study natural systems. They are intended in part to serve as gene pools for rare and endangered species and as examples of significant natural ecosystems. Some wilderness lands are maintained by states or private organizations. For example, the state of New York has long preserved a region of the Adirondacks as wilderness.

Habitat Restoration, Remediation, and Reclamation

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (Figure $23.6.8$) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

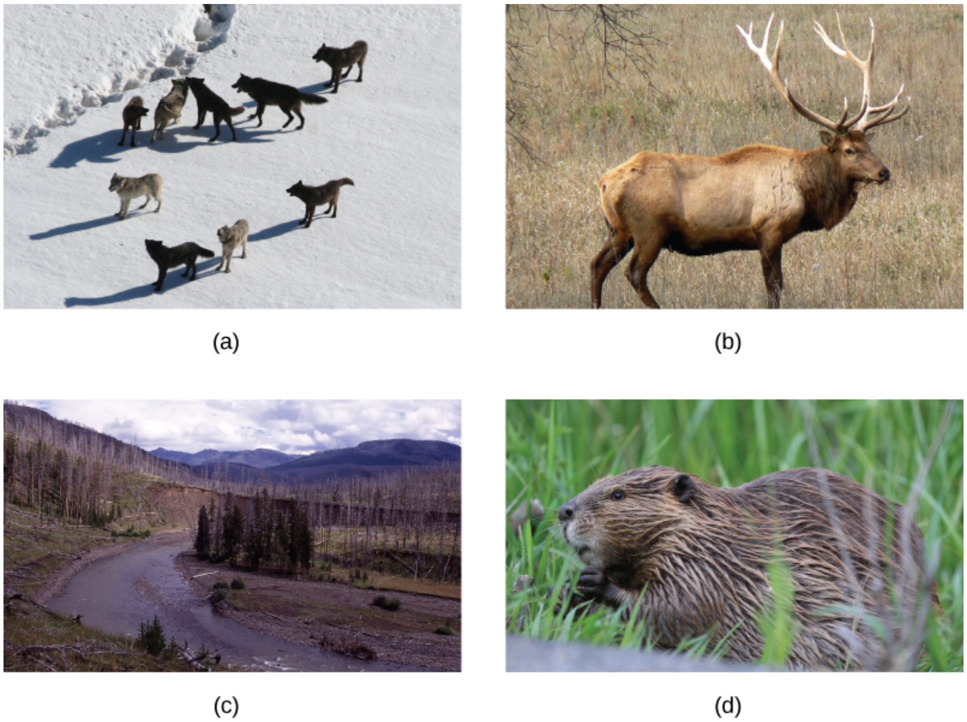


Figure 23.6.8: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by “Shiny Things”/Flickr).

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

Besides physical processes, socioeconomic factors must also be considered in a restoration project. Actions of humans have historically been important in shaping ecosystems, and are important in determining the success of restoration efforts. Because the cost to restore an individual site can involve millions of dollars, government support is a necessity.

Danger to human health from both historic and modern pollution requires that cleanup measures be implemented. **Remediation** is aimed at neutralization, containment, and/or removal of the polluting chemicals. The goal is to prevent the spread of the pollution, or to reduce it to levels that will not appreciably risk human health. Many times, it is physically impossible or financially unfeasible to completely clear all contamination. Often, experts and the public disagree on how clean is clean enough.

Many communities are struggling to find the funds and technological expertise needed to clean up polluted areas. Some settings, such as brownfields, can be remediated fairly easily. **Brownfields** are abandoned industrial or commercial facilities or blighted urban areas that need to be cleansed of contamination before they can be redeveloped. Other areas, because of their size or the extreme toxicity of their contaminants, require very expensive, complex, and long-term remediation. Many of these have been designated as Superfund sites.

Superfund sites are areas with the most toxic contamination in the United States. The contamination may not only make the site itself too dangerous to inhabit, but often leaks toxic levels of pollutants into the surrounding soil, water, or air. An example of a Superfund site is Love Canal in Niagara Falls, New York (Figure $23.6.9$). The canal was a chemical waste dump for many years, then in the 1950's was covered with soil and sold to the city. Over time, many homes and a school were built over the former dump. In the 1970's, heavy rains raised the water table and carried contaminants back to the surface. Residents noticed foul smells, and gardens and trees turned black and died. Soon after, rates of birth defects, cancer, and other illnesses began to rise sharply. In 1977, the State of New York and the federal government began remediation work. Buildings were removed, and all residents were bought out and relocated, contaminated deposits and soils were excavated, and remaining soils and groundwater were treated and sealed off to prevent further spread of the contamination. Remediation activities have now been completed at this site.

Figure $23.6.9$: Love Canal. *Source: US Environmental Protection Agency.*

The type of pollution and the medium affected (air, water, or soil) determine remediation methods. Methods include incineration, absorption onto carbon, chemical methods, or bioremediation. **Bioremediation** is the use of plants, bacteria, or fungus to "digest" the contaminant to a non-toxic or less toxic form. All of these methods tend to be expensive and time-consuming.

Reclamation involves salvaging some features of a degraded habitat, but it may not restore the ecosystem fully (Figure $23.6.10$). For example, instead of abandoning a mined area once resources have been collected, it can be reclaimed by planting vegetation, reshaping the landscape, and redirecting water flow. However the reclaimed land still lacks many features of the original ecosystem, such as complex topography, vegetation that took tens or hundreds of years to grow, soil quality, and an intricate network of streams.

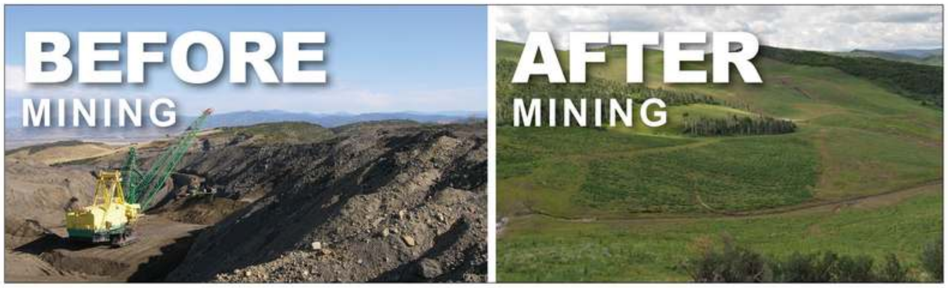


Figure 23.6.10: The Seneca Yoast coal once land has been cleared in preparation for mining (left) and after reclamation (right). Image by Peabody Energy, Inc. (CC-BY).

Sometimes, actions can be taken to avoid, reduce or compensate for the effects of environmental damage. Such **mitigation** efforts have been taken by the Army Corps of Engineers during construction projects. The native plants are removed from a site before construction begins and transplanted at a special holding site. After the construction project is completed, the native plants are replanted using those from the holding site. Another example of mitigation might involve the creation or enhancement of wetlands in one area, in order to compensate for permitted wetland losses in another area. Mitigation often goes hand-in-hand with restoration. Texaco, in conjunction with environmental groups and the United States Fish and Wildlife Service, restored 500 acres of agricultural lands in the lower Mississippi Delta to bottomland hardwoods. Texaco received environmental credits for the mitigating effects of the new woodlands on air quality.

The Role of Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education (Figure 23.6.11). The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing and gaining strength. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. However, captive breeding programs have yielded some success stories, such as the California condor reintroduction to the Grand Canyon and the reestablishment of the Whooping Crane along the Midwest flyway. Unfortunately, zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people’s attitudes and actions regarding conservation; at present, the results tend to be mixed.

Figure 23.6.11: Zoos and captive breeding programs help preserve many endangered species, such as this golden lion tamarin (credit: Garrett Ziegler).

Economic Influences on Conservation

Economics greatly impacts conservation success. Short-term profits can incentivize individuals, companies, or governments to harvesting resources at an unsustainable rate and at the expense of ecosystem health. In impoverished regions, compromising habitat to grow high-value crops, such as coffee or oil palms, or poaching endangered species may seem like the only source of income. One solution is **debt-for-nature swaps** through which one country forgives the debt of another if the latter agrees to protect natural areas. These conservation efforts can provide a new source of income for residents near the protected areas. For example, the United States forgave $20 million in debt from Costa Rica. In exchange, Costa Rica invested in expanding its protected areas and developing the ecotourism industry, which provides jobs to many of its residents (Figure 23.6.12). **Ecotourism** involves visiting and enjoying natural areas while minimizing ecological damage. Ecotourism can benefit local economies and alleviate poverty especially if the earnings from it are reinvested into the communities living near tourist destinations. It generates jobs such as park operators, sellers of local crafts, and tour guides.

Figure 23.6.12: A tourist ziplines over the Costa Rican rainforest. Image by Khaufle at the English language Wikipedia (CC-BY-SA).

Supplemental Reading

America's Public Lands Explained. 2016. U.S. Department of the Interior.

References

1. MacArthur, R.H., & Wilson, E. O. (1967). The theory of island biogeography. *Princeton, N.J.: Princeton University Press*.

Contributors and Attributions

Modified by Kyle Whittinghill and Melissa Ha from the following sources

- Preserving Biodiversity by OpenStax is licensed under CC BY 4.0 by

  Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

- Threatened and Endangered Species by California Department of Fish and Wildlife (public domain)
- Marine Mammal Protection by NOAA Fisheries (public domain)
- Ecotourism from *Life Sciences Grade 10* by Siyavula (licensed under CC-BY)
- Preserving Biodiversity and Case Study - The Love Canal Disaster from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Issues and Opinions, Biological and Land from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Multiple Use Lands. 12 May 2015. The United States Department of Justice. Accessed 28 March 2021 (public domain)

CHAPTER OVERVIEW

24: Human Impact on Global Climate

Learning Objectives

- Describe how humans have changed greenhouse gas concentrations in the Earth's atmosphere and how scientists have identified this as the cause of recent changes in climate.
- Discuss how humans have changed Earth's energy balance through changes in albedo.
- Characterize feedbacks to climate change from changes in temperature, carbon cycling, and albedo.
- Explain predictions for future changes in temperature, precipitation, storm events, ice cover and permafrost.
- Define ocean acidification and how it will change with changes in atmospheric carbon dioxide concentrations.
- Describe changes in plant productivity, species interactions, and diseases that may occur with changes in climate.

Summary

This chapter discusses recent changed in climate caused by human activity and how scientists have attributed those changes to increases in greenhouse gas concentrations in the atmosphere from human activities. Section 24.1 also describes changes in the earths reflectivity (albedo) due to humans and feedbacks to global climate. Section 24.2 characterizes future climate changes expected due to the changes in greenhouse gas concentrations in the atmosphere including changes in temperature, precipitation, storm events, ice cover and permafrost, sea level, ocean acidification, plant productivity, species interactions, and disease prevalence. For more information on Earth's energy balance, atmospheric and oceanic circulation, natural climate forcings, and past climate change, see the chapter on "The Physical Environment".

24.1: Anthropogenic Climate Change

When we talk about anthropogenic climate change, we are generally thinking of the industrial era, which really got going when we started using fossil fuels (coal to begin with) to drive machinery and trains. That was around the middle of the 18th century. The issue with fossil fuels is that they involve burning carbon that was naturally stored in the crust over hundreds of millions of years. Some climate scientists argue that anthropogenic climate change actually goes back much further than the industrial era, and that humans began to impact the climate by clearing land to grow grains in Europe and the Middle East around 8,000 years BCE and by creating wetlands to grow rice in Asia around 5,000 years BCE. Clearing forests for crops is a type of climate-forcing because the CO_2 storage capacity of the crops is generally lower than that of the trees they replace, and creating wetlands is a type of climate forcing because the anaerobic bacterial decay of organic matter within wetlands produces CH_4.

In fact, whether anthropogenic climate change started with the agricultural revolution or the industrial revolution is not important, because the really significant climate changes didn’t start until the early part of the 20th century, and although our activities are a major part of the problem, our increasing numbers are a big issue as well. Figure $24.1.1$ shows the growth of the world population from around 5 million, when we first started growing crops, to about 18 million when wetland rice cultivation began, to over 800 million at the start of the industrial revolution, to over 7,700 million in 2019. A big part of the incredible growth in our population is related to the availability of the cheap and abundant energy embodied in fossil fuels, which we use for transportation, heating and cooling, industry, and food production.

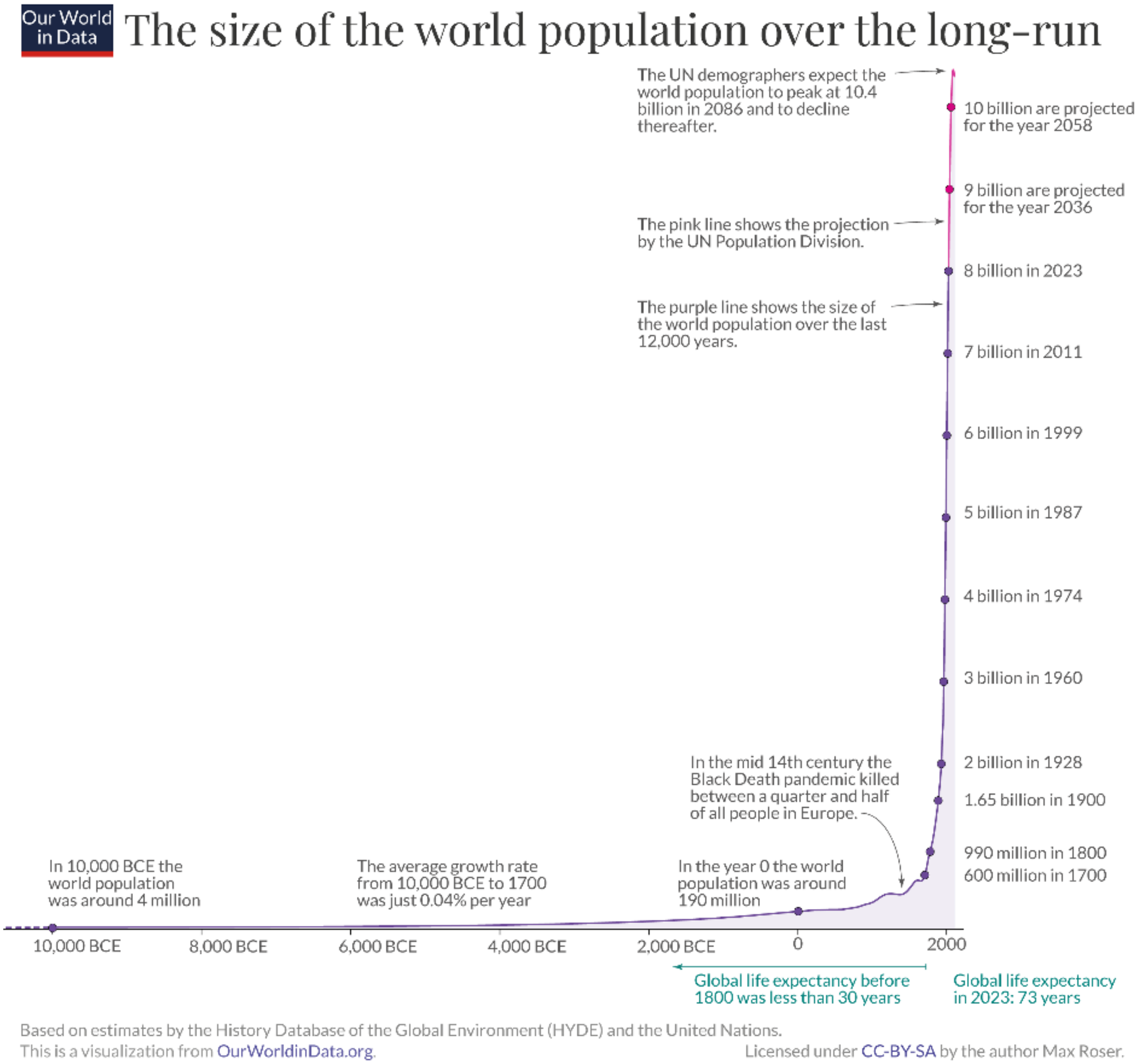


Figure 24.1.1: World population growth over the past 12,000 years. Based on estimates by the History Database of the Global Environment (HYDE) and the United Nations. This visualization is from OurWorldinData.org and is liscensed under CC-BY-SA by the author Max Roser.

A rapidly rising population, the escalating level of industrialization and mechanization of our lives, and an increasing dependence on fossil fuels for transportation and energy generation have driven the anthropogenic climate change of the past century. The trend of mean global temperatures since 1880 is shown in Figure 24.1.2 For approximately the past 55 years, the temperature has increased at a relatively steady and rapid rate, especially compared to past changes. The average temperature now is approximately 1.0°C higher than before industrialization, and two-thirds of this warming has occurred since 1975.

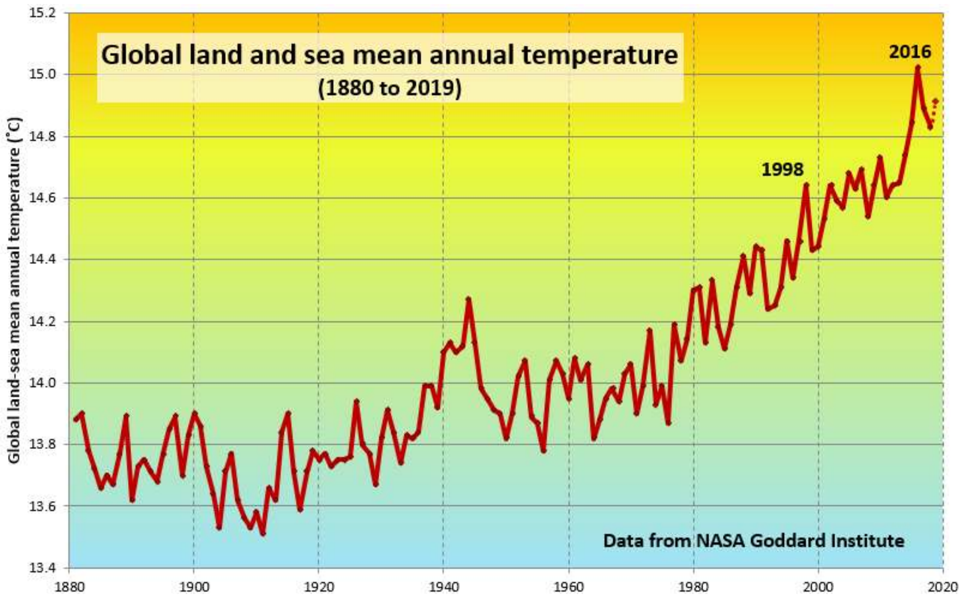


Figure $24.1.2$: Global mean annual temperatures for the period from 1880 to 2019. The value for 2019 is projected, based on only 6 months of data. 1998 and 2016 were strong El Niño years. © Steven Earle. CC BY. Based on data from NASA.

Changes in land surface or ocean surface temperatures can be expressed as temperature **anomalies**. A temperature anomaly is the difference in average temperature measurement from a predetermined datum (or baseline). This datum is the average temperature of a particular date range, for example, 1951 to 1980. Another common datum is the last century (1900-2000). Therefore, an anomaly of 1.25 ℃ for 2015 (last century datum) means that the average temperature for 2015 was 1.25 ℃ greater than the 1900-2000 average. In 1950, the temperature anomaly was -0.28 ℃, so this is -0.28 ℃ lower than the 1900-2000 average [3]. These temperatures are annual average surface temperatures. Figure $24.1.3$ shows the global mean temperature estimates for the period of 1880 to 2020 using the datum of the 1951-1980 average temperature.

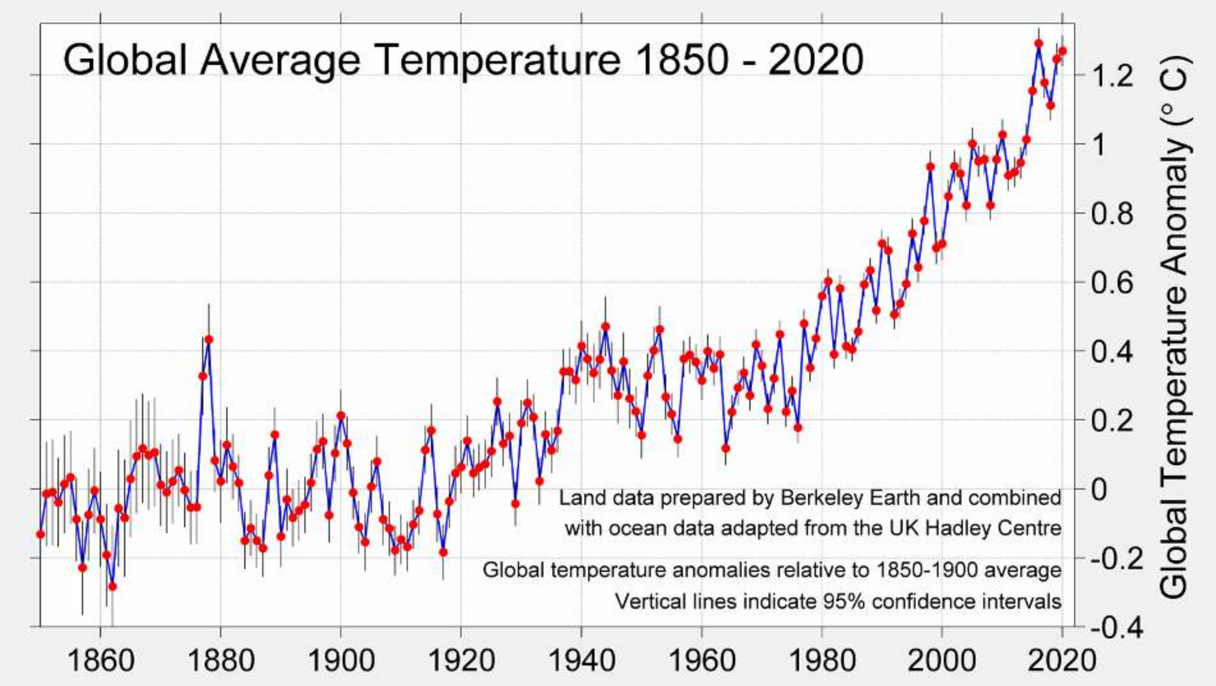


Figure 24.1.3: Land-ocean temperature index, 1880 to 2020, with a base time 1951-1980. The solid black line is the global annual mean and the solid red line is the five-year lowess smooth. The blue uncertainty bars (95% confidence limit) account only for incomplete spatial sampling.
[From https://berkeleyearth.org/global-temperature-report-for-2020/]

Since 1880, average global surface temperatures have trended upward and most of that warming has occurred since 1970 (see this NASA animation). Since the ocean is absorbing a lot of the additional trapped heat, surface temperatures include both land surface and ocean temperatures [13]. This video figure also shows worldwide temperature changes since 1880. The more blue, the cooler; the more yellow and red, the warmer.

Scientific Consensus: Global Climate Change is Real

The **Intergovernmental Panel on Climate Change** (IPCC)—established by the United Nations Environment Programme and the World Meteorological Organization in 1988—is responsible for reviewing the scientific literature on climate change and issuing periodic reports on several topics, including the scientific basis for understanding climate change, our vulnerability to observed and predicted climate changes, and what we can do to limit climate change and minimize its impacts. The IPCC uses this information to evaluate current impacts and future risks, in addition to providing policymakers with assessments. These assessments are released about once every every six years. The most recent report, the 6th Assessment, was released in 2023. Hundreds of leading scientists from around the world are chosen to author these reports. Over the history of the IPCC, these scientists have reviewed thousands of peer-reviewed, publicly available studies. The scientific consensus according to the last IPCC assessment is clear: global climate change is real and humans are very likely the cause for this change.

Additionally, the major scientific agencies of the United States, including the National Aeronautics and Space Administration (NASA) and the National Oceanic and Atmospheric Administration (NOAA), also agree that climate change is occurring and that humans are driving it. In 2010, the US National Research Council concluded that “Climate change is occurring, is very likely caused by human activities, and poses significant risks for a broad range of human and natural systems”. Many independent scientific organizations have released similar statements, both in the United States and abroad. This doesn’t necessarily mean that every scientist sees eye to eye on each component of the climate change problem, but broad agreement exists that climate change is happening and is primarily caused by excess greenhouse gases from human activities. The scientific consensus is clear: through alterations of the carbon cycle, humans are changing the global climate by increasing the effects of something known as the greenhouse effect.

Comparing modeling results to the historical climate record shows that, in general, climate changes prior to the Industrial Revolution in the 1700s can be explained by natural causes, such as changes in solar energy, volcanic eruptions, and natural changes in greenhouse gas (GHG) concentrations (Figure 24.1.4). However, recent changes in climate, especially warming since the mid-20th century, cannot be explained by natural causes alone and models need to include the effects of human activities, especially our combustion of fossil fuels, to explain the current warming (Figure 24.1.4).

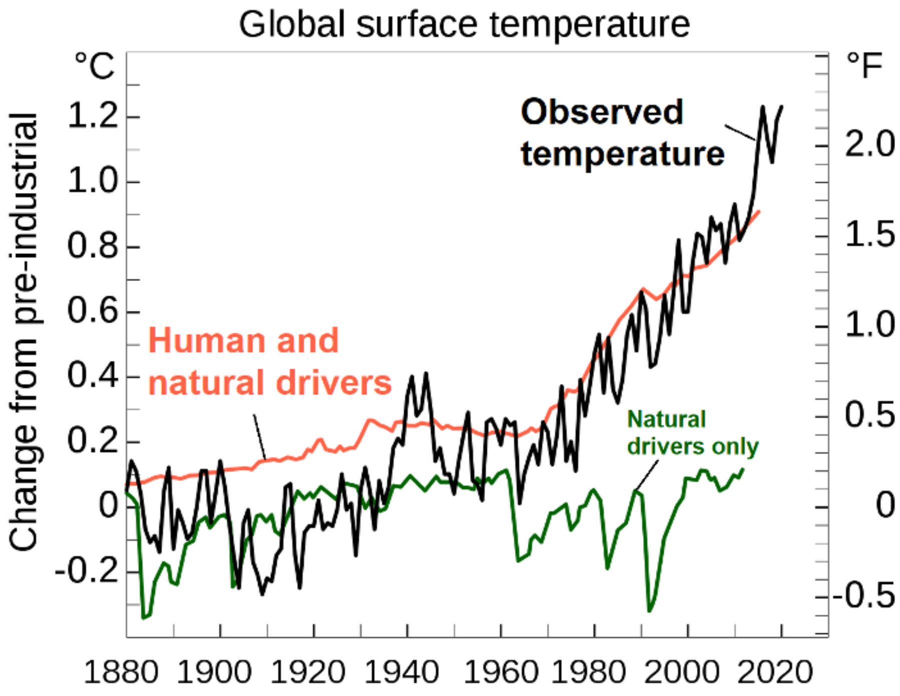


Figure 24.1.4: This graph shows the predicted temperatures from two climate models and observed temperatures from 1880 to 2020. The first model considered only natural factors that could influence temperature and is represented by the green line (bottom). It shows some fluctuations in temperature by no overall increase or decrease. The second model considered both human and natural factors and is represented by the orange line (top). It shows an overall increase in temperature. Actual observations (black, jagged line; middle) more closely match the second model. Overall, temperature has increased about 1.2 degrees Celsius (2.1 degrees Fahrenheit) since pre-industrial times. Image relabeled from Efbrazil (CC-BY-SA).

Human Impact on Greenhouse Gases

Recall that greenhouse gases are probably the most significant drivers of the climate. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere as thermal energy. Greenhouse gases absorb much of the thermal energy near the Earth's surface so the more greenhouse gases there are in the atmosphere, the more thermal energy is retained by the Earth.

Water vapor is the most abundant greenhouse gas and also the most important in terms of its contribution to the natural greenhouse effect, despite having a short atmospheric lifetime. Some human activities can influence local water vapor levels. However, on a global scale, the concentration of water vapor is controlled by temperature, which influences overall rates of evaporation and precipitation. Therefore, the global concentration of water vapor is not substantially affected by direct human emissions.

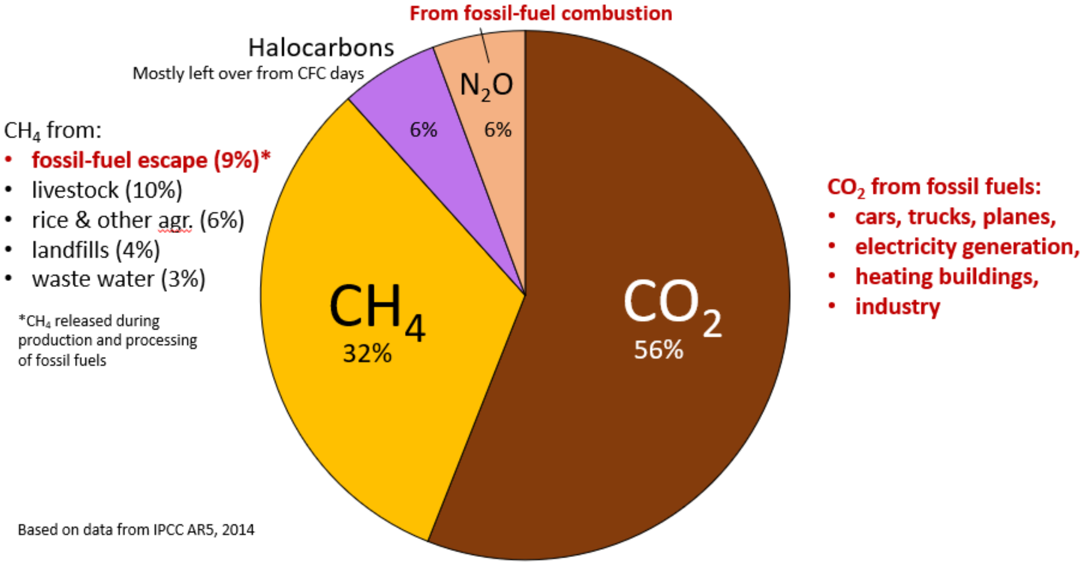


Figure 24.1.5: The relative climate-warming effects of the various greenhouse gases. (Effects listed in red are all related to fossil fuels.)

© Steven Earle. CC BY. Based on data in IPCC AR 5, 2014.

Figure 24.1.5, which is based on data from the fifth assessment report of the IPCC, issued in 2014, shows the relative contributions of various long-lasting anthropogenic GHGs to current climate forcing, based on the changes from levels that existed in 1750. Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The biggest anthropogenic contributor to warming is CO_2, which accounts for 56% of positive forcing. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure 24.1.6). CH_4 accounts for 32%, and the halocarbon gases (mostly leaked from older air-conditioning appliances that still contain CFCs) and nitrous oxide (N_2O) (from burning fossils fuels) account for 6% each. CO_2 emissions come mostly from coal- and gas-fired power stations, motorized vehicles (cars, trucks, and aircraft), and industrial operations (e.g., smelting). CH_4 emissions come from production of fossil fuels (escape from coal mining and from gas and oil production and processing), livestock farming (mostly beef), landfills, waste water, and wetland rice farming. N_2O is derived almost entirely from the combustion of fossil fuels. In summary, most (by far) of our current GHG emissions come from fossil fuel production and use.

Figure 24.1.6: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere (credit: "Smoke Plume" by Pöllö is licensed under CC BY 3.0).

Carbon Dioxide

Carbon dioxide (CO_2) is the primary greenhouse gas that is contributing to recent global climate change. CO_2 is a natural component of the carbon cycle, involved in such activities as photosynthesis, respiration, volcanic eruptions, and ocean-atmosphere exchange. Human activities, primarily the burning of fossil fuels and changes in land use, release very large amounts of CO_2 to the atmosphere, causing its concentration in the atmosphere to rise. Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm (Figure 24.1.7). Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration.

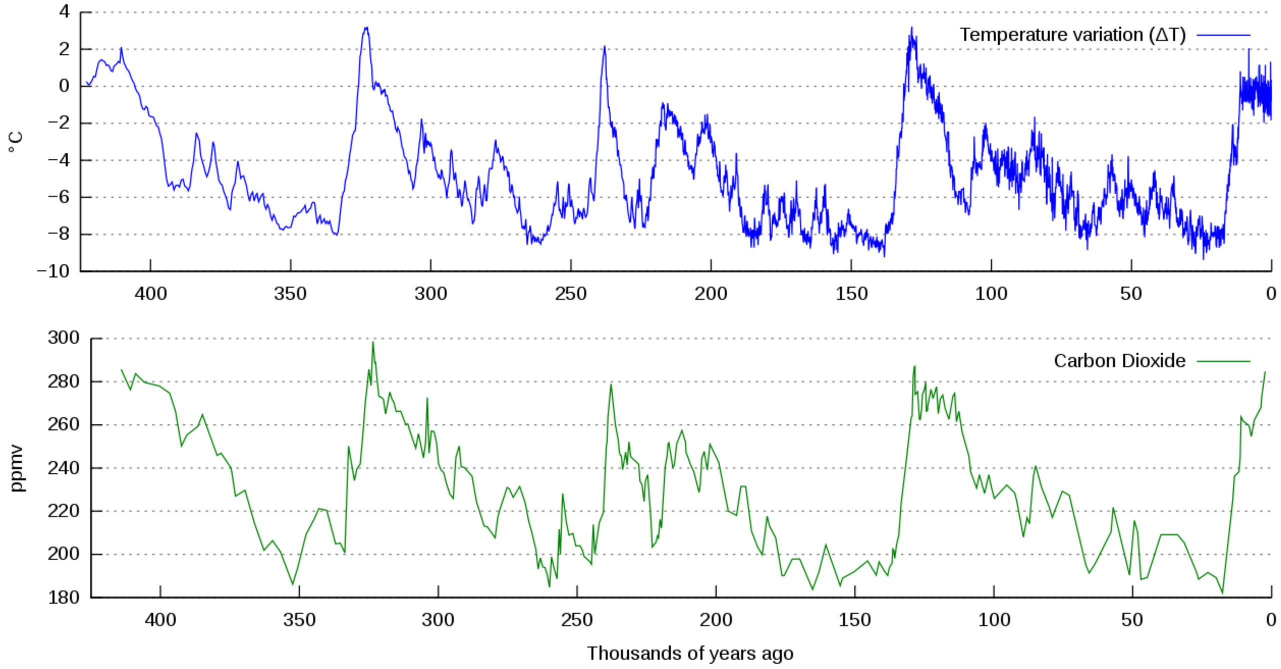


Figure 24.1.7: Graph of change in temperature in degrees Celsius (top, blue line) and carbon dioxide concentration in parts per million by volume (bottom, green line) measured from the Vostok, Antarctica ice core. These have been associated for over 400,000 years. As carbon dioxide concentration increased, so did temperature. As carbon dioxide concentration decreased, so did temperature. These data were collected in 1999. Since then, carbon dioxide concentrations have increased to 409.8 ppm (2019 average). Image and caption (modified) by NOAA/Autopilot (CC-BY-SA).

However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm (Figure 24.1.8 – 9). Atmospheric CO_2 concentrations have increased by 45% since pre-industrial times, from approximately 280 parts per million (ppm) in the 18th century to 409.8 ppm in 2019 (Figures 24.1.8 – 9).

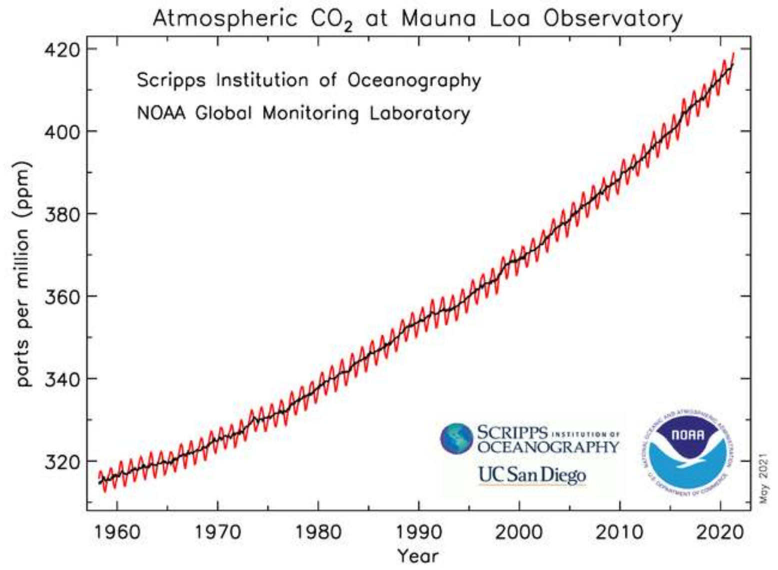


Figure 24.1.8: Monthly mean carbon dioxide concentration in parts per million (ppm) measured at Mauna Loa Observatory, Hawaii. The carbon dioxide data on Mauna Loa constitute the longest record of direct measurements of CO_2 in the atmosphere. The fluctuating red line represents the monthly mean values, centered on the middle of each month. Carbon dioxide concentrations

dip every summer due to increased photosynthesis. The smoother black line represents the same, after correction for the average seasonal cycle. Image and caption (modified) by NOAA (public domain).

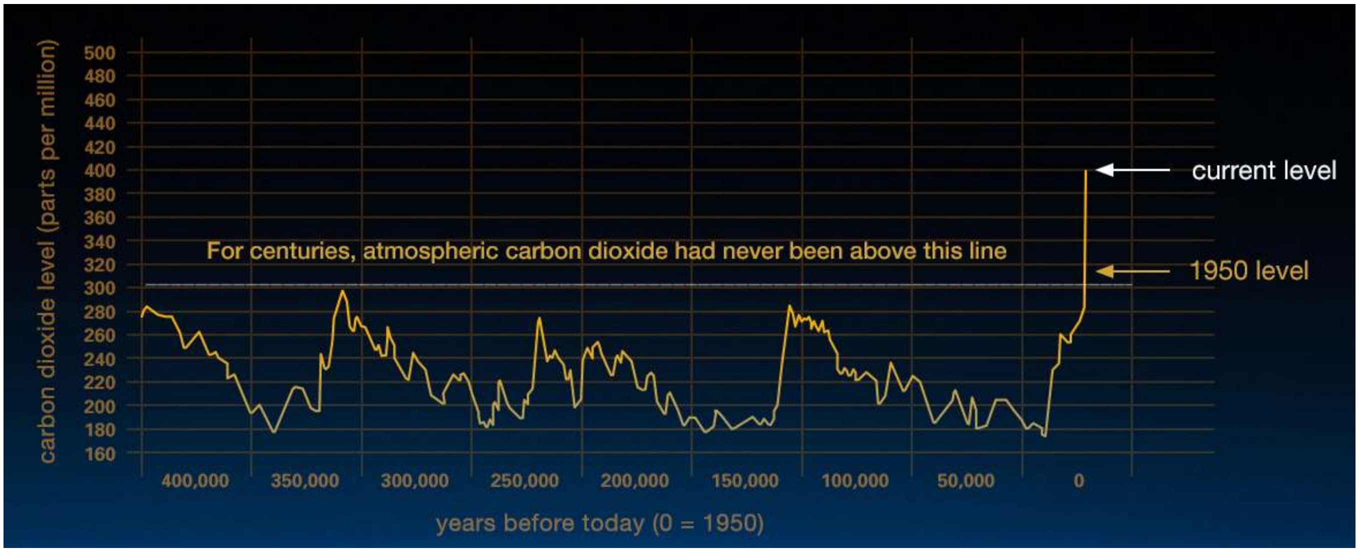
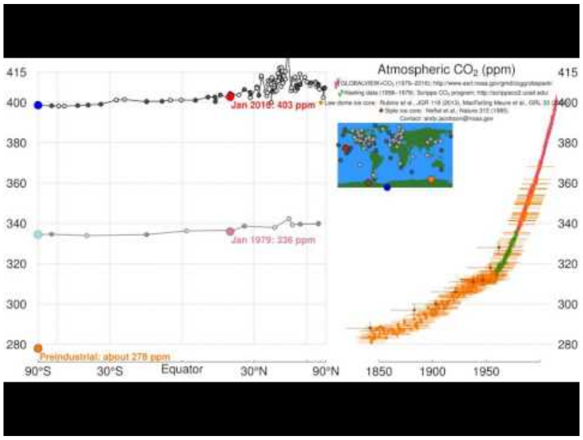


Figure 24.1.9: This graph, based on the comparison of atmospheric samples contained in ice cores and more recent direct measurements, provides evidence that atmospheric CO2 has increased since the Industrial Revolution. On the x-axis are the years before today (0 = 1950). It begins 400,000 years prior to 1950. On the y-axis is the carbon dioxide level in parts per million. Carbon dioxide levels have fluctuated over the years, but they never exceeded 300 parts per million until 1950. In 2018, carbon dioxide levels reached 409.8 ppm. This graph is a few years old and shows the current CO_2 level at 400 ppm; Credit: Vostok ice core data/J.R. Petit et al.; NOAA Mauna Loa CO2 record.

The current CO_2 level is higher than it has been in at least 800,000 years, based on evidence from ice cores that preserve ancient atmospheric gases. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude. Human activities currently release over 30 billion tons of CO_2 into the atmosphere every year. While some volcanic eruptions released large quantities of CO_2 in the distant past, the U.S. Geological Survey (USGS) reports that human activities now emit more than 135 times as much CO_2 as volcanoes each year. This human-caused build-up of CO_2 in the atmosphere is like a tub filling with water, where more water flows from the faucet than the drain can take away.

The following video shows how atmospheric CO_2 has varied recently and also over the last 800,000 years as determined by many CO_2 monitoring stations (shown on the insert map). It is also instructive to watch the CO_2 variation of the Keeling portion of the video by latitude. This shows that most of the human sources of CO_2 are in the Northern Hemisphere.



Methane

Although this concentration is far less than that of CO2, **methane** (CH_4) is 28 times as potent a greenhouse gas. Methane is produced when bacteria break down organic matter under anaerobic conditions and can be released due to natural or anthropogenic processes. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Anthropogenic causes now account for 60% of total methane release. Examples include agriculture, fossil fuel extraction and transport, mining, landfill use, and burning of forests. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Specifically, raising cattle releases methane due to fermentation in their rumens produces methane that is expelled from their GI tract. Methane is more abundant in Earth's atmosphere now than at any time in at least the past 650,000 years, and CH_4 concentrations increased sharply during most of the 20th century. They are now more than two and-a-half times pre-industrial levels (1.9 ppm), but the rate of increase has slowed considerably in recent decades.

Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.

Other Greenhouse Gases

Nitrous oxide (N_2O) is produced through natural and human activities, mainly through agricultural activities and natural biological processes. Fuel burning and some other processes also create N_2O. Concentrations of N_2O have risen approximately 18% since the start of the Industrial Revolution, with a relatively rapid increase towards the end of the 20th century. [3] In contrast, the atmospheric concentration of N_2O varied only slightly for a period of 11,500 years before the onset of the industrial period, as shown by ice core samples.

Ground-level ozone (O_3), which also has a short atmospheric lifetime, is a potent greenhouse gas. Chemical reactions create ozone from emissions of nitrogen oxides and volatile organic compounds from automobiles, power plants, and other industrial and commercial sources in the presence of sunlight. In addition to trapping heat, ozone is a pollutant that can cause respiratory health problems and damage crops and ecosystems.

Chlorofluorocarbons (CFCs), hydrochlorofluorocarbons (HCFCs), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), and sulfur hexafluoride (SF6), together called F-gases, are often used in coolants, foaming agents, fire extinguishers, solvents, pesticides, and aerosol propellants. Unlike water vapor and ozone, these F-gases have a long atmospheric lifetime, and some of these emissions will affect the climate for many decades or centuries.

Human Induced Changes in Albedo

When sunlight energy reaches Earth it can be reflected or absorbed. The amount that is reflected or absorbed depends on Earth's surface and atmosphere. Light-colored objects and surfaces, like snow and clouds, tend to reflect most sunlight, while darker objects and surfaces, like the ocean and forests, tend to absorb more sunlight. The term **albedo** refers to the amount of solar radiation reflected from an object or surface, often expressed as a percentage. Earth as a whole has an albedo of about 30%, meaning that 70% of the sunlight that reaches the planet is absorbed. Sunlight that is absorbed warms Earth's land, water, and atmosphere.

Albedo is also affected by aerosols. **Aerosols** are small particles or liquid droplets in the atmosphere that can absorb or reflect sunlight. Unlike greenhouse gases (GHGs), the climate effects of aerosols vary depending on what they are made of and where they are emitted. Those aerosols that reflect sunlight, such as particles from volcanic eruptions or sulfur emissions from burning coal, have a cooling effect. Those that absorb sunlight, such as black carbon (a part of soot), have a warming effect. In addition, human activities have generally increased the number of aerosol particles in the atmosphere. Overall, human-generated aerosols have a net cooling effect offsetting about one-third of the total warming effect associated with human greenhouse gas emissions. Reductions in overall aerosol emissions can therefore lead to more warming. However, targeted reductions in black carbon emissions can reduce warming.

Human changes in land use and land cover have changed Earth's albedo. Processes such as deforestation, reforestation, desertification, and urbanization often contribute to changes in climate in the places they occur. These effects may be significant regionally, but are smaller when averaged over the entire globe.

Climate Feedbacks

When sea ice melts, as it has done in the Arctic Ocean at a disturbing rate over the past decade, the albedo of the area affected changes dramatically, from around 80% down to less than 10%. This is a positive feedback because much more solar energy is absorbed by the water than by the pre-existing ice, and the temperature increase is amplified. The same applies to ice and snow on land, but the difference in albedo is not as great.

When ice and snow on land melt, sea level rises. Sea level is also rising because the oceans are warming and that increases their volume. A higher sea level means a larger proportion of the planet is covered with water, and since water has a lower albedo than land, more heat is absorbed and the temperature goes up a little more. Since the last glaciation, sea-level rise has been about 125 m; a huge area that used to be land is now flooded by heat-absorbent seawater. During the current period of anthropogenic climate change, sea level has risen only about 20 cm, and although that doesn't make a big change to albedo, sea-level rise is accelerating.

Figure 24.1.10: A degrading permafrost site on the north coast of Alaska.

Most of northern Canada has a layer of permafrost that ranges from a few centimeters to hundreds of meters in thickness; the same applies in Alaska, Russia, and Scandinavia. Permafrost is a mixture of soil and ice (Figure 24.1.10), and it also contains a significant amount of trapped organic carbon that is released as CO_2 and CH_4 when the permafrost breaks down. Because the amount of carbon stored in permafrost is in the same order of magnitude as the amount released by burning fossil fuels, this is a feedback mechanism that has the potential to equal or surpass the forcing that has unleashed it.

In some polar regions, including northern Canada, permafrost includes methane hydrate, a highly concentrated form of CH_4 trapped in solid form. Breakdown of permafrost releases this CH_4. Even larger reserves of methane hydrate exist on the sea floor, and while it would take significant warming of ocean water down to a depth of hundreds of meters, this too is likely to happen in the future if we don't limit our impact on the climate. There is strong isotopic evidence that the Paleocene-Eocene thermal maximum was caused, at least in part, by a massive release of sea-floor methane hydrate.

There is about 45 times as much carbon in the ocean (as dissolved bicarbonate ions, HCO_3^-) as there is in the atmosphere (as CO_2), and there is a steady exchange of carbon between the two reservoirs. But the solubility of CO_2 in water decreases as the temperature goes up. In other words, the warmer it gets, the more of that oceanic bicarbonate gets transferred to the atmosphere as CO_2. That makes CO_2 solubility another positive feedback mechanism.

Vegetation growth responds positively to both increased temperatures and elevated CO_2 levels, and so in general, it represents a negative feedback to climate change because the more the vegetation grows, the more CO_2 is taken from the atmosphere. But it's not quite that simple because when trees grow bigger and more vigorously, forests become darker (they have lower albedo) so they absorb more heat. Furthermore, climate warming isn't necessarily good for vegetation growth; some areas have become too hot, too dry, or even too wet to support the plant community that was growing there, and it might take centuries for something to replace it successfully.

All of these positive (and negative) feedbacks work both ways. For example, during climate cooling, growth of glaciers leads to higher albedos, and formation of permafrost results in storage of carbon that would otherwise have returned quickly to the atmosphere.

References

3. Lindsey, R. (2009). Climate and Earth's energy budget: Feature articles.. Available at: http://earthobservatory.nasa.gov. (Accessed: 14th September 2016)

6. Pachauri, R.K. *et al.* (2014). Climate change 2014: Synthesis report. contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. *IPCC.*

7. Oreskes, N. (2004). The scientific consensus on climate change. *Science*, *306*, pp. 1686–1686.

11. Earle, S. (2015). Physical geology OER textbook. *BC Campus OpenEd.*

12. Callendar, G.S. (1938). The artificial production of carbon dioxide and its influence on temperature. *Q.J.R. Meteorol. Soc.*, *64*, pp. 223–240.

13. Hansen, J., Sato, M., Kharecha, P., et al. (2011). Earth's energy imbalance and implications. *Atmospheric*.

14. Foster, G., & Rahmstorf, S. (2011). Global temperature evolution 1979–2010. *Environ. Res. Lett.*, *6*, 044022.

15. Kosaka, Y., & Xie, S.-P. (2013). Recent global-warming hiatus tied to equatorial Pacific surface cooling. *Nature*, *501*, pp. 403–407.

16. Easterling, D.R., & Wehner, M.F. (2009). Is the climate warming or cooling? *Geophys. Res. Lett.*, *36*.

17. Zemp, M. et al. (2015). Historically unprecedented global glacier decline in the early 21st century. *J. Glaciol.*, *61*, pp. 745–762.

18. Karl, T.R. & Knight, R.W. (1998). Secular trends of precipitation amount, frequency, and intensity in the United States. *Bull. Am. Meteorol. Soc.*, *79*, pp. 231–241.

19. Santer, B.D., et al. (2007). Identification of human-induced changes in atmospheric moisture content. *Proc. Natl. Acad. Sci. U.S.A.*, *104*, pp. 15248–15253.

Further "Reading"

For more information, watch this six-minute video on climate change by two professors at a North Carolina State University.

Contributors and Attributions

Modified by Kyle Whittinghill (University of Vermont) from the following sources:

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).
- Kyle Whittinghill (University of Pittsburgh)
- ”Physical Geology” by Steven Earle used under a CC-BY 4.0 international license. Download this book for free at http://open.bccampus.ca
- Contributed by Melissa Ha and Rachel Schleiger Faculty (Biological Sciences) at Yuba College & Butte College
- Contributed by Paul Webb Professor (Biology) at Rodger Williams University
- Contributed by Chris Johnson, Matthew D. Affolter, Paul Inkenbrandt, & Cam Mosher Faculty (Geology) at Salt Lake Community College
- Sourced from OpenGeology from *An Introduction to Geology* Chapter Chapter 15: Global Climate Change
- 12.4 Climate Change from *Essentials of Environmental Science* by CK-12 and Kamala Doršner (licensed under CC BY 4.0.)
- Climate and the Effects of Global Climate Change from *General Biology* by OpenStax (licensed under CC-BY)
- Climate Change from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Carbon Cycle from *Biology* by John W. Kimball (licensed under CC-BY)

24.2: Implications of Climate Change

Past and Present-day GHG Emissions Will Affect Climate Far into the Future

Many greenhouse gases stay in the atmosphere for long periods of time. As a result, even if emissions stopped increasing, atmospheric greenhouse gas concentrations would continue to remain elevated for hundreds of years. Moreover, if we stabilized concentrations and the composition of today's atmosphere remained steady (which would require a dramatic reduction in current greenhouse gas emissions), surface air temperatures would continue to warm. This is because the oceans, which store heat, take many decades to fully respond to higher greenhouse gas concentrations. The ocean's response to higher greenhouse gas concentrations and higher temperatures will continue to impact climate over the next several decades to hundreds of years.

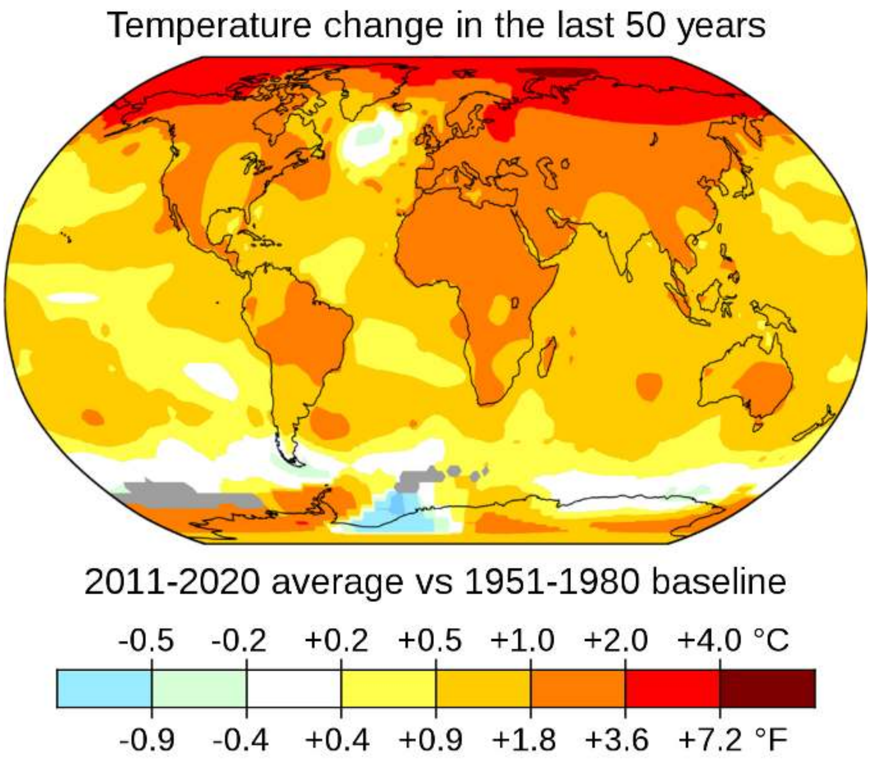


Figure 24.2.1: Temperature increases have been most pronounced in northern latitudes and over land masses. The colors represent the temperature difference between the 2011-2020 average and the 1951-1980 baseline, with warmer colors (yellow, orange, red) representing increases, and cool colors (green, blue) representing decreases. The image uses longer term averages of at least a decade to smooth out climate variability due to factors such as El Niño. Grey areas in the image have insufficient data for rendering. Image and caption (modified) from NASA's Scientific Visualization Studio/Eric Fisk (public domain).

Future Temperature Changes

Climate models project the following key temperature-related changes:

- Average global temperatures are expected to increase by 2°F to 11.5°F by 2100, depending on the level of future greenhouse gas emissions, and the outcomes from various climate models.
- By 2100, global average temperature is expected to warm at least twice as much as it has during the last 100 years.
- Ground-level air temperatures are expected to continue to warm more rapidly over land than oceans.
- Some parts of the world are projected to see larger temperature increases than the global average.

These changes will impact our food supply, water resources, infrastructure, ecosystems, and even our own health. The magnitude and rate of future climate change will primarily depend on the following factors:

- The rate at which levels of greenhouse gas concentrations in our atmosphere continue to increase,

- How strongly features of the climate (e.g., temperature, precipitation, and sea level) respond to the expected increase in greenhouse gas concentrations,
- Natural influences on climate (e.g., from volcanic activity and changes in the sun’s intensity) and natural processes within the climate system (e.g., changes in ocean circulation patterns).

Future Precipitation and Storm Events

Patterns of precipitation and storm events, including both rain and snowfall are likely to change. However, some of these changes are less certain than the changes associated with temperature. Because warm air is able to hold more water than cold air, the general global trend over the past century has been one of increasing precipitation (Figure 24.2.2).

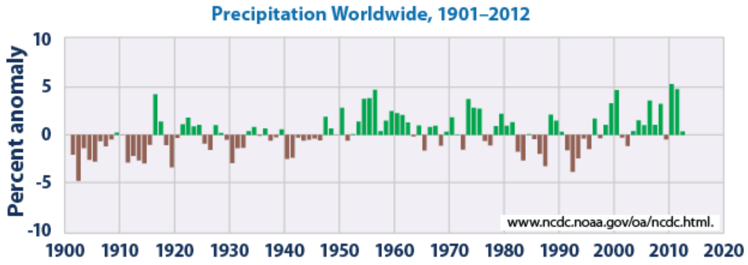


Figure 24.2.2: *Global precipitation anomalies compared with the average over the period from 1901 to 2012.* [“Precipitation Worldwide, 1901-2013” by NASA. Public domain.]

Projections show that future precipitation and storm changes will vary by season and region. Some regions may have less precipitation, some may have more precipitation, and some may have little or no change. The amount of rain falling in heavy precipitation events is likely to increase in most regions, while storm tracks are projected to shift towards the poles. Climate models project the following precipitation and storm changes:

- Global average annual precipitation through the end of the century is expected to increase, although changes in the amount and intensity of precipitation will vary by region.
- The intensity of precipitation events will likely increase on average. This will be particularly pronounced in tropical and high-latitude regions, which are also expected to experience overall increases in precipitation.
- The strength of the winds associated with tropical storms is likely to increase. The amount of precipitation falling in tropical storms is also likely to increase.
- Annual average precipitation is projected to increase in some areas and decrease in others.

Occurrence and intensity of extreme weather events such as hurricanes, precipitation, and heatwaves are increasing [3; 6]. Since the 1980s, hurricanes, which are generated from warm ocean water, have increased in frequency, intensity, and duration and connections to a warmer climate are likely. Since 1910, average precipitation has increased by 10% in the contiguous United States, and much of this increase is associated with heavy precipitation events like storms [18]. However, the distribution is not even and more precipitation is projected for the northern United States while less precipitation is projected for the already dry southwest [3]. Further, heatwaves have increased and rising temperatures are already affecting crop yields in northern latitudes [6]. Increased heat allows for greater moisture capacity in the atmosphere, increasing the potential for more extreme events [19].

One of the other risks for coastal populations, besides sea-level rise, is that climate warming is also associated with an increase in the intensity of tropical storms (e.g., hurricanes or typhoons), which almost always bring serious flooding from intense rain and storm surges. Some recent examples are New Orleans in 2005 with Hurricane Katrina, and New Jersey and New York in 2012 with Hurricane Sandy (Figure 24.2.3).

Figure 24.2.3: Damage to the Casino Pier, Seaside Heights, New Jersey, from Hurricane Sandy, November 2012 ["Hurricane Sandy New Jersey Pier" © Master Sgt. Mark C. Olsen/U.S. Air Force/New Jersey National Guard. CC BY.]

Tropical storms get their energy from the evaporation of warm seawater in tropical regions. In the Atlantic Ocean, this takes place between 8° and 20° N in the summer. Figure 24.2.4 shows the variations in the sea-surface temperature (SST) of the tropical Atlantic Ocean (in blue) versus the amount of power represented by Atlantic hurricanes between 1950 and 2008 (in red). Not only has the overall intensity of Atlantic hurricanes increased with the warming since 1975, but the correlation between hurricanes and sea-surface temperatures is very strong over that time period.

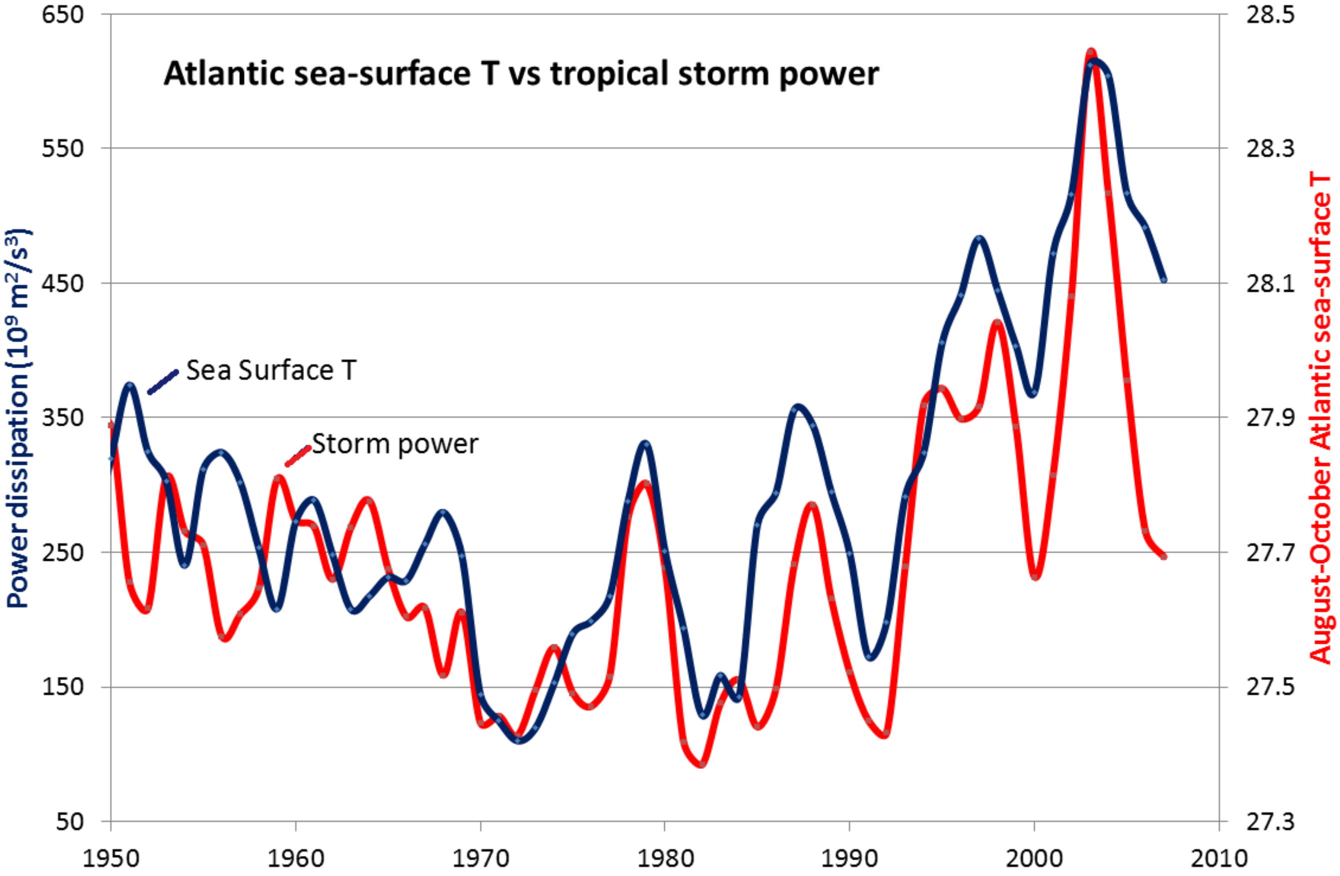


Figure 24.2.4: Relationship between Atlantic tropical storm cumulative annual intensity and Atlantic sea-surface temperatures ["Atlantic sea-surface T vs. tropical storm power" © Steven Earle. CC BY. Based on data from Papers, Data, and Graphics Pertaining to Tropical Cyclone Trends and Variability.]

For several weeks in July and August of 2010, a massive heat wave affected western Russia, especially the area southeast of Moscow, and scientists have stated that climate change was a contributing factor. Temperatures soared to over 40°C, as much as 12°C above normal over a wide area, and wildfires raged in many parts of the country. Over 55,000 deaths are attributed to the heat and to respiratory problems associated with the fires. A summary of the impacts of climate change on natural disasters is given in Figure 24.2.5. The major types of disasters related to climate are floods and storms, but the health implications of extreme temperatures are also becoming a great concern. In the decade 1971 to 1980, extreme temperatures were the fifth most common natural disasters; by 2001 to 2010, they were the third most common.

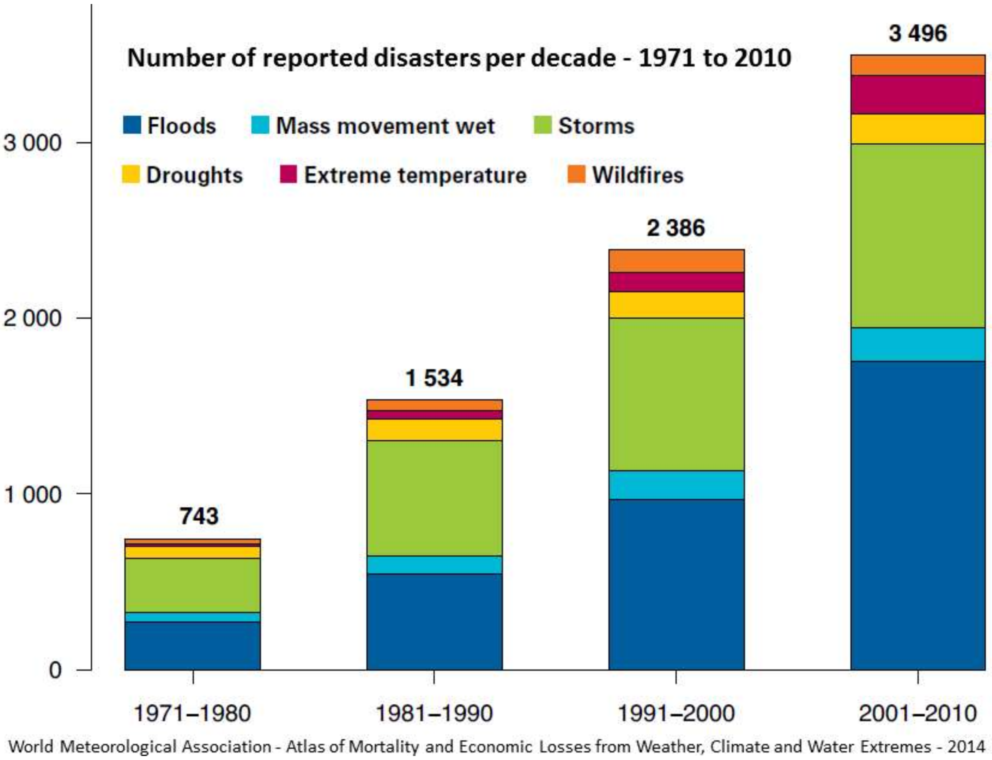


Figure 24.2.5: Numbers of various types of disasters between 1971 and 2010 (WMO Atlas of Mortality and Economic Losses from Weather, Climate and Water Extremes, 2014. CC BY-NC-ND).

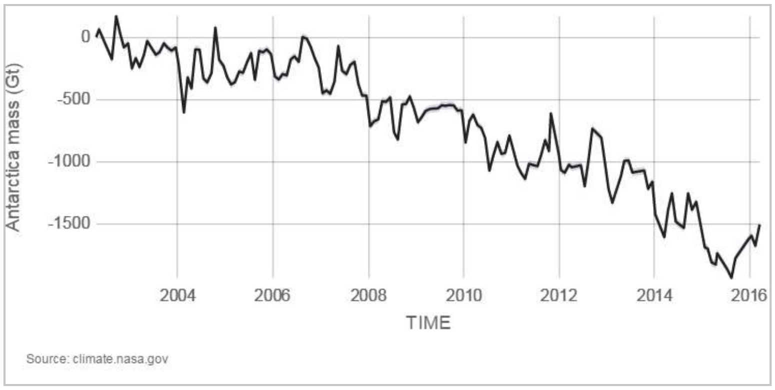
We've all experienced the effects of climate change over the past decade. However, it's not straightforward for climatologists to make the connection between a warming climate and specific weather events, and most are justifiably reluctant to ascribe any specific event to climate change. In this respect, the best measures of climate change are those that we can detect over several decades, such as the temperature changes shown in Figure 24.2.1, or the sea level rise shown in Figure 24.2.8.

Future Ice, Snowpack, and Permafrost

Arctic sea ice is already declining. The area of snow cover in the Northern Hemisphere has decreased since 1970. Permafrost temperature has increased over the last century, making it more susceptible to thawing. Over the next century, it is expected that sea ice will continue to decline, glaciers will continue to shrink, snow cover will continue to decrease, and permafrost will continue to thaw.

For every 2°F of warming, models project about a 15% decrease in the extent of annually averaged sea ice and a 25% decrease in September Arctic sea ice. The coastal sections of the Greenland and Antarctic ice sheets are expected to continue to melt or slide into the ocean. If the rate of this ice melting increases in the 21st century, the ice sheets could add significantly to global sea level rise. Glaciers are expected to continue to decrease in size. The rate of melting is expected to continue to increase, which will contribute to sea level rise.

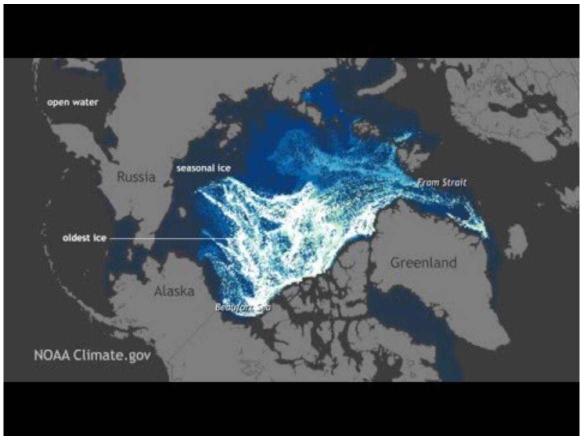
Glaciers are ice on top of the land. Alpine glaciers, ice sheets, and sea ice are all melting. Almost all major alpine glaciers are shrinking, deflating, and retreating and the rate of ice mass loss is unprecedented (never observed before) since the 1940's when quality records for most began.Before anthropogenic warming, glacial activity was variable with some retreating and some advancing [17]. The extent of spring snow cover has decreased. Satellites have recorded that Antarctica is melting at 118 gigatons per year and Greenland is melting at 281 gigatons per year (1 gigaton is over 2 trillion pounds) (Figure 24.2.6).



Source: climate.nasa.gov

Figure 24.2.6 : Decline of Antarctic ice mass from 2002 to 2016.

In addition, the extent of sea ice is shrinking. Sea ice is ice floating in the ocean (not on land like a glacier). Most sea ice is at the North Pole which is only occupied by the Arctic Ocean and sea ice [3; 6]. Below, the NOAA animation shows how perennial sea ice has declined from 1987 to 2015. The oldest ice is white and the youngest (seasonal) ice is dark blue. The amount of old ice has declined from 20% in 1985 to 3% in 2015.



This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

A number of global events have occurred that may be attributed to climate change during our lifetimes. Explore melting glaciers at NASA's interactive Global Ice Viewer. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure 24.2.7) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.

Figure 24.2.7: The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems (credit: modification of work by USGS).

Future Sea Level Change

Warming temperatures contribute to sea level rise by expanding ocean water, melting mountain glaciers and ice caps, and causing portions of the Greenland and Antarctic ice sheets to melt or flow into the ocean. Since 1870, global sea level has risen by about 8 inches. Estimates of future sea level rise vary for different regions, but global sea level for the next century is expected to rise at a greater rate than during the past 50 years. The contribution of thermal expansion, ice caps, and small glaciers to sea level rise is relatively well-studied, but the impacts of climate change on ice sheets are less understood and represent an active area of research. Thus, it is more difficult to predict how much changes in ice sheets will contribute to sea level rise. Greenland and Antarctic ice sheets could contribute an additional 1 foot of sea level rise, depending on how the ice sheets respond.

Sea-level is rising 3.4 millimeters (0.13 inches) per year and has risen 0.19 meters (7.4 inches) from 1901 to 2010 (Figure 24.2.8). This is thought largely to be from both the melting of glaciers and thermal expansion. Thermal expansion means that as objects such as solids, liquids, and gases heat up, they expand in volume. Since 1970, the melting of glaciers and thermal expansion account for 75% of the sea-level rise [6].

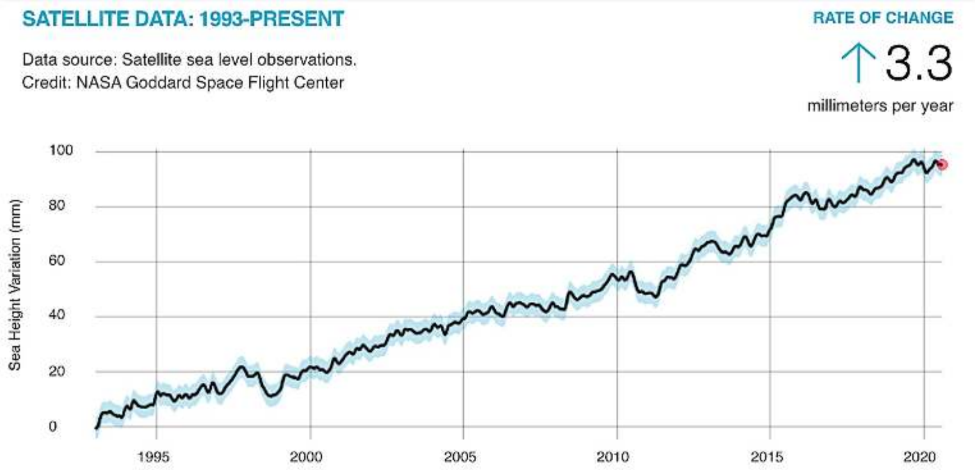


Figure 24.2.8: Sea height variation (mm) over time. Sea height has increased about 3.3 millimeters per year on average since 1993. Data is from satellite sea level observations by the NASA Goddard Space Flight Center. Image by NASA (public domain).

Projections for sea level rise to the end of this century vary widely. This is in large part because we do not know which of the above climate change scenarios (Figure 24.2.9) we will most closely follow, but many are in the range from 0.5 m to 2.0 m. One of the problems in predicting sea level rise is that we do not have a strong understanding of how large ice sheets, such as Greenland and Antarctica, will respond to future warming. Another issue is that the oceans don't respond immediately to warming. For example, with the current amount of warming, we are already committed to a future sea level rise of between 1.3 m and 1.9 m, even if we could stop climate change today. This is because it takes decades to centuries for the existing warming of the atmosphere to be transmitted to depth within the oceans and to exert its full impact on large glaciers. Most of that committed rise would take place over the next century, but some would be delayed longer. And for every decade that the current rates of climate change continue, that number increases by another 0.3 m. In other words, if we don't make changes quickly, by the end of this century we'll be locked into 3 m of future sea level rise. In a 2008 report, the Organization for Economic Co-operation and Development (OECD) estimated that by 2070 approximately 150 million people living in coastal areas could be at risk of flooding due to the combined effects of sea level rise, increased storm intensity, and land subsidence. The assets at risk (buildings, roads, bridges, ports, etc.) are in the order of $35 trillion ($35,000,000,000,000). Countries with the greatest exposure of population to flooding are China, India, Bangladesh, Vietnam, U.S.A., Japan, and Thailand. Some of the major cities at risk include Shanghai, Guangzhou, Mumbai, Kolkata, Dhaka, Ho Chi Minh City, Tokyo, Miami, and New York.

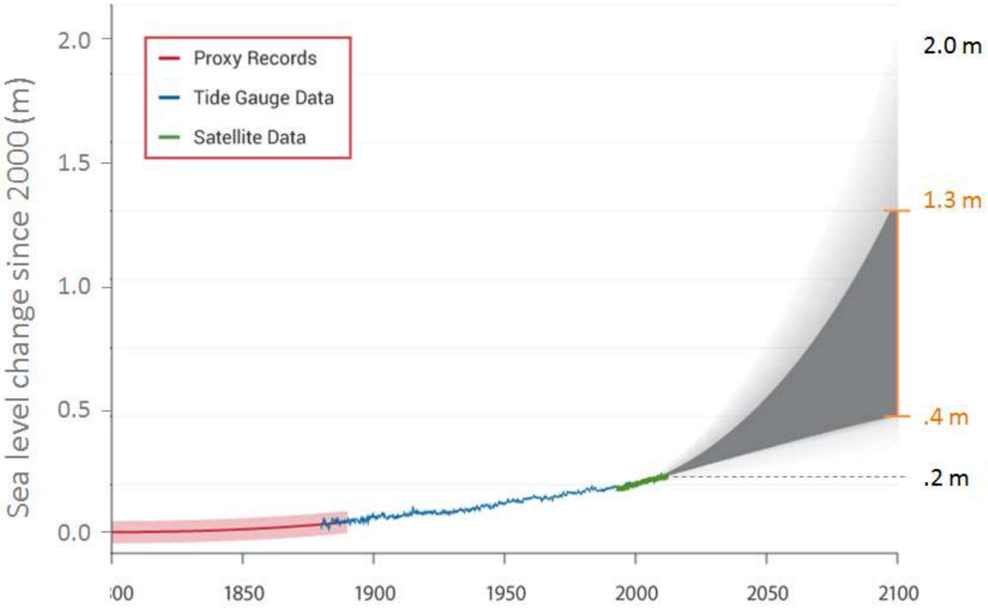


Figure 24.2.9: Projected sea-level increases to 2100, showing likely range (grey) and possible maximum [Adapted by Steven Earle from “[Past and Projected Changes in Global Sea Level Rise](#)” based on data from Parris et al. 2012 with input from NASA Jet Propulsion Laboratory.]

Regional and local factors will influence future relative sea level rise for specific coastlines around the world (Figure 24.2.10). For example, relative sea level rise depends on land elevation changes that occur as a result of subsidence (sinking) or uplift (rising). Relative sea level rise also depends on local changes in currents, winds, salinity, and water temperatures, as well as proximity to thinning ice sheets. Assuming that these historical geological forces continue, a 2-foot rise in global sea level by 2100 would result in the following relative sea level rise:

- 2.3 feet at New York City
- 2.9 feet at Hampton Roads, Virginia
- 3.5 feet at Galveston, Texas
- 1 foot at Neah Bay in Washington state

Figure 24.2.10: The United States government paid for the residents of Isle De Jean Charles, an island south of Louisiana (that is also part of Louisiana), to relocate when it became inhabitable due to sea level rise. Image by Karen Apricot (CC-BY-SA).

Future Ocean Acidification

Since 1750, about 40% of the new anthropogenic carbon dioxide has remained in the atmosphere. The remaining 60% gets absorbed by the ocean and vegetation. Therefore, the ocean has absorbed about 30% of new anthropogenic carbon dioxide. When carbon dioxide gets absorbed in the ocean, it creates carbonic acid which makes the ocean more acidic. **Ocean acidification** is the process of ocean waters decreasing in pH. Oceans become more acidic as carbon dioxide (CO_2) emissions in the atmosphere dissolve in the ocean. This change is measured on the pH scale, with lower values being more acidic. The pH level of the oceans has decreased by approximately 0.1 pH units since pre-industrial times, which is equivalent to a 25% increase in acidity (see the EPA website for a more detailed explanation). The pH level of the oceans is projected to decrease even more by the end of the century as CO_2 concentrations are expected to increase for the foreseeable future. Ocean acidification adversely affects many marine species, including plankton, mollusks, shellfish, and corals. As ocean acidification increases, the availability of calcium carbonate will decline. Calcium carbonate is a key building block for the shells and skeletons of many marine organisms. Acidification combined with warmer temperature and lower oxygen levels is expected to have severe impacts on marine ecosystems and human-used fisheries, possibly affecting our ocean-derived food sources [6].

Corals require the right combination of temperature, light, and the presence of calcium carbonate (which they use to build their skeletons). As atmospheric carbon dioxide (CO_2) levels rise, some of the excess CO_2 dissolves into ocean water, reducing its calcium carbonate saturation. Calcium carbonate saturation has already been reduced considerably from its pre-industrial level, and model projections suggest much greater reductions in the future. If atmospheric CO_2 concentrations double, coral calcification rates are projected to decline by more than 30%. If CO_2 concentrations continue to rise at their current rate, corals could become rare on tropical and subtropical reefs by 2050. Under projections for the future, it is very unlikely that calcium carbonate saturation levels will be adequate to support coral reefs in any U.S. waters.

Plant Productivity

Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Mismatched Interactions

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the *geographic distribution* and *phenology* of plants and animals. **Phenology** is the study of the effects of climatic conditions on the timing of periodic life cycle events, such as flowering in plants or migration in birds.

Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present. Likewise, migratory birds rely on day length cues, which are not influenced by climate change. Their insect food sources, however, emerge earlier in the year in response to warmer temperatures. As a result, climate change decreases food availability for migratory bird species.

Spread of Disease

This rise in global temperatures will increase the range of disease-carrying insects and the viruses and pathogenic parasites they harbor. Thus, diseases will spread to new regions of the globe. This spread has already been documented with dengue fever, a disease the affects hundreds of millions per year, according to the World Health Organization. Colder temperatures typically limit the distribution of certain species, such as the mosquitoes that transmit malaria, because freezing temperatures destroy their eggs. West Nile virus and Lyme disease are two examples that already directly affect North Americans, while dengue fever could be an issue in the future (dengue became a “nationally notifiable condition” in the United States in 2010).

Not only will the range of some disease-causing insects expand, the increasing temperatures will also accelerate their lifecycles, which allows them to breed and multiply quicker, and perhaps evolve pesticide resistance faster. In addition to dengue fever, other diseases are expected to spread to new portions of the world as the global climate warms. These include malaria, yellow fever, West Nile virus, zika virus, and chikungunya.

Climate change does not only increase the spread of diseases in humans. Rising temperatures are associated with greater amphibian mortality due to chytridiomycosis (see Invasive Species). Similarly, warmer temperatures have exacerbated bark beetle infestations of coniferous trees, such as pine an spruce.

Climate Change Affects Everyone

Our lives are connected to the climate**.** Human societies have adapted to the relatively stable climate we have enjoyed since the last ice age which ended several thousand years ago. A warming climate will bring changes that can affect our water supplies, agriculture, power and transportation systems, the natural environment, and even our own health and safety. Carbon dioxide can stay in the atmosphere for nearly a century, on average, so Earth will continue to warm in the coming decades. The warmer it gets, the greater the risk for more severe changes to the climate and Earth's system. Although it's difficult to predict the exact impacts of climate change, what's clear is that the climate we are accustomed to is no longer a reliable guide for what to expect in the future

References

3. Lindsey, R. (2009). Climate and Earth's energy budget: Feature articles. Available at: http://earthobservatory.nasa.gov. (Accessed: 14th September 2016)

6. Pachauri, R.K. et al. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC.

7. Oreskes, N. (2004). The scientific consensus on climate change. *Science*, *306*, pp. 1686–1686.

11. Earle, S. (2015). Physical geology OER textbook. *BC Campus OpenEd.*

12. Callendar, G.S. (1938. The artificial production of carbon dioxide and its influence on temperature. *Q.J.R. Meteorol. Soc.*, *64*, pp. 223–240.

13. Hansen, J., Sato, M., Kharecha, P., et al. (2011). Earth's energy imbalance and implications. *Atmospheric*.

14. Foster, G., & Rahmstorf, S. (2011). Global temperature evolution 1979–2010. *Environ. Res. Lett.*, *6*, 044022.

15. Kosaka, Y., & Xie, S.P. (2013). Recent global-warming hiatus tied to equatorial Pacific surface cooling. *Nature*, *501*, pp. 403–407.

16. Easterling, D.R. & Wehner, M.F. (2009). Is the climate warming or cooling? *Geophys. Res. Lett.*, *36*.

17. Zemp, M. et al. (2015). Historically unprecedented global glacier decline in the early 21st century. *J. Glaciol.*, *61*, pp. 745–762.

18. Karl, T.R. & Knight, R.W. (1998). Secular trends of precipitation amount, frequency, and intensity in the United States. *Bull. Am. Meteorol. Soc.*, *79*, pp. 231–241.

19. Santer, B.D., et al. (2007). Identification of human-induced changes in atmospheric moisture content. *Proc. Natl. Acad. Sci. U.S.A.*, *104*, pp. 15248–15253.

Suggested Supplementary Reading

Intergovernmental Panel on Climate Change. 2013. 5th Assessment: Summary for Policymakers.

NASA. 2018. Global Climate Change: Vital Signs of the Planet. This website by NASA provides a multi-media smorgasbord of engaging content. Learn about climate change using data collected by NASA satellites and more.

Contributors and Attributions

Modified by Kyle Whittinghill and Melissa Ha from the following sources:

- Contributed by Chris Johnson, Matthew D. Affolter, Paul Inkenbrandt, & Cam Mosher Faculty (Geology) at Salt Lake Community College
- Sourced from OpenGeology from *An Introduction to Geology* Chapter Chapter 15: Global Climate Change
- ”Physical Geology” by Steven Earle used under a CC-BY 4.0 international license. Download this book for free at http://open.bccampus.ca
- 12.4 Climate Change from *Essentials of Environmental Science* by CK-12 and Kamala Dorsner (Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0.)
- Climate and the Effects of Global Climate Change from *General Biology* by OpenStax (licensed under CC-BY)

- Climate Change from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Carbon Cycle from *Biology* by John W. Kimball (licensed under CC-BY)

- **10.4: Climate Change** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **44.5: Climate and the Effects of Global Climate Change** by OpenStax is licensed CC BY 4.0.

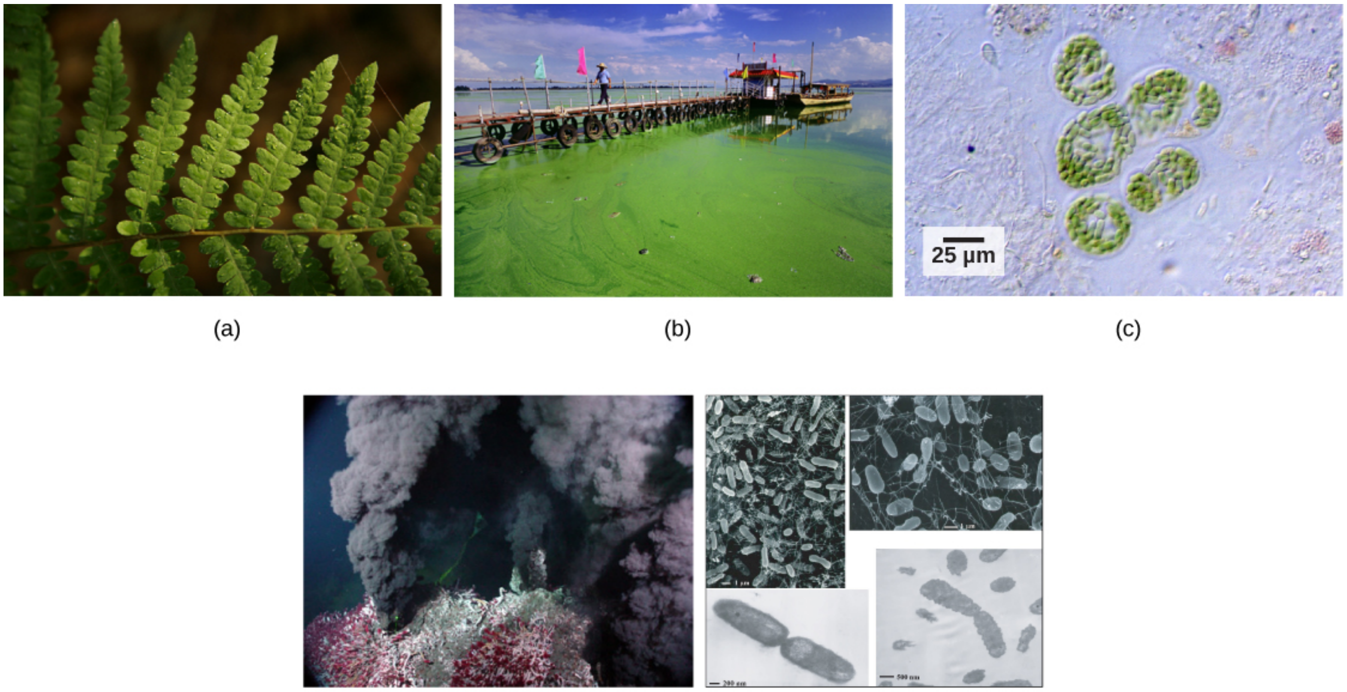
25: Light and Photosynthesis

Learning Objectives

- Define photosynthesis and photoautotrophs
- Describe properties of light important for photosynthesis
- Outline the steps in both the light-dependent and light-independent reactions in photosynthesis
- Explain photorespiration and the three major photosynthetic pathways used by plants

Photoautotrophs

Plants, algae, and certain bacteria (cyanobacteria and green and purple sulfur bacteria) are among the organisms capable of performing photosynthesis (Figure 25.1). Because they use light to manufacture their own food, they are called **photoautotrophs** (literally, “self-feeders using light”, Greek autos = self and trophe = nutrition). Other organisms, such as animals, fungi, and most other bacteria, are termed **heterotrophs** (“other feeders”), because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight’s energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as **chemoautotrophs**.



(a) (b) (c)

(d) (e)

Figure 25.1: Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopi that derive energy from the bacteria. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA).

Photosynthesis is the process on which photoautotrophs rely to capture the energy in solar radiation (the “photo-” part) as high-energy electrons and use it to produce the carbon-carbon bonds of carbohydrate molecules (the “-synthesis” part). The carbon used to make these molecules comes from the carbon dioxide (CO_2) in the atmosphere. Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via cellular respiration. Because photosynthesis removes carbon from the atmosphere and incorporates it into organic molecules which eventually become the plant’s leaves, stems, roots, and fruits, photosynthesis is sometimes said to **fix** carbon. **Fix**, in this sense, means to secure or sequester rather than to repair.

Properties of Light

Recall that light travels in waves and that light is made up of particles are called photons. The length of the wave is measured from one peak to the next and is called the **wavelength**, which differs for different colors of light (Figure 25.2. Within the visible wavelengths of light, the longest wavelengths are red light; outside the visible range of wavelengths, even longer wavelengths include infrared radiation, microwaves, and radio waves. Shorter visible wavelengths include blue and purple light, and beyond the visible range even shorter wavelengths include UV light, X-rays, and Gamma rays.

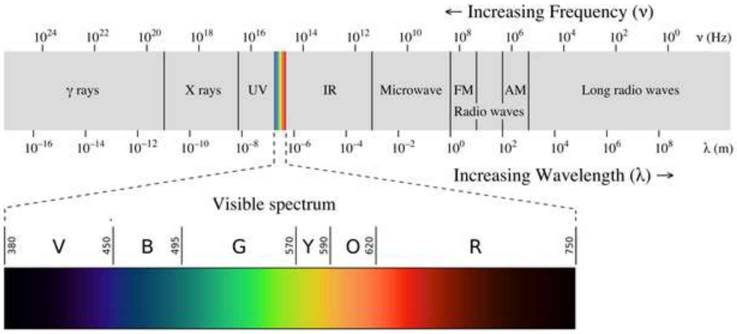


Figure 25.2: Visible spectrum. "EM spectrum revised" by Philip Ronan is licensed under CC BY-SA 3.0.

Steps of Photosynthesis

The photons in light provide the energy that drives photosynthesis. The chemical formula is the same for the two types of simple sugars produced by photosynthesis: glucose and fructose: $C_6H_{12}O_6$. The equation that summarizes photosynthesis is:

water + carbon dioxide -> oxygen, water, and simple sugars

$$\mathbf{12H_20 + 6CO_2 \text{ -> } 6O_2 + 6H_2O + C_6H_{12}O_6}$$

This balanced equation tells us that 12 molecules of water plus 6 molecules of carbon dioxide, in the presence of chlorophyll, accessory pigments, and light, produces 6 molecules of oxygen gas, returns 6 molecules of water back to the cell, and produces one molecule of a simple sugar like glucose or fructose.

Photosynthesis takes place in two sequential stages: the **light-dependent reactions** and the **light independent-reactions** (Calvin cycle). In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. Light-dependent reactions require water and produce oxygen and energy in the form of ATP and NADPH. In the light-independent reactions, the chemical energy harvested during the light-dependent reactions drive the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, several enzymes of the light-independent reactions are activated by light. ATP and NAPDH move energy from light-dependent reactions to light-independent reactions. In all autotrophic eukaryotes, photosynthesis takes place inside the **chloroplast**. Figure 25.3 illustrates the components inside the chloroplast (a membrane bound organelle in plant cells) where the light-dependent and light-independent reactions take place.

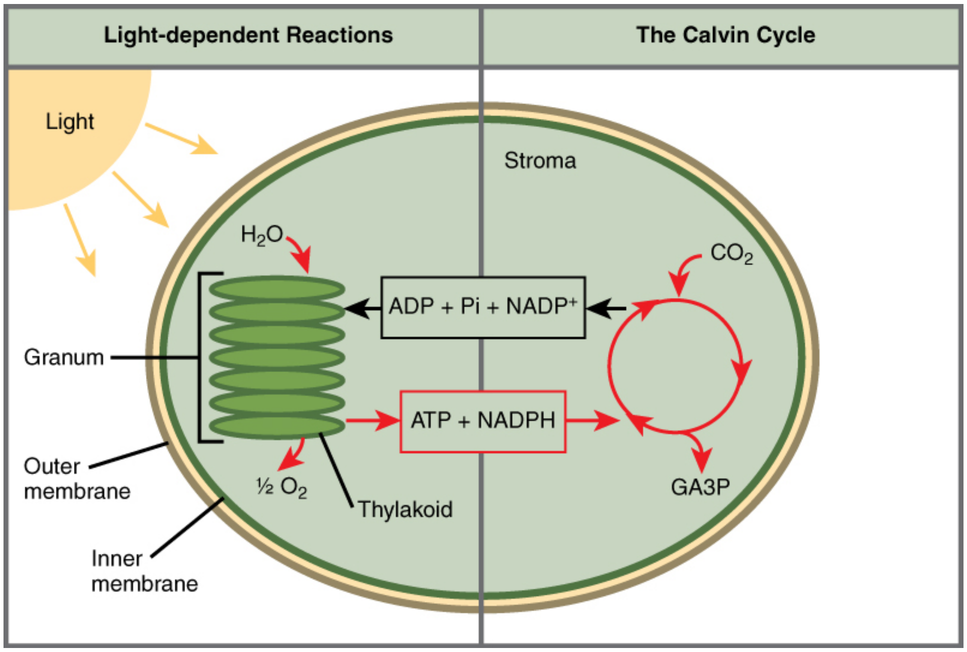


Figure 25.3: Photosynthesis takes place in two stages: light-dependent reactions and the light-independent reactions (Calvin cycle or Calvin-Benson cycle). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. In the process, water is used and oxygen is produced. Energy from ATP and NADPH are used to power the Calvin cycle, which produces GA3P from carbon dioxide. ATP is broken down to ADP and Pi, and NADPH is oxidized to $NADP^+$. The cycle is completed when the light reactions convert these molecules back into ATP and NADPH.

Light-Dependent Reactions

There are two types of **chlorophyll**, a green pigment that captures light for photosynthesis, Chlorophyll *a* and Chlorophyll *b*.

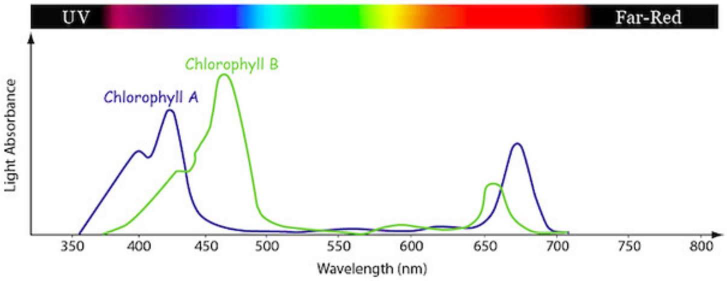


Figure 25.4: Chlorophyll A & B Absorption Spectrum. Image by byr7 is licensed under CC BY 2.0

The graph above shows % absorbance of different wavelengths by these two chlorophylls (Figure 25.4). The Y axis (the vertical one) shows the percentage of the light that is absorbed (rather than reflected). High levels of absorption mean that the chlorophyll molecule uses that wavelength of light for energy. Low absorption means that the molecule does not use that wavelength, and is thus reflected away. The X axis indicates the wavelength of light in nanometers (nm) and the bar at the top represents the color of the light at the wavelength shown. The blue line is a typical absorption curve for chlorophyll a, while the green line shows chlorophyll *b*. Both chlorophyll *a* and *b* absorb blue and red light wavelengths and reflect green. Chlorophyll *a* has a peak in the violet and red regions and chlorophyll *b* in the blue and orange regions. Notice how their absorbance is very low in the green region. That’s why we think of chlorophyll as green, and why we perceive leaves, which have chlorophyll as the predominant pigment, as green.

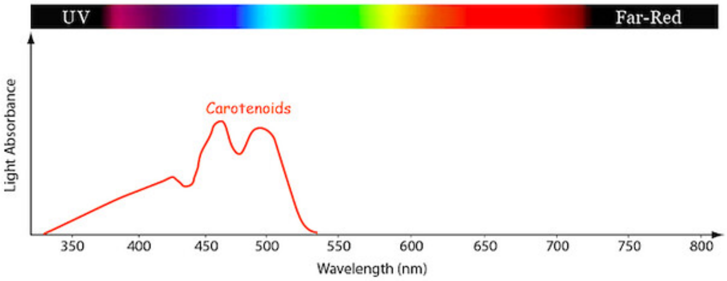


Figure 25.5: Carotenoids absorption spectrum. Image by byr7 is licensed under CC BY 2.0.

The graph above shows the absorbance of carotenoid pigments, which are an accessory pigment in photosynthesis and present throughout the growing season (Figure 25.5). **Carotenoids** absorb light in the green range, but reflect in yellow and red. We don't see these pigments during the growing season because they are much lower in concentration than the chlorophylls, so the green reflected light overwhelms the orange, and we see green. But when the chlorophyll fades in the fall the orange can be seen in beautiful fall leaf colors.

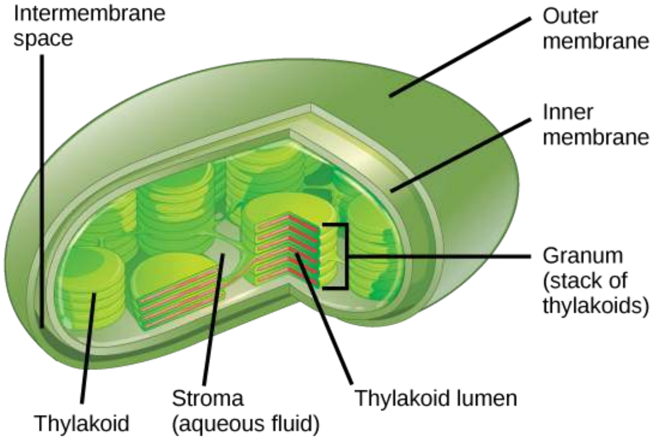


Figure 25.6: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. The space between the outer and inner membranes is called the intermembrane space. Stacks of thylakoids called grana form a third membrane layer. The thylakoids form stacks called grana. The liquid inside the inner membrane is called the stroma, and the space inside the thylakoid is called the thylakoid lumen.

The chloroplast has a double membrane envelope (composed of an outer membrane and an inner membrane) with an interior called the stroma (Figure 25.6). Within the stroma are coin-like thylakoids and stacks of thylakoids are called grana. The thylakoids are also surrounded by a membrane, called the thylakoid membrane. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. Embedded in the thylakoid membrane is chlorophyll, as well as the accessory pigments, and numerous proteins that make up the **electron transport chain** (Figure 25.7. In the light-dependent reactions protein complexes and pigment molecules work together to produce NADPH and ATP.

Figure 25.7: A diagram of the electron transport chain. Image by Jen Valenzuela (CC-BY).

When light hits a pigment molecule in the thylakoid membrane, the energy from the light photon promotes (pushes up) an electron in one of the pigment's atoms to a higher orbital as seen in the cartoon and energy is gained (Figure 25.7. The electron can't stay in that higher orbital indefinitely, and when it drops back to its home orbital it releases the energy it absorbed from light, denoted as **energy loss**. This released energy can be passed to another pigment molecule. This resonance energy travels down the antenna complex to the reaction center, where the captured energy pulls electrons out of water molecules, and water is split into oxygen gas, hydrogen ions, and electrons. This process of one pigment capturing the photon's energy and passing that energy onto adjacent pigment molecules is the crucial step in energy transformation that takes place in photosynthesis. This is the step that takes light energy and converts it into chemical energy — one of the only known biological processes that allows this type of energy transformation.

Recall that the overall equation for photosynthesis is:

water + carbon dioxide -> oxygen, water, and simple sugars

$$12H_20 + 6CO_2 \rightarrow 6O_2 + 6H_2O + C_6H_{12}O_6$$

This equation is made up of two parts called **half-reactions**. The half-reaction for the Light Reaction is as follows:

$$12H_2O \rightarrow 6O_2 + 24e^- + 24H^+$$

Light-Independent reactions

The Light-Independent Reactions is the second part of photosynthesis. It takes place in the stroma of the chloroplast. Unlike the Light-Dependent Reaction, it does not require light. In the Light-Independent Reactions, two compounds, NADPH and ATP, carry the energy from light that was originally transformed into hydrogen ions and electrons through the splitting of water. The NADPH and ATP, along with carbon dioxide from the atmosphere, enter a process called the **Calvin Cycle**, where the energy is used to fix carbon into a molecule abbreviated G3P as shown in Figure 25.8. This process requires the help of an important protein abbreviated RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) that catalyzes the step in the process where the carbon from atmospheric CO_2 is incorporated into an organic molecule. RuBisCO is the most abundant protein in leaves and, given the number of leaves in the world, likely the most abundant protein on the planet.

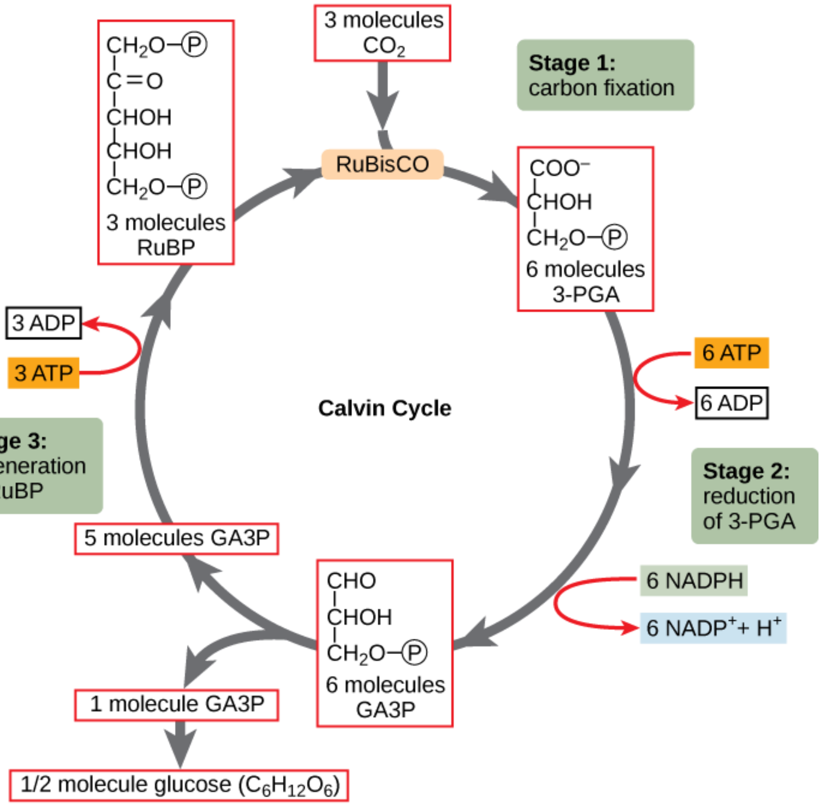


Figure 25.8: The light-independent reactions (Calvin cycle) has three stages. In stage 1, the enzyme RuBisCO adds carbon dioxide to RuBP, which immediately splits, producing two three-carbon 3-PGA molecules. In stage 2, two NADPH and two ATP are used to reduce 3-PGA to GA3P. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. One ATP is used in the process. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

RuBisCO catalyzes a reaction between CO_2 and RuBP (**ribulose-1,5-bisphosphate**). For each CO_2 molecule that reacts with one RuBP, two molecules of another compound, **3-phosphoglycerate** (3-PGA), form. 3-PGA has three carbon atoms and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from 3 CO_2 + 15 atoms from 3 RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called **carbon fixation**, because CO_2 is “fixed” from an inorganic form into organic molecules.

Six molecules of both ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called **glyceraldehyde 3-phosphate** (G3P). The G3P produced by the carbon fixation process is called a triose phosphate, meaning it is a 3-carbon sugar (triose) with phosphorus and oxygen atoms (phosphate) attached. Triose phosphate moves out of the chloroplast into the mesophyll cell's cytoplasm, where two of these three-carbon molecules are combined to produce the 6-carbon molecules glucose and fructose. The glucose and fructose molecules then combine to form sucrose, a 12-carbon organic molecule. Sucrose is important because it is the sugar that is transported by the phloem throughout the plant to provide energy and building blocks for other organic molecules like starch and cellulose.

Interestingly, at this point, only one of the G3P molecules leaves the light-independent reactions and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the cycle to fix enough net carbon to export one G3P. But each turn makes two G3P, thus three turns make six G3P. One of these six is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

Recall that the overall equation for photosynthesis is:

water + carbon dioxide -> oxygen, water, and simple sugars

$$\mathbf{12H_20 + 6CO_2 \text{ -> } 6O_2 + 6H_2O + C_6H_{12}O_6}$$

The half-reaction for the Light-Independent Reactions is:

$$\mathbf{24H^+ + 24e^- + 6CO_2 \text{ -> } C_6H_{12}O_6 + 6H_2O}$$

Photorespiration and other Photosynthetic Pathways

Different plant species have adaptations that allow them to do different variations of the light-independent reactions. These are called **photosynthetic pathways**. Plants are classified as C_3, C_4, or CAM depending on their use of these pathways, but note that some plants can switch photosynthetic pathways depending on environmental conditions. The process for light-independent reactions described in the previous section was the **C_3 pathway**: the compound formed during fixation (3-PGA) has three carbon atoms. Before discussing the details of the C_4 pathway, it is important to understand the circumstances that led to these adaptations.

As its name suggests, **ribulose-1,5-bisphosphate carboxylase/oxygenase** (**RuBisCO**) catalyzes two different reactions (Figure 25.9).. The first is adding CO_2 to ribulose-1,5- bisphosphate (RuBP) — the **carboxylase** activity. The second is adding O_2 to RuBP — the **oxygenase** activity. The oxygenase activity of RuBisCO forms the three-carbon molecule 3-phosphoglycerate (3-PGA), just as in the light-independent reactions, and the two-carbon molecule glycolate. The glycolate enters peroxisomes, where it uses O_2 to form intermediates that enter mitochondria where they are broken down to CO_2. So this process uses O_2 and ATP and liberates CO_2 as aerobic cellular respiration does, which is why it is called **photorespiration**. It undoes the work of photosynthesis, which is to build sugars, and wastes ATP which could be more useful to the plant in other ways.

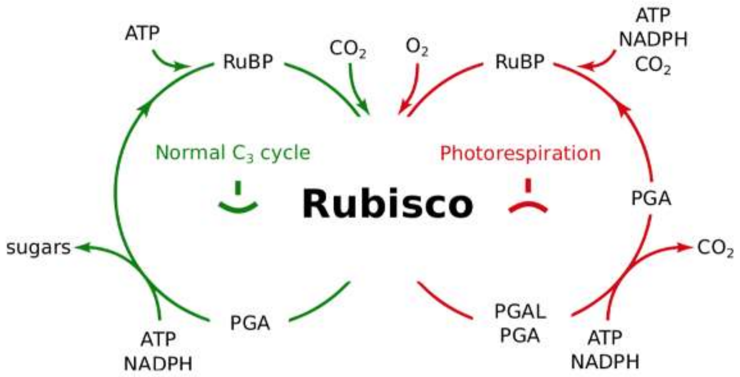


Figure 25.9: Rubisco is a two-faced enzyme.

Which action of RuBisCO predominates depends on the relative concentrations of O_2 and CO_2 with high CO_2, low O_2 favoring the carboxylase action and high O_2, low CO_2 favoring the oxygenase action. The light reactions of photosynthesis liberate oxygen, and more oxygen dissolves in the cytosol of the cell at higher temperatures. Therefore, high light intensities and high temperatures (above ~ 30°C) favor the second reaction and result in photorespiration.

If concentration of CO_2 is high enough, assimilation will overcome photorespiration. Consequently, to minimize the amount of photorespiration plants employ **Le Chatelier's principle** ("**Equilibrium Law**") and increase concentration of carbon dioxide near RuBisCO. One solution to increased concentrations of carbon dioxide in leaf tissues is for plants to open their stomata to release O_2 and obtain CO_2. However, if conditions are hot or dry, this will result in too much water loss (**transpiration**). For this reason, C_3 plants do best in cool, moist areas. Rice and potatoes are examples of C_3 plants.

Plants can also increase the concentration of carbon dioxide near RuBisCO by temporarily bonding carbon dioxide with **phosphoenolpyruvic acid** (**PEP,** C_3) using carboxylase enzyme; this results in C_4 molecules, like malate or malic acid, with four carbons in the skeleton. When plant needs it, that C_4 splits into pyruvate (C_3) plus carbon dioxide, and the release of that carbon dioxide will increase its concentration. On the final step, pyruvate plus ATP react to restore PEP; recovery of PEP does cost ATP. This entire process is called the "**C_4 pathway**" (Figure 25.10). These plants are called **C_4 plants**.

C_4 plants have structural changes in their leaf anatomy so that synthesizing the four-carbon sugar (the C_4 pathway) and resuming the light-independent reactions (C_3 pathways) are separated in different parts of the leaf with RuBisCO sequestered where the CO_2 level is high and the O_2 level low. After entering through stomata, CO_2 diffuses into a mesophyll cell (Figure 25.10) where it undergoes the C_4 pathway. Being close to the leaf surface, these cells are exposed to high levels of O_2, but they have no RuBisCO so cannot start photorespiration (nor the light-independent reactions). Then the four carbon molecules are transported in to **bundle sheath cells** (Figure 25.11) deep in the leaf, so atmospheric oxygen cannot diffuse easily to them. In the bundle sheath cells, the four-carbon compound is broken down into carbon dioxide, which enters the light-independent reactions (C_3 pathway) to form sugars, and pyruvic acid, which is transported back to a mesophyll cell where it is converted back into **PEP**.

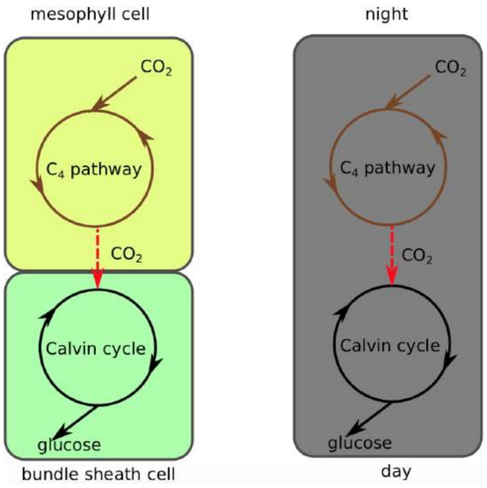


Figure 25.10: C_4 plants (left) conduct the C_4 pathway in the mesophyll cells and the Calvin cycle (C_3 pathway) in the bundle sheath cells, meaning they spatially separate the two . CAM plants (right) conduct the C_4 pathway at night and the Calvin cycle (C_3 pathway) during the day, resulting an a temporal separation of the two.

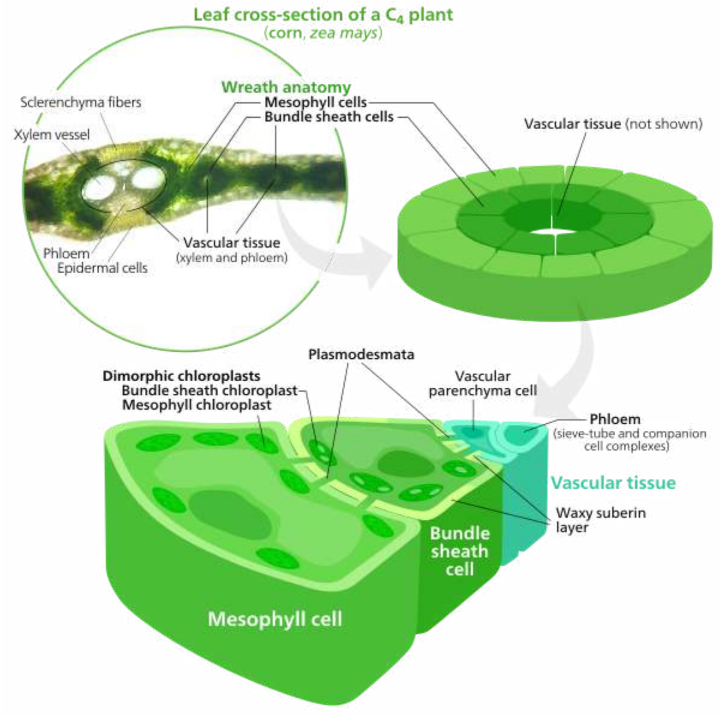


Figure 25.11: Cross section and diagram of a C_4 plant, showing mesophyll cells surrounding bundle sheath cells in concentric circles. The bundle sheath cells are larger and have more chloroplasts than in other plants. This arrangement is called Kranz anatomy (wreath anatomy). Vascular bundles contain xylem (vessel elements and tracheids) and phloem (sieve-tube and companion cell complexes). A vascular parenchyma is also shown in the vascular bundle. Waxy suberin borders the bundle sheath cells. The chloroplasts in the mesophyll cells are distinct from those in the bundle sheath cells, and the chloroplasts are thus called dimorphic. Sclerenchyma fibers are just above and below the vascular bundle, and epidermal cells surround the entire leaf. Image by Kelvinsong (CC-BY-SA).

These C_4 plants are well adapted to (and likely to be found in) habitats with high daytime temperatures and intense sunlight. Because they use the C_4 pathway to prevent photorespiration, they do not have to open their stomata to the same extent as C_3 plants and can thus conserve water. Some examples crabgrass, corn (maize), sugarcane, and sorghum. Although comprising only ~3% of the angiosperms by species, C_4 plants are responsible for ~25% of all the photosynthesis on land.

CAM stands for **c**rassulacean **a**cid **m**etabolism because it was first studied in members of the plant family Crassulaceae. **CAM plants** also do the C_4 pathway. However, instead of segregating the C_4 and C_3 pathways in different parts of the leaf, CAM plants separate them in **time** instead (Figure 25.10, Table 25.1). As a result, CAM plants do not need to open their stomata in the daytime to reduce photorespiration because they have already formed a four-carbon molecule at night that can be broken down to release carbon dioxide during the day.

Table 25.1: Activities of CAM plants at night and in the morning.

Night	Morning
• CAM plants take in CO_2 through their open stomata (they tend to have reduced numbers of them). • The CO_2 joins with PEP to form the four-carbon oxaloacetic acid. • This is converted to four-carbon **malic acid** that accumulates during the night in the central vacuole of the cells.	• The stomata close (thus conserving moisture as well as reducing the inward diffusion of oxygen). • The accumulated malic acid leaves the vacuole and is broken down to release CO_2. • The CO_2 is taken up into the light-independent reactions (C_3 pathway).

CAM plants thus thrive in conditions of high daytime temperatures, intense sunlight, and low soil moisture. Some examples of CAM plants include cacti (Figure 25.12), pineapples, all epiphytic bromeliads, sedums, and the "ice plant" that invade the California coast line.

Figure 25.12: Cultivated cacti in the Singapore Botanic Gardens. Image by Calvin Teo (CC-BY-SA).

Summary

This chapter defines photosynthesis, autotrophs, and heterotrophs and describes key properties of light for the reactions of photosysnthesis. The chapter outlines the important steps in the photosynthesis reactions and differentiates between the light-dependent reactions and the light-independent reactions in photosynthesis. Finally, the chapter explains the concepts of photorespiration and compares the three major photosynthetic pathways used by plants (C3, C4, and CAM).

Contributors and Attributions

Modified by Kyle Whittinghill (University of Pittsburgh) from the following sources

- 11.2: Light and Photosynthesis by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe. Original source: *The Science of Plants: Understanding Plants and How They Grow* by Tom Michaels; Matt Clark; Emily Hoover; Laura Irish; Alan Smith; and Emily Tepe
- Some of the explanations and pictures used in this section came from Introduction to photosynthesis and other pages at that McDaniel College site.
- 8.1 Overview of Photosynthesis, 8.2 The Light-Dependent Reactions of Photosynthesis, and 8.3 Using Light Energy to Make Organic Molecules from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 3.1 Discovery of Photosynthesis and 3.3 Enzymatic Stage from *Introduction to Botany* by Alexey Shipunov
- **13.3: Photosynthesis Overview and Equation**, **13.5: The Light-dependent Reactions**, **13.6: Light-independent Reactions**, and **13.7: Photorespiration and Photosynthetic Pathways** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.
- 16.2E Photorespiration and C4 Plants from *Biology* by John W. Kimball (licensed CC-BY)

- **4.1.3: Photosynthesis Overview and Equation** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.
- **11.2: Light and Photosynthesis** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.
- **4.1.6: Light-independent Reactions** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.
- **4.1.7: Photorespiration and Photosynthetic Pathways** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

26: TEAM - PA Ecology

Funding:

Ecology for All! was developed thanks to a grant from the Commonwealth of Pennsylvania's PA GOAL program. Funding for PA GOAL was provided by the Governor's Emergency Education Relief Fund (GEER) by the state Department of Education (PDE) through the Office of Commonwealth Libraries (OCL). Additional funding was also provided by the Gettysburg College Johnson Center for Creative Teaching and Learning and the Office of the Provost's Open Educational Research grant initiative at the University of Pittsburgh.

Acknowledgments:

We thank Drs. Rebecca Ekert, David Outomuro Priede, and Marion Holmes for providing feedback on the book. At the University of Pittsburgh Cathy Barr, Lynn Rago, Matthew Rager and Vivian Lin provided support with the administration of the grant. At Gettysburg College, Katie Weigle, Laura Runyan, and Dawn Helsing provided administrative support and Janelle Wertzberger and Mary Elmquist provided expertise on open educational resources. Drs. Walt Carson and Martin Turcotte generously supported the involvement of graduate students on the project.

We are also incredibly thankful to all of the authors who have contributed to the open access resources that we relied on for this project. In particular, we benefited greatly from previously developed open textbooks including Biology 2e on OpenStax (by M.A. Clark, M. Douglas, and J. Choi), Conservation Biology in Sub-Saharan Africa (J.W. Wilson and R.B. Primack), and Spreadsheets Exercises in Ecology and Evolution (T.M. Donovan and C. Weldon).

Last, but certainly not least, we are grateful to the staff at Libretexts for building this open educational resource plaftorm and for their patience with our many, many emails throughout the development of this textbook.

Nathan Brouwer		Nathan Brouwer is a lecturer in the Department of Biological Sciences at the University of Pittsburgh, where he teaches intro biology, computational biology, biostatistics, and scientific writing. Prior to graduate school he served as a Peace Corps Volunteer with the National Agricultural Research Institute of The Gambia, West Africa. A first-generation PhD, he obtained his doctorate from the University of Pittsburgh studying the impacts of invasive species and overabundant deer on the native plants of western Pennsylvania. He did his post-doctoral work at the National Aviary of Pittsburgh with Dr. Steve Latta, where he modeled long-term monitoring data of tropical bird communities.

Hannah Connuck		Hannah Connuck (she/her), is an undergraduate student at Franklin & Marshall College ('23), where she is head biology tutor and does research involving plant physiology and hydrology. She has a specific interest in tropical systems and climate in Costa Rican cloud forests.
Hayden Dubniczki		Hayden Dubniczki worked on Ecology for All! while an undergraduate student at Gettysburg College, where she earned a BS in Environmental Science. She is pursuing a Master of Environmental Management at Duke University's Nicholas School of the Environment. Her program concentration is Coastal Environmental Management.

Natasha Gownaris		Natasha (Tasha) Gownaris (she/her) is an Assistant Professor of Environmental Studies at Gettysburg College. At Gettysburg, Tasha teaches Ecology, Marine Ecology, Marine and Freshwater Fisheries, and Oceanography. Her research focuses on seabird foraging ecology and diet and the response of these species to climate change. She earned her BS in Biology and Environmental Studies at Gettysburg College in 2009 and a PhD in Marine Sciences from Stony Brook University in 2015. Before joining the Gettysburg faculty, she spent three years as a postdoctoral researcher at the University of Washington, where she studied Magellanic penguin demography and chick growth.

Aaron Howard		Aaron Howard (he/him) is a teaching professor at Franklin & Marshall College. He teaches throughout the biology core including introductory courses and Biostatistics. He also teaches upper-level electives on evolution and ecological data science. Aaron earned a BS in Biology and Education from Grove City College and a PhD in Biology from Georgetown University with a research focus on pollination biology. Specifically, I study how floral display – the size, arrangement, color, etc. of flowers, influences pollinator behavior and plant reproduction.

Leah Nath		Leah Nath is an Environmental Studies major at Gettysburg College (Class of '26), where she is interested in both the natural sciences and the humanities. She is working to edit and improve the accessibility of the Ecology for All! textbook and, as a student who has used the book herself, to add new learning tools for future students.

Castilleja Olmsted		Castilleja (Cassie) Olmsted (she/her) is a graduate student at the University of Pittsburgh. Cassie conducts field research in Pennsylvania on the impact of natural and anthropogenic disturbance on forest soil seed banks, and on the role of traditional agriculture in preserving genetic diversity in South America. She double-majored in Biology and Spanish at Earlham College.

Dan Wetzel		Dan Wetzel (he/his) is a lecturer and academic advisor in the Department of Biological Sciences at the University of Pittsburgh, where he teaches ecology, biostatistics, and scientific writing in addition to meeting with hundreds of biology students each year. Dan earned a PhD at the University of Kentucky and a MS degree from Georgia Southern University, both focused on understanding individual differences in levels of parental care in birds. While he still dabbles in biological research, he's currently studying the perception and usage of office hours in large introductory science courses.

Kyle Whittinghill		Kyle Whittinghill is a lecturer and academic advisor in the Department of Geology and Environmental Science at the University of Pittsburgh. Kyle teaches Environmental Science, Environmental Geochemistry, Statistics for Earth, Ecosystem Modeling and Environmental Science and Communication in Geosciences. Kyle also an instructor for the University of Pittsburgh's summer Wyoming Field Studies in Ecology course. Additionally, Kyle has edited and written an introductory environmental science book on LibreText, *Environmental Science*.

Andy Wilson		Andy Wilson (he/him/his) is an Associate Professor in the Environmental Studies Department at Gettysburg College, where he teaches Ecology, Wildlife Ecology, Conservation Biology, and Geographic Information Systems. A first-generation college student, Andy earned his PhD at Penn State, before which he worked as an ecologist for 10 years at the British Trust of Ornithology, a non-governmental organization. His research focuses on large-scale studies of birds, often involving large numbers of citizen scientists, and the use of new technologies in Ecology.

Taylor Zallek		Taylor Zallek is a graduate student at the University of Pittsburgh where he studies the implications of rapid evolutionary change during experimental invasions on plant communities. Taylor has previously taught as a lecturer and lab instructor for undergraduate ecology courses in the University of Pittsburgh's Department of Biological Sciences. He has a Bachelor's degree from St. John's University and a Master's from Michigan Tech.

Index

Glossary

Sample Word 1 | Sample Definition 1

R Practice: Building Interdisciplinary Skillsets to Understand Environmental Attitudes (Part I: Word Clouds)

Technical Learning Objective: In this module, students will learn how to prepare a .txt file for the purpose of text analysis in R and will learn how to make a word cloud with the resulting textual data.

Word Cloud Analysis of Silent Spring

Note: This is an Module is focused on the preparation of a .txt file for purposes of text analysis. Please refer to the accompanying module 'Sentiment Analysis' to see how the product of this is used.

When we think of coding, we often associate it heavily with STEM. Coding is used in a wide range of fields, however, including in the humanities. Often, we need to think critically about how to analyze large amounts of text without having to perform a close reading on them. Several methods in R allow us summarize these large amounts of textual data into meaningful patterns.

A corpus is the term used for a set of text files of interest in an analysis. For this particular module, we will be focus on the famous book 'Silent Spring' by Rachel Carson. This book sparked a massive environmental movement - including the creation of the Environmental Protection Agency in 1970 and the banning of DDT (an insecticide that wrecked havoc on natural environments, particularly on birds). The impact of this one book is a testament to the power of individuals in conservation. Here, we will conduct a "sentiment analysis" of Silent Spring. Sentiment analysis is used to determine the "tone" of a corpus, whether it is positive, negative, or neutral.

Rachel Carson by U.S. Fish and Wildlife Service is licensed under CC-BY.

This module will focus first on the often overlooked, but critical, stage of any analysis - data cleaning and preparation. We are trying to identify sentiment as much as possible in our corpus, so we have to take into account factors that influence the sentiment of text. While you continue with this module, please take into account the comments and how each line of code in our text preparation aids in our quest of complete objectivity and preciseness in the preparation of our corpus analysis.
The analysis below is based on guidance from an article written by Mhatre 2020.

Loading Packages and Data

Before we get to work, we have to download the appropriate packages for this type of analysis. Because these are specialized packages, we do need to install most of them before loading them. This stage might take a minute! The more common packages, which are already built in to Libretexts, have been commented out of the install.packages commands with a #. When you run R on your computer, you only need to install packages once (but you do need to load them each time).

```
# Install
install.packages("tm")  # this package is used for text mining or taking information
install.packages("SnowballC") # for text stemming which is to reduce the words to the
install.packages("wordcloud") # word-cloud generator
#install.packages("RColorBrewer") # provides color pallets for our study which will ma
#install.packages("ggplot2") # for plotting graphs

# Load
library("tm")
library("SnowballC")
library("wordcloud")
library("RColorBrewer")
library("ggplot2")
```

run restart restart & run all

Now that our packages are ready, let's load our data.

```
# When working with R on Libretexts, we upload our file to the website, then can call
text <- readLines(url("https://bio.libretexts.org/@api/deki/files/66199/SilentSpring.
# Load the data as a corpus which aids with the analysis
TextDoc <- Corpus(VectorSource(text))
```

run restart restart & run all

Cleaning and Preparing Our Data

After we load out .txt file we have to make sure that we eliminate anything that is not purely a text file. We will go line by line and denote what needs to be removed in order to create a proper corpus.

```
#Replacing "/", "@" and "|" with space, this is because the processing packages can't
toSpace <- content_transformer(function (x , pattern ) gsub(pattern, " ", x))
TextDoc <- tm_map(TextDoc, toSpace, "/")
TextDoc <- tm_map(TextDoc, toSpace, "@")
TextDoc <- tm_map(TextDoc, toSpace, "\\|")
# Convert the text to lowercase so that there is all text in the corpus is uniform an
TextDoc <- tm_map(TextDoc, content_transformer(tolower))
# Remove numbers because we still only need strings of text in the data
TextDoc <- tm_map(TextDoc, removeNumbers)
# Remove english common stopwords, stopwords are words that appear commonly in the en
TextDoc <- tm_map(TextDoc, removeWords, stopwords("english"))
# Remove punctuation
TextDoc <- tm_map(TextDoc, removePunctuation)
# Eliminate extra white spaces
TextDoc <- tm_map(TextDoc, stripWhitespace)
```

```
# Text stemming - which reduces words to their root form which can be used to amplify
TextDoc <- tm_map(TextDoc, stemDocument)
```

run restart restart & run all

Note: You will get a warning message, but that is because the corpus is being altered. If you get these messages you are going in the right direction.

All if these preparations can be used for many other purposes, for example, we can generate a word cloud or get statistical word association values.

Now that we have understood how the preparation of a text corpus works, analyze the corpus for after the publishing of Silent Spring. We challenge you to come up with 1-3 custom stopwords and rerun your analysis to see whether it changes anything. This specific work of pre-preocessing texts can be used for the creation of different word analysis and visualizations. For example, the most popular visualization is the word cloud. If we think about the preprocessing, without the elimination of common English stopwords, we would have words like 'the', 'and', and 'or' as the most frequent in the word cloud.

```
# Remove your own stop word
# specify your custom stopwords as a character vector, if you have/think a word appea
TextDoc <- tm_map(TextDoc, removeWords, c(""))
```

run restart restart & run all

Thanks to the preprocessing we have the following:

```
# Build a term-document matrix
TextDoc_dtm <- TermDocumentMatrix(TextDoc)
dtm_m <- as.matrix(TextDoc_dtm)
# Sort by descending value of frequency, this will aid in the visualization of the wo
dtm_v <- sort(rowSums(dtm_m),decreasing=TRUE)
dtm_d <- data.frame(word = names(dtm_v),freq=dtm_v)
# Display the top 5 most frequent words
head(dtm_d, 5)
```

run restart restart & run all

Above, we see the most common words, now we will visualize these in a word cloud.

```
#generate word cloud, here we are just setting the parameters for the creation of our
set.seed(1234)
wordcloud(words = dtm_d$word, freq = dtm_d$freq, min.freq = 5,
          max.words=100, random.order=FALSE, rot.per=0.40,
          colors=brewer.pal(8, "Dark2"))
```

run restart restart & run all

While you may be wondering what this has to do explicitly with ecology, we have to think about the interdisciplinary nature of Environmental Studies. Humanities intertwine with the ecological perspectives of people which would normally be analyzed through close reading and mass analysis of individual texts. With coding we can still achieve those results and make the analysis of various data forms widely available and accessible. Think about the possibilities of doing this for other disciplines and data forms.

Food for Thought

What themes and ideas can you conclude from the word cloud? How can this be applied to broader studies on ecology?

References:
Carson, R. (1962). Silent Spring. Crest Book.
Mhatre, S., Sampaio, J., Torres, D., & Abhishek, K. (2021, September 15). Text mining and sentiment analysis: Analysis with R. Simple Talk. Retrieved November 18, 2022, from https://www.red-gate.com/simple-talk...alysis-with-r/

Detailed Licensing

Overview

Title: Ecology for All!

Webpages: 166

Applicable Restrictions: Noncommercial

All licenses found:

- CC BY-NC-SA 4.0: 91% (151 pages)
- Undeclared: 7.8% (13 pages)
- CC BY-NC-SA 3.0: 1.2% (2 pages)

By Page

- Ecology for All! - *CC BY-NC-SA 4.0*
  - Front Matter - *CC BY-NC-SA 4.0*
    - TitlePage - *CC BY-NC-SA 4.0*
    - InfoPage - *CC BY-NC-SA 4.0*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Introduction to Ecology - *CC BY-NC-SA 4.0*
    - 1.1: Biology and The Scientific Method - *CC BY-NC-SA 4.0*
    - 1.2: What is Ecology? - *CC BY-NC-SA 4.0*
    - 1.3: History of Ecology - *CC BY-NC-SA 4.0*
    - 1.4: Subdisciplines of Ecology - *CC BY-NC-SA 4.0*
    - 1.5: An Overview of Essential Mathematics Used in Science - *CC BY-NC-SA 4.0*
      - 1.5.1: Essential mathematical and statistical terms and concepts - *CC BY-NC-SA 4.0*
      - 1.5.2: Summarizing data--Descriptive statistics - *CC BY-NC-SA 4.0*
      - 1.5.3: Testing hypotheses--Inferential statistics - *CC BY-NC-SA 4.0*
  - 2: The Physical Environment - *CC BY-NC-SA 4.0*
    - 2.1: Properties of Water - *CC BY-NC-SA 4.0*
    - 2.2: Water (Hydrologic) Cycle - *CC BY-NC-SA 4.0*
    - 2.3: Soils - *CC BY-NC-SA 4.0*
    - 2.4: The Atmosphere - *CC BY-NC-SA 4.0*
    - 2.5: Earth's Energy Balance - *CC BY-NC-SA 4.0*
    - 2.6: Atmospheric and Oceanic Circulation - *CC BY-NC-SA 4.0*
    - 2.7: What Makes the Climate Change - *CC BY-NC-SA 4.0*
    - 2.8: Past Climate Change - *CC BY-NC-SA 4.0*
  - 3: Introduction to Evolution - *CC BY-NC-SA 4.0*
    - 3.1: Evolution - *CC BY-NC-SA 4.0*
    - 3.2: Understanding Evolution - *CC BY-NC-SA 4.0*
    - 3.3: Scientist Spotlight - Ynes Enriquetta Julietta Mexia - *CC BY-NC-SA 4.0*
    - 3.4: Mechanisms of Evolution - *CC BY-NC-SA 4.0*
    - 3.5: Adaptive Evolution - *CC BY-NC-SA 4.0*
    - 3.6: Common Misconceptions about Evolution - *CC BY-NC-SA 4.0*
  - 4: Adaptations to the Physical Environment - *CC BY-NC-SA 4.0*
    - 4.1: What is adaptation? - *CC BY-NC-SA 4.0*
    - 4.2: Strategies for dealing with a changing environment - *CC BY-NC-SA 4.0*
    - 4.3: Adaptations to avoid harsh conditions - *CC BY-NC-SA 4.0*
    - 4.4: Physiological optima and critical limits - *CC BY-NC-SA 4.0*
  - 5: Terrestrial and Aquatic Biomes - *CC BY-NC-SA 4.0*
    - 5.1: Biogeography - *CC BY-NC-SA 4.0*
    - 5.2: Terrestrial Biomes - *CC BY-NC-SA 4.0*
    - 5.3: Aquatic Biomes - *CC BY-NC-SA 4.0*
  - 6: The Evolution of Populations and Species - *CC BY-NC-SA 4.0*
    - 6.1: Introduction - *CC BY-NC-SA 4.0*
    - 6.2: Population Evolution - *CC BY-NC-SA 4.0*
    - 6.3: The Hardy-Weinberg Equilibrium - *CC BY-NC-SA 3.0*
    - 6.4: Population Genetics - *CC BY-NC-SA 4.0*
    - 6.5: Formation of New Species - *CC BY-NC-SA 4.0*
    - 6.6: Reconnection and Rates of Speciation - *CC BY-NC-SA 4.0*
  - 7: Phylogenies and the History of Life - *CC BY-NC-SA 4.0*
    - 7.1: Introduction - *CC BY-NC-SA 4.0*
    - 7.2: Organizing Life on Earth - *CC BY-NC-SA 4.0*
    - 7.3: Determining Evolutionary Relationships - *CC BY-NC-SA 4.0*
    - 7.4: Perspectives on the Phylogenetic Tree - *CC BY-NC-SA 4.0*

R Practice: Building Interdisciplinary Skillsets to Understand Environmental Attitudes (Part II: Sentiment Analysis)

Technical Learning Objective: In this module, students will learn how to run a Sentiment Analysis for textual data (a "corpus") in R.

Sentiment Analysis of Silent Spring

This is the second part of a two-part analysis. Please see Part I: Word Cloud prior to completing this activity.

As a reminder, in the first part of this module we looked at a word cloud of the impactful book "Silent Spring", by Rachel Carson. In this follow-up module, we will run another common analysis used for textual data - a sentiment analysis. Sentiment analysis is used to determine the "tone" of a corpus, whether it is positive, negative, or neutral.

Loading Packages and Data

As always, we first need to install and load all necessary packages and data.

```
# Install
install.packages("syuzhet") # for sentiment analysis - this specialized package needs

# Load
library("RColorBrewer")
library("syuzhet")
library("ggplot2")

# here we are loading in the text file from a url, as the file has been uploaded to L
text <- readLines(url("https://bio.libretexts.org/@api/deki/files/66200/SilentSpring.
```

run restart restart & run all

Exploring Emotional Sentiments in Silent Spring

Now, let's use the get_ncr_sentiment command, a specialized function in the syuzhet package, which will tell us which sentiments are tracked in our textual data. The head command allows us to explore the first 10 rows of data for the emotional sentiment in Silent Spring. Run the code below to figure out what emotions are classified by this package.

```
# run nrc sentiment analysis to return data frame with each row classified as one of
d<-get_nrc_sentiment(text)

# head(d,10) - to see top 10 lines of the get_nrc_sentiment dataframe, or display the
head (d,10)

# [fill in the emotions here, there should be 8]
```

run restart restart & run all

Visualizing Emotional Sentiments in Silent Spring

Now we can visualize the sentiment frequency with a bar graph. Pay attention to the perceived sentiment values for each emotion. What conclusions can you draw from the graph? Where can you see some of this code being applicable in other fields?

```
#transpose the text file with the data frame for the calculated sentiment.
td<-data.frame(t(d))

#The function rowSums computes column sums across rows for each level of a grouping va
td_new <- data.frame(rowSums(td[2:253]))

#Transformation and cleaning the data to make it easier to graph
names(td_new)[1] <- "count" #here we are labeling the new data frame with a sting
td_new <- cbind("sentiment" = rownames(td_new), td_new) # here we are adding the senti
rownames(td_new) <- NULL
td_new2<-td_new[1:8,] #Here we are including the sentiments into the new graphable dat

#Plot One - count of words associated with each sentiment
quickplot(sentiment, data=td_new2, weight=count, geom="bar", fill=sentiment, ylab="cou
```

run restart restart & run all

Food for Thought

What sentiments are most common in Silent Spring? What does this tell you about the approach taken by Rachel Carson?

Sources

Carson, R. (1962). Silent Spring. Crest Book. Mhatre, S., Sampaio, J., Torres, D., & Abhishek, K. (2021, September 15). Text mining and sentiment analysis: Analysis with R. Simple Talk. Retrieved November 18, 2022, from https://www.red-gate.com/simple-talk...alysis-with-r/

R Practice: Using Chi-Square to Test for Underrepresentation in STEM

Technical Learning Objective: In this module, you will learn how to use loops to repeat processes in R and to use grep to match patterns among two datasets (in this case, bird species names and European surnames).

Underrepresentation in STEM

In science, technology, engineering, and mathematics (STEM), some groups are disproportionately underrepresented. For example, from 2010-2018, only around 9% of masters students in the STEM fields in the United States were Black students (Funk & Parker, 2018). Similarly, Hispanic students also only accounted for about 9% of those degrees during the same time frame (Funk & Parker, 2018). White students received 62% of STEM masters degrees. Though we have made progress in reducing opportunity gaps in some STEM fields, we have seen less progress in others.

Why does underrepresentation occur? There are several factors that contribute to underrepresentation of some groups (underrepresented and minority groups, URM) in STEM, one of which is a sense of belonging. It is important that URM groups feel a strong sense of belonging in STEM, as this can positively impact retention (Kricorian et al., 2020). However, studies have shown that students from URM groups tend to feel more uncertain about their belonging to their academic field compared to students from well-represented groups (Kricorian et al., 2020). Academic opportunity is another aspect of a student's background that can influence their participation in STEM fields (Beasley & Fischer, 2012). White students typically have access to higher quality teachers and curricula in their primary and secondary educations compared to Black or Hispanic students (Beasley & Fischer, 2012). Understanding the drivers of underrepresentation may help us to develop effective strategies to promote diversity and inclusion in STEM.

In this module, we will be analyzing a 2018 data set from the National Science Foundation (NSF) that quantifies the number of science and engineering graduate students by field, sex, degree, citizenship, ethnicity, and race. NSF releases these data as part of the "Diversity and STEM" report, which is updated every two years. Our goal is to test the null hypothesis that participation in STEM fields does not differ by racial identity. To do this, we will be using a chi-square test. If our p-value is <0.05, we will reject our null hypothesis.

When to Use Chi-Square Tests: Chi-square tests are used when analyzing the relationship between two categorical variables and often rely on count data. In the case of our data, the two categorical variables tested are academic field and racial group.

Loading Packages and Data

Let's begin by downloading and installing the necessary packages. We will use the tidyverse package, which you've seen before, to wrangle our data. We will also install and load a new package, "gplots", that will help us to visualize our data.

```
#Let's first load the tidyverse package
library(tidyverse)

#Now let's load and install the gplots package
install.packages("gplots") # The gplots package allows us to create a balloon plot
library("gplots")  #loads the gplots package

#Next, we will import and clean our dataset
NSF_STEMDiversity = read.csv(url("https://bio.libretexts.org/@api/deki/files/70893/NS
NSF_STEMDiversity #let's take a look at our data to make sure it loaded okay
```

run restart restart & run all

Running a Chi-Square Test

The goal of this module is to familiarize you with a "for" loop and with the function "grep", a pattern matching function. The code below creates an empty table (or "data frame"), then fills that table with two bits of information: the European surname of interest, and the number of bird species names based on the European surname.

```
#Step 1 - Create a Contingency Table
rownames(NSF_STEMDiversity) = NSF_STEMDiversity$Field #Creates a column that has the
NSF_STEMDiversity = NSF_STEMDiversity %>% select(-Field) # Removes the excess field

#Step 2 - Run Your Test
chisq.test(NSF_STEMDiversity) # Performs a chi-square test, where the null hypothesis
```

run | restart | restart & run all

Our p-value is less than 0.05 ($p = 2.2x10^{-16}$), which allows us to reject the null hypothesis that there is equal participation of racial identities across STEM fields. Instead, the data published by NSF suggests the alternative, that participation across different STEM fields varies by race.

Creating a Balloon Plot

Though we now know that participation in different STEM fields varies by race, the chi-squared test only gives us one value. Visualizing our data will help us to better understand where these discrepancies lie.

```
dt <- as.table(as.matrix(NSF_STEMDiversity)) # The first step to creating a balloon p

balloonplot(t(dt), main ="Diversity in STEM", #This creates a balloon plot using the
            xlab ="", ylab="", # xlab and ylab are used to set their respective axis
            label = FALSE, # label is set to true when you want to show the values on
            show.margins = FALSE, text.size = .5, # Deletes the margin lines and sett
            rowmar = 5.5, colmar = 6, # Changes the amount of space for the row and
            dotsize=1.5/max(strwidth(20),strheight(20)), # Changes the dot size, sett
            dotcolor = "blue", # We can also set the dot color
            label.lines = FALSE, # Removes the label lines from the graph
            cum.margins = FALSE, # Removes marginal fractions
            colsrt = 90 ) # Changes the angle of the column titles to 90 degrees
```

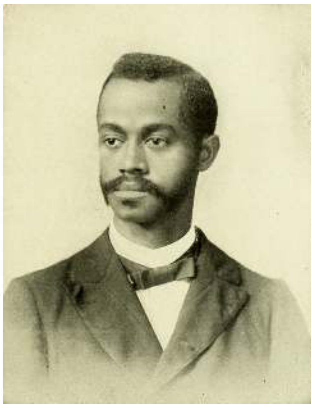
run | restart | restart & run all

This figure confirms that, within STEM, most fields are dominated by White graduate students.

What Next? Supporting Diversity and Inclusion in STEM

What can we do to improve representation in STEM? One idea is to provide these students with STEM-related opportunities earlier in their academic career. Many URM students do not receive adequate preparation for college level STEM courses in high school (Ghazzawi, 2018). This opportunity gap could impact students' self-confidence and motivation going into a STEM major (Ghazzawi, 2018). STEM intervention programs provide students with intensive instruction prior to college that strengthens their background in math and science concepts (Ghazzawi, 2018). Another way to improve URM participation in STEM programs is by strengthening peer and faculty mentorships. These relationships can allow URM students to feel more connected with their field and help them in developing important time management and other skills (Ghazzawi, 2018). Kendricks et al. (2013) found that faculty mentoring was the factor that had the overall highest impact on URM students academic success in STEM. Lastly, representation is a key factor in improving URM student belonging in STEM - the motivation for the "Scientist Spotlights" you will see throughout this book!

Case Study: Charles Henry Turner



Charles Henry Turner was a biologist, neurologist, and psychologist who dedicated much of his life to studying animal cognition (CBC Radio, 2021). He was the first Black scientist to be published in the highly prestigious journal *Science* back in 1892. Throughout his life, he was able to publish a total of 71 papers. Thanks to him, we know that insects are able to hear and honey bees are capable of recognizing patterns and perceiving color (Bolt, n.d.). Despite his impressive resume of accomplishments, Turner was never able to secure a job as an academic or researcher due to racial disparities at the time (CBC Radio, 2021). Even without the ability to use a lab or research materials, Turner was able to achieve revolutionary findings in the field of animal behavior. Specifically, his work supported the idea that animals were capable of complex cognition, a finding that went against the popular beliefs at the time (CBC Radio, 2021). Unfortunately, his work was paid little attention and ended up being mostly forgotten, resulting in White scientists "re-discovering" the same findings many years later (CBC Radio, 2021).

References

Beasley, M. A., & Fischer, M. J. (2012). Why they leave: The impact of stereotype threat on the attrition of women and minorities from science, math and engineering majors. *Social Psychology of Education*, *15*(4), 427-448.

Bolt, C. (n.d.). *More than mere insects: The brilliant mind of Charles Henry Turner*. WWF. Retrieved January 5, 2023, from https://www.worldwildlife.org/storie...s-henry-turner

CBC Radio. (2021, August 13). *Meet 7 groundbreaking black scientists from the past | CBC radio*. CBC. Retrieved January 5, 2023, from https://www.cbc.ca/radio/quirks/blac...tory-1.5918964

Elassar, A. (2022, April 3). *California once prohibited Native American fire practices. now, it's asking tribes to use them to help prevent wildfires*. CNN. Retrieved January 5, 2023, from https://www.cnn.com/2022/04/03/us/ca...20the%20canopy.

Funk, C., & Parker, K. (2018, January 9). *Blacks in STEM jobs are especially concerned about diversity and discrimination in the workplace*. Pew Research Center's Social & Demographic Trends Project. Retrieved January 5, 2023, from https://www.pewresearch.org/social-t...the-workplace/

Ghazzawi, D., Pattison, D., & Horn, C. (2021, July). Persistence of Underrepresented Minorities in STEM Fields: Are Summer Bridge Programs Sufficient?. In *Frontiers in Education* (Vol. 6, p. 224). Frontiers.

Kendricks, K., Nedunuri, K. V., & Arment, A. R. (2013). Minority student perceptions of the impact of mentoring to enhance academic performance in STEM disciplines. *Journal of STEM Education: Innovations and Research*, *14*(2).

Kricorian, K., Seu, M., Lopez, D., Ureta, E., & Equils, O. (2020). Factors influencing participation of underrepresented students in STEM fields: matched mentors and mindsets. *International Journal of STEM Education*, *7*(1), 1-9.

R Practice: Using Linear Models Determine the Relationship Between Biodiversity and Socioeconomic Status (Part I: Exploring Linear Model Outputs)

Technical Learning Objective: In this module, readers should gain a better understanding of when to use linear regressions and how to collect and interpret linear regression statistics using R.

The Biodiversity Implications of Socioeconomic Inequality

The socioeconomic status (SES) of an area is known to have a strong influence on the lives of those who reside within it. Extensive evidence has indicated that economic inequality negatively impacts a variety of social outcomes and institutions (Holland et al. 2009). For example, in Mexico, villages with an unequal economic structure were much more likely to have poorly managed forests (Holland et al. 2009). These quality of life differences have lead ecologists to wonder how the SES of an area impacts biodiversity. While there have been few studies analyzing the relationship between SES and biodiversity, research on similar concepts provides guidance on what we might expect to see. One concept known as the "Luxury Effect" states that wealth can allow people to live in areas with higher biodiversity thanks to access to things such as private gardens (Hope et al. 2003). The "Hierarchy of Need" concept mentions that residents with a lower SES often struggle to produce diverse edible and medicinal plants, while those with a higher SES don't face this issue (Kuras et al. 2020).

Mikkelson et. al. (2007) aimed to examine the degree to which socioeconomic factors impact biodiversity loss. One aspect of this study was to test for a correlation between the number of permanent resident bird species experiencing population decline and each state's Gini Ratio of income inequality, which is a value used to estimate economic inequality. The Gini Ratio ranges from 0 (perfect equality) to 1 (perfect inequality). Mikkelson et. al. (2007) used linear regression plots and statistics to better understand this relationship, which we will recreate using R.

When to use Linear Regressions: Linear regressions are used to test the relationship between two or more continuous variables of interest. In the case of our analysis, the two variables we are interested in are the number of declining permanent resident bird species and the Gini Ratio of income inequality.

Mikkelson, G. M., Gonzalez, A., & Peterson, G. D. (2007). Economic inequality predicts biodiversity loss. *PloS one*, *2*(5), e444.

Loading Packages and Data

First, let's load any libraries we will be using (here just tidyverse) and our dataset.

```
library(tidyverse) #Loads the tidyverse package into R's brain. This pacakge contains

bird <- read.csv(url("https://bio.libretexts.org/@api/deki/files/65130/GINI_BIRDS.csv
#This loads in the dataset and stores it in R's "brain," that way we can use the data

tibble(bird) # Visualizes the dataset in a table.
```

run restart restart & run all

Creating a Regression Plot

Now, let's *visualize* the relationship using a linear regression. Afterwards, we will have to test whether this relationship is statistically significant.

```
bird %>%
  ggplot(aes(x = GiniRatio_1969, y = DecResBird_1966)) + #plotting two continuous var
  geom_point() + #adding points to my plot.
```

```
  geom_smooth( method = "lm" ) # Creates a regression line for a linear model.
```

run | restart | restart & run all

Before we move on, we should take a look at our plot and see whether it is likely to fit the assumptions of a linear model. Is the relationship linear? Are the data homoscedastic (e.g., the variance of points stays similar across values of the y-axis). Learn more about the assumptions of linear models on Wikipedia.

Running a Linear Model

The code below generates some key linear regression statistics, including the p-value, the slope of the relationship, and the r-squared value. The p-value tells us how likely it is that our data occurred due to chance. A higher p-value indicates a stronger probability that the results we see are due to chance. Most fields used a cut-off off p-value of 0.05 to consider a relationship statistically significant. Anything less than 0.05 means that the probability of our results occurring by chance is less than 5%. The R-squared value is tells us how much of the dependent variable can be explained by the independent variable. For example, if we were to calculate an r^2 value of .75, that would mean that 75% of the variance in the declining resident bird population can be explained by the Gini Ratio. Lastly, the slope tells us how fast the dependent variable increases or decreases with every one unit change in the independent variable.

To find the linear regression statistics, we use the formula:
new_data_frame = lm(y-axis_Variable ~ x-axis_Variable, data = old_data_frame)

We then have to display the summary statistics, which we do by using the code:
summary(new_data_frame)

Now let's try it our with our data!

```
bird_mod = lm(DecResBird_1966 ~ GiniRatio_1969, data = bird) # creates a new data fra

summary(bird_mod) # shows us a summary of the statistics present in bird mod.
```

run | restart | restart & run all

Interpreting a Linear Model

Now we have our linear regression statistics, what can we interpret from them?
First, let's take a look at our p-value. Our p-value is 0.05266, which presents an interesting dilemma. As mentioned previously, many scientists infer that there is statistically significant correlation between two variables if the p-value is less than 0.05. This cut-off is somewhat arbitrary, however, and has received a lot of pushback from some scientists. Our p-value means that there was a 5.266 percent likelihood of our results occurring by chance. So while we cannot claim our results are statistically significant, it does seem like there might be a pattern here.
Next, let's look at our r-squared value. We can determine that there is a weak positive correlation between the Gini Ratio and declining resident bird species given our low r^2 value of 0.08454. This value suggests that only 8.5% of the difference in %declining resident bird species across states can be explained by the Gini Ratio.
The last value we want to look at is our Estimate, or our slope. Here, our Estimate is 22.578. This represents the slope between the Gini Ratio and the % of declining resident bird species. In other words, for every increase of 1 in the Gini Ratio, the percent of resident bird species showing population decline increases by 22.58%. Because the Gini Ratio ranges from 0 to 1, this suggests that a state with perfect inequality (Ratio = 1) has 22.58% more of its resident bird species declining than a state with perfect equality (Ratio = 0).

We can also use this table to write out the linear model that describes the relationship we are observing, using the form y = mx + b where:

- y is our dependent variable (declining resident bird species)
- x is our independent variable (Gini Ratio)
- m is our slope
- b is out y-intercept

In the R outline, the column Estimate gives us our slope and y-intercept. The y-intercept is the estimate for "intercept", while the slope is the Estimate for "GiniRatio_1969".

? Equation for a Linear Model

What would the equation for your resulting linear model be?

Answer

DecResBird_1966 = (22.6 * GiniRatio_1969) + (-4.8)

A male Kirtland's Warbler in a jack pine forest in Michigan, USA by snowmanradio is licensed under CC BY 2.0. Kirkland's Warblers are near threatened species that are dependent on jack pine habitat.

References:

Holland, T. G., Peterson, G. D., & Gonzalez, A. (2009). A cross-national analysis of how economic inequality predicts Biodiversity loss. *Conservation Biology*, *23*(5), 1304–1313. https://doi.org/10.1111/j.1523-1739.2009.01207.x

Hope, D., Gries, C., Zhu, W., Fagan, W. F., Redman, C. L., Grimm, N. B., Nelson, A. L., Martin, C., & Kinzig, A. (2003). Socioeconomics Drive Urban Plant Diversity. *Proceedings of the National Academy of Sciences*, *100*(15), 8788–8792. https://doi.org/10.1073/pnas.1537557100

Kuras, E. R., Warren, P. S., Zinda, J. A., Aronson, M. F. J., Cilliers, S., Goddard, M. A., Nilon, C. H., & Winkler, R. (2020). Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landscape and Urban Planning*, *198*. https://doi.org/10.1016/j.landurbplan.2020.103799

Mikkelson, G. M., Gonzalez, A., & Peterson, G. D. (2007). Economic inequality predicts biodiversity loss. *PloS one*, *2*(5), e444.

R Practice: Using Loops and Pattern Matching to Understand Colonial Histories of Species Names

Technical learning objective: In this module, you will learn how to use loops to repeat processes in R and to use grep to match patterns among two datasets (in this case, bird species names and European surnames).

What's in a name?

In their 2021 publication, Trisos et al. (2021) explore the history of colonialism in the field of ecology and how we, as scientists, can make ecology a more inclusive space.

The code below is a modification of one of their analyses, which focused on the number of bird species whose scientific names have a European influence. They found that many bird species *outside of Europe* contain European surnames, and that this pattern was most prominent in areas formally colonized by European countries. Exploring links between European surnames and species names helps us to recognize the colonial nature of this field, and this recognition is a first step towards decolonization.

One considerable issue is that these names often convey little ecological information, as compared to the indigenous names for these species, and create a barrier for indigenous involvement in local ecology. There is a movement in ecology to include indigenous names for species alongside their scientific names and, in some cases, to rename species with local ecological knowledge in mind.

The authors list several approaches to more inclusive ecology: decolonizing access, decolonizing expertise, decolonizing your mind, practice ethical and inclusive ecology, and knowing your histories. Language is a key consideration in this process because of the important role it plays in our understanding of the world.

So, what can you do? You can learn more about decolonizing conservation here. Educating yourself on the issues and solutions is the first step towards making a difference.

Below, we use a pattern-matching tool in R, grep, to compare two datasets, one with species names of birds and one with European surnames. We also learn about how to set up a "for loop" in R. Loops are used to repeat tasks multiple times across different rows or columns of a dataset and can be extremely useful for streamlining analyses.

Trisos, C. H., Auerbach, J., & Katti, M. (2021). Decoloniality and anti-oppressive practices for a more ethical ecology. *Nature Ecology & Evolution*, *5*(9), 1205-1212.

Loading Packages and Data

Today, we'll be working with the package "tidyverse" to manipulate our data. We will be loading in two datasets, one on bird names and one on European surnames. Both are saved as a csv, or a comma-separated value.

```
#Let's first load the tidyverse package
library(tidyverse)

#Load bird species names (names follow Taxonomy of Jetz et al. 2012 http://birdtree.o
birdnames <- read.csv(url("https://bio.libretexts.org/@api/deki/files/65125/bird_spec

#We are going to read in our csv files, and tell R that there is no column heading (h

#Load list of surnames
peoplenames <- read.csv(url("https://bio.libretexts.org/@api/deki/files/65127/europea

#Now let's make sure out data loaded correctly by examining the first few rows with t
head(peoplenames)
```

run restart restart & run all

Learning About Loops and "grep"

The goal of this module is to familiarize you with a "for" loop and with the function "grep", a pattern matching function. The code below creates an empty table (or "data frame"), then fills that table with two bits of information: the European surname of interest, and the number of bird species names based on the European surname.

```
#Step 1: Setting up the length of the loop
npeople = nrow(peoplenames) #When we are running a loop, we want to first figure out


#Step 2: Creating a table for the loop to put data into
matches = matrix(nrow = npeople, ncol = 2) #We also need to create an empty data tabl


#Step 3: Let's give the empty table some useful column names
colnames(matches) = c("Name", "NMatches") #here we use the "colnames" labelling functi


#Step 4: Creating our loop
for (i in 1:npeople) #The "for" loop says "do the tasks below for each of these elemen
  {
  matching_birds = grep(peoplenames[i,1], unlist(birdnames), ignore.case=TRUE, value=
  number_matches = length(matching_birds) #This counts the number of matches using th
  matches[i,1] = peoplenames[i,1] #In R, data are indexed as [row,column]. Here we ar
  matches[i,2] = number_matches #And, lastly, we are putting the number of matches fo
}


#Step 5: Reorder our dataframe
data.frame(matches) %>% #here we are using the "pipe" to direct our dataset into the
  arrange(desc(NMatches)) #the arrange function allows us to sort our data by a colum
```

run restart restart & run all

What did you find?

Based on your outputs, which surnames shows up most in bird species names? Using Google to help, what is the origin of that surname?

Answer

Dutch naturalist Coenraad Jacob Temminck
British naturalist John Edward Gray

Case Study: Rudolf Grauer

Rudolf Grauer was a German Zoologist whose research focused on the Belgian Congo. The Belgian Congo was a Belgian colony in Central Africa from 1908 until independence in 1960. Four species in the Democratic Republic of Congo are still named after Grauer today: Grauer's Cuckoo Shrike (*Coracina graueri*), Grauer's Swamp Warbler (*Bradypterus graueri*), Grauer's warbler (*Graueria vittata*), and Grauer's Broadbill (*Pseudocalyptomena graueri*). A photo of Grauer's Broadbill is included below.

Grauer's Broadbill *Pseudocalyptomena graueri* by Nik Borrow is licensed under CC BY-NC 2.0

R Practice: Using Linear Models Determine the Relationship Between Biodiversity and Socioeconomic Status (Part II: Visualizing Linear Models)

Technical Learning Objective: In this module, students will gain a better understanding of how to create and interpret linear regression plots using R.

The Biodiversity Implications Implications of Socioeconomic Inequality - Visualization

In the previous model, we used a linear model to test for the relationship betwee the Gini Ratio of Income Equation, which ranges from 0 (perfect equality) to 1 (complete inequality) and the percentage of declining resident bird species in a state. In this follow-up module, we are going to learn how to effectively visualize the results of these models.

Data from: Mikkelson, G. M., Gonzalez, A., & Peterson, G. D. (2007). Economic inequality predicts biodiversity loss. *PloS one*, *2*(5), e444.

Note: This is the second part of a two-part exercise. Please see Part I for guidance on interpreting linear model outputs.

Loading Our Packages and Data

First let's start by loading in our packages! For this module, we will be using rstatix and tidyverse.

```
library(tidyverse) #First, let's load the tidyverse packages, which we will use for d

bird <- read.csv(url("https://bio.libretexts.org/@api/deki/files/66201/GINI_BIRDS.csv
#read.csv loads our data file, and setting it to "bird" stores it in R's "brain" so t

head(bird) # Head allows us to visualize the first few rows of the dataset, so that w
```

run restart restart & run all

We can also get a quick feel for our data using the summary command. This is a quick way, for example, to get an idea of the range of each of our data columns and to see whether there are any extreme outliers.

```
summary(bird) # Shows the summary statistics containing a summary of each column in t
```

run restart restart & run all

The Components of a ggplot object

After we've loaded in our data and gotten a quick feel for it, we can begin to visualize our data. A ggplot object is made up of three components:

- the data - the dataframe being plotted, which can be piped into the figure or defined within the ggplot command
- the aesthetics (aes) - the aesthetics of the geometric object, such as color and shape, as well as the columns to be used for the x and y axes
- the geometries (geom) - the type of plot (e.g. point, boxplot, histogram)

The type of plot you use (the geom) will depend on what type of data you are working with. Here, we are looking for the relationship between two continuous variables, so we will be using a scatterplot. We know from our previous analysis (Part I: Exploring Linear Model Outputs) that the linear relationship between these two variables is borderline insignificant. Generally, you would only include a linear model line on a regression plot if the relationship is significant. We will add a linear model line here, however, for learning purposes.

The first step is to pipe our data into a plot. We do so by using the formula:
Name of Data %>%
ggplot(aes(x = independent variable, y = dependent variable))

In the case of our experiment, we are testing whether the % declining species *depends* on the Gini Ratio. We will therefore place the % declining species on the y axis and the Gini Ratio on our x-axis.

IMPORTANT: After each line of code, it's important to include a brief description of what your code does to keep track of it all. This is called commenting. Any line of code that starts with a # will be treated as a comment by R.
Your code should look something like this:

```
bird %>%
  ggplot(aes(x = GiniRatio_1969, y = DecResBird_1966)) #plotting two continuous varia
```

run | restart | restart & run all

You now have data added to your plot and your aesthetics set, but the plot is blank because you have not yet chosen a geom. Next, we need to add data points and a regression line. To add data points, we will use the function geom_point(). To add a regression line, we will use the function geom_smooth(method = "lm"). The reason why we use "method = "lm" is because this is a linear model. The grey area surrounding the line represents your model's error. There are several other model types that can be added with geom_smooth (e.g., a generalized additive model), but these models are beyond the goals of this module.

IMPORTANT: Before each addition to the ggplot command, you have to use a "+" rather than a pipe (%>%).

Awesome, the regression has all the data needed!

Effective Data Visualization

There is still a long way to go to make our plot look nicer, however. Here are just a few ways to improve our visualization:

- We can change the labels of the x and y axes to be more descriptive using xlab("Text") and ylab("Text"). Make sure to include units for your variables where relevant!
- We can customize the text size for the axes. We do this within our plot "theme"

  theme(axis.title.x = element_text(size = number), axis.title.y = element_text(size = number))

- We can change the color or size of our points by setting the color and size within geom_point.

Note: Effective ata visualization is a complex skill to learn! There are a lot of online resources to help you on this journey.

- For a full list of colors in R, visit this Colors in R Cheatsheet
- For more ways to make prettier plots, visit this Data Visualization in R Cheatsheet
- To explore some additional types of plots in R and figure out which are best for your data, visit datatoviz

After you've run this code, try out some of your own changes by replacing the color blue and the size of the axis titles.

```
bird %>%
  ggplot(aes(x = GiniRatio_1969, y = DecResBird_1966)) + #plotting two continuous var
  geom_point(size = 2, color = "blue") + #adding points/creating a scatterplot and ma
  geom_smooth(method = "lm") + #adds the best fit line for the linear model between t
  ylab("Declining Resident Bird Species, 1966-2005 (%)") +
```

```
  xlab("Gini Ratio of Family Income Inequality 1969") +
  theme(axis.title.x = element_text(size = 14), ## Changes x-axis font size to 14
  axis.title.y = element_text(size = 14)) ## Changes y-axis font size to 14
```

run | restart | restart & run all

Finally, let's add a theme to the regression plot. There are several set themes available for you to use, but for this regression lets use a simple black and white theme.
To do so, use the function: theme_bw()

Here are some other themes. Go ahead and try them out by changing and rerunning the code!
theme_gray()
theme_classic()
theme_minimal()

Here is the code again, including the theme.

```
bird %>%
  ggplot(aes(x = GiniRatio_1969, y = DecResBird_1966)) + #plotting two continuous vari
  geom_point(size = 2, color = "blue") + #adding points/creating a scatterplot and mak
  geom_smooth(method = "lm") + #adds the best fit line for the linear model between th
  ylab("Declining Resident Bird Species, 1966-2005 (%)") +
  xlab("Gini Ratio of Family Income Inequality 1969") +
  theme(axis.title.x = element_text(size = 14), ## Changes x-axis font size to 14
  axis.title.y = element_text(size = 14)) +  ## Changes y-axis font size to 14
  theme_bw()
```

run | restart | restart & run all

Visualizing Model Fit

Looking at the graph, what can you say about the fit of this linear model?

Answer

The data points are widely scattered around the line of best fit, indicating that there is a weak correlation between the Gini Ratio and % declining resident bird species. There seem to be some outliers that might be skewing this relationship (e.g., the state that has 10% declining resident bird species). These data are unlikely to fit the assumptions of a linear model without additional statistical consideration.

A male Kirtland's Warbler in a jack pine forest in Michigan, USA by snowmanradio is licensed under CC BY 2.0. Kirkland's Warblers are near threatened species that are dependent on jack pine habitat.

References:

Holland, T. G., Peterson, G. D., & Gonzalez, A. (2009). A cross-national analysis of how economic inequality predicts Biodiversity loss. *Conservation Biology*, *23*(5), 1304–1313. https://doi.org/10.1111/j.1523-1739.2009.01207.x

Hope, D., Gries, C., Zhu, W., Fagan, W. F., Redman, C. L., Grimm, N. B., Nelson, A. L., Martin, C., & Kinzig, A. (2003). Socioeconomics Drive Urban Plant Diversity. *Proceedings of the National Academy of Sciences*, *100*(15), 8788–8792. https://doi.org/10.1073/pnas.1537557100

Kuras, E. R., Warren, P. S., Zinda, J. A., Aronson, M. F. J., Cilliers, S., Goddard, M. A., Nilon, C. H., & Winkler, R. (2020). Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landscape and Urban Planning*, *198*. https://doi.org/10.1016/j.landurbplan.2020.103799

Mikkelson, G. M., Gonzalez, A., & Peterson, G. D. (2007). Economic inequality predicts biodiversity loss. *PloS one*, *2*(5), e444.

R Practice: Using Pattern Matching and Metadata to Connect with Local Ecology (Part I: Locally Endangered Fishes)

Technical learning objective: In this module, you will learn how to use a variety of common tidyverse functions (filter, group_by, summarize) and specialized pattern matching functions (grepl). You will also be asked to use metadata to interpret your dataset. Whenever you see text that is highlighted in orange, you are being asked to add code of your own!

Local Endangered Species

When thinking of the word "endangered", what species comes to mind?

Likely, we first think of large, charismatic species whose conservation is most likely to make headlines. But, many of us live in areas with much less visible endangered species. In this activity, we help to cultivate a sense of local connection by improving knowledge of the species endangered in your home state. We will do this using a data set that lists endangered fishes based on state.

Loading Packages and Data

Let's start off my loading our packages and data. Here, we are going to do something a little different and have you name your dataset.

```
library(tidyverse) #loading the tidyverse package into the R workspace

#name# = read.csv(url("https://bio.libretexts.org/@api/deki/files/70943/EndangeredFis

#name#
```

run restart restart & run all

Focusing on Your State

Now that we have loaded the data as a file in our workspace, we will begin to isolate the data we want to work with. Let's start by looking at a specific state. Fill in your state below and save it to the object 'my_state'. The way you enter your state must match exactly with the format used in the table (i.e., an all-caps, two-letter code). This type of data will represent a character "string" and needs to be surrounded by quotation marks (e.g., "AZ" for Arizona.)

```
my_state = #"yourstate"#  #fill in the two-letter code for your chosen state here, ma
```

run restart restart & run all

If you take a look at fishes data set, you will notice that some of the entries contain multiple states. These entries represent waterways that occur across state boundaries. Now that the chosen state has been stored as the object 'state' we have to find a way to include all entries that contain your chosen state, including those which contain multiple states under them.

If each entry only ever included one state, this would be much easier, as we could use the following code (make sure to replace #name# with your data set name):

```
#name# %>%
  filter(HU_8_STATE == my_state)
```

run restart restart & run all

Unfortunately, this code only filters for rows that exclusively contain the specified state. This is where we would like to introduce the concept of the grepl() function, which allows us to conduct pattern matching in R. This function searches for matches with a specified pattern from a specific vector or column within a data set. Pattern matching can manifest itself in many forms and have many internal arguments, but we will only be looking at the following:
grepl(pattern, x), this is a function of pattern matching which focuses on the identifying portion of pattern matching.
The first argument within the function focuses on the character string of the 'pattern' that we are trying to identify within a vector or column within our data set. What would go in the pattern section of our code? That's right, we will use the state object we created.
x is the second argument within the grepl() pattern matching function which is used to determine vector or column in which the function should be applied. What is the name of the state column within the data set? This will be important for the next portion of the coding exercise.
More information on pattern matching can be found online.

Now let's give this pattern matching a try. First we will start by giving what we will code a name so that we have an output table, we will name it state_fish for simplicity. Then we apply the functions under the data set we loaded and using a pipe (%>%) we will apply the filter() and grepl() functions.
Remember how we said that filter wouldn't work. Well, it wouldn't work by itself. It does, however, work perfectly for our purposes if combined with the grepl function. After the pipe, we insert the filter() function and within it the grepl() function. Using what was explained in the last paragraph, we will code for the grepl() pattern matching function. The shell of the code has been provided, but it is up to you to finish the code block by telling the grepl function the column it is searching for the pattern in.

```
state_fish = #naming the functions we are using to have an output table
#name# %>% #please insert the chosen name for the data set
 filter(grepl(my_state, )) #using the filter and grepl functions we are coding to onl
```

run | restart | restart & run all

Using Metadata to Understand Your Columns

Now that we have isolated the data for your desired state, we will answer the following question: Which place within your chosen state has the highest proportion of endangered fish species? Now, we have to figure out how to code the endangered species proportion for the desired region. There are many columns within the data set, so your job now is to find the two columns necessary to calculate a "proportion endangered".
But, how do you even know where to start with choosing these two columns? This brings us to the metadata, the data about the data, which is a key component of any dataset. The metadata is important because it contains the meaning and units of the columns in the data set. Please run the following code chunk to access the metadata within your workspace.

```
fish_readme = read.csv(url("https://bio.libretexts.org/@api/deki/files/70942/readme_E
#loading in the metadata file, please read it and pay attention to the columns and th

fish_readme #now, take a look at your metadata
```

run | restart | restart & run all

Now that you have access to the metadata, we are going to group by basins within your state (BASIN) and calculate the percentage of species endangered. We will first pipe our data set into a group_by function, then we will use summarize to calculate the percentage of species endangered.
Within the summarize function, we need to give our name column a name (per_endangered). We will set this equal to an equation that calculates the percentage of species endangered using two other columns in the data set. Hint: You will want to use a column regarding ESA designation and a column for the total fish counts for thsi calculation.
Putting the data in descending order will allow us to more easily answer the question we posed at the beginning of this exercise. We do this using the arrange() function. As a default, arrange sorts the data by ascending order with a column name as an argument

within the function. By adding desc() as a function within the arrange() function, we will see the data sorted by descending order. To specify a column just add it within the desc() function. In this case, we will use the per_endangered column that we created. Now, you will practice the previous block of code on your own. The chosen region size and percent endangered columns must be different from the example. If you are having trouble please refer to the previous examples and metadata to get and output.

For this code to run, you must replace #column1# and #column2# with the relevant columns from the dataset!

```
state_fish %>% #specifying the data frame we are working with
  group_by(BASIN) %>% #using the function to group by specific regions
  summarize(per_endangered = (#column1#/#column2#) * 100) %>% #Here we are coding the
  arrange(desc(per_endangered)) #arranging our data by descending order with the perce
```

run restart restart & run all

Great work! You can now continue onto Part II of this module, which will allow you to visualize your findings.

Hint for Endangered Species Equation $RPractice.1$

Which two columns did you need to use to calculate the percentage of endangered species?

Answer

Your equation should read as follows: per_endangered = ESA_E/TOTAL_SP * 100

Formulas Summary

Name	Formula	Interpretation
Fundamental equation of population growth	$N_{t+1} = N_t + B_t - D_t + I_t - E_t$	N_t = population size at time t B = births; D = deaths; I = immigrant
Net reproductive rate - average total number of female offspring per female over the course of her lifetime	$R_0 = I_x m_x$	increasing pop: R_0 > 1 stable population: R_0 = 1 decreasing pop: R_0 < 1
Generation time	$T = x I_x m_x R_0$	T = average age of reproduction
Intrinsic/ per capita growth rate	$r = T ln(R_0)$	increasing pop: r > 0 stable population: r = 0 decreasing pop: r < 0
Rule of 70	$t = 70(100r)$	t = time (in years) for population size
F_x	$F_x = S_x m_{x+1}$	age-specific fecundity
T_x	$T_x = x L_x$	T_x = years left to live
E_x	$E_x = T_x n_x$	E_x = life expectancy
L_x	$L_x = (n_x + n_x + 1)/2$	L_x = number surviving
Geometric population growth - growth rate of population with pulsed (seasonal) reproduction patterns	$\lambda = N_{t+1}/N_t$	increasing pop: > 1 stable population: = 1 decreasing pop: < 1
Geometric growth model future population estimation	$N_t = N_0 \lambda^t$	N_t = population size at time t
Exponential population growth - growth by a population with continuous reproduction (rate of population size change over time)	$dN/dt = rN$	increasing population: r > 0 stable population: r = 0 decreasing population: r < 0
Exponential growth model future population estimation	$N_t = N_0 e^{rt}$	N = population size at time t $(e \approx 2.71828)$
Logistic population growth - exponential growth limited by carrying capacity	$\frac{dN}{dt} = rN \frac{(K - N_t)}{K}$	increasing pop: N < K stable population: N = K decreasing pop: N > K
Bioenergetics model	$S = IE - (FE + UE) - M$	S = energy storage (growth and repro
Lincoln-Peterson Index (Mark-Recapture Model)	$N = \frac{(M * S)}{R}$	N = population size estimate M = # of animals marked and release S = # of animals recaptured R = size of sample on 2nd visit
Leslie Matrix formula	$N_{t+1} = L * N^t$	N_{t+1} = population size at time t L = Leslie Matrix N_t = age-specific population at initia
Simpson's Index of Diversity (measure of probability): the less diversity, the greater the probability that two randomly selected individuals will be the same	$D = \sum_{i=1}^{S} \left(\frac{n_i}{N}\right)^2$	n_i = number of individuals of specie N = total number of individuals of all 1 - D: if D is closer to zero, then less diversity
Shannon-Wiener Diversity Index (measure of certainty): more common species, more uncertain which one will be selected	$H = -\sum_{i=1}^{S} p_i * \ln p_i$	$n_i/N = p_i$ = proportion of individua H = 0 in the absence of diversity
Species richness	$H_{\max} = ln(S)$	H_{max} = maximum number of differe S = number of different species
Species evenness	$J = \frac{H}{H_{\max}}$	if J is closer to 0, then less evenness;
1. alpha 2. beta 3. gamma	1. average number of species 2. gamma / alpha 3. total # of species	1. diversity within a specific habitat 2. comparison of diversity within ha 3. measure of diversity at landsca region)