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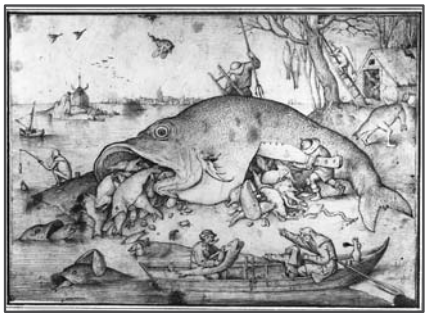

The feeding relationships between species can often be complicated.

Communities and Ecosystems

When scientists first began studying biological communities, they were so fascinated with the interactions and dependencies between species that they saw the biological community as a superorganism. Whole species were viewed as organs that performed specific functions for the complete ecological superorganism. The integration and communication between these "organs" was thought to be deliberate and well tuned. One way to think of this idea is to imagine a stitched-together Frankenstein, each sewn-on body part a distinct species.

Today biologists find the analogy between biological communities and organisms superficial. To be sure, there are populations within communities that are highly dependent on each other. And it is also true that biological communities and their physical environments support all life on Earth by such processes as recycling nutrients. The impact of this recycling can be profound. For instance, atmospheric levels of carbon dioxide depend on plant photosynthesis and the respiration of all aerobic organisms. Global temperatures and weather are in turn dependent on atmospheric carbon dioxide levels, which are covered in Chapter 16 (The Biosphere and the Physical Environment). The coordination and integration of biological communities has vast implications for the Earth.

For this reason, there are few biological topics as important for the future of life on Earth as the functioning of ecosystems. In this chapter, we survey how ecosystems function, from the flow of energy in Module 15.1 (Energy Flow) and the recycling of nutrients in Module 15.15 (Ecosystems) to the portentous problem of the fragility of ecosystems. In Modules 15.8 (Community Organization) and 15.4 (Equilibrium and Nonequilibrium Communities), we consider the factors that determine the number of species in a community. Surprisingly, in some communities predation and environmental disturbance may promote increased species diversity. Islands represent interesting communities, because virtually all species on an island must travel there from some larger mainland. Species diversity on islands is a consequence of dynamic processes. Understanding these forces has important practical applications for the design of ecological preserves, to be covered in Chapter 17 (Conservation). ❖

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Energy Flow

15.1 The flow of energy is a central organizing theme in community ecology

We have all strolled through forests or walked along the seashore or lakeside. Even the untrained person will notice a variety of plants in a forest or the many insects and birds near lakes and oceans. These interacting plant and animal populations are part of a biological **community**. The members of such a community will be apparent from their associations or their geographic location. As we have seen in the previous chapter, some plants and animals may interact very closely and affect each other's evolution. While the details of processes such as coevolution were unknown to early ecologists, there was a strong sense that there was a mutual interdependence among the members of a community.

FIGURE 15.1A The Initial Stages of Succession in a Temperate Forest .

Communities

Early in the twentieth century, F. E. Clements developed some of the first ideas about communities. If a tract of land is cleared but then left undisturbed, it will be recolonized by plants over time. This recolonization, or **succession**, may follow a predictable pattern, with some species appearing early in the sequence of recolonization, but later giving way to different species. (Figure 15.1A shows one example of succession.) In studying ecological succession, Clements thought that the species that appeared during succession made up a superorganism, with strong interdependencies much like the organs of a single plant or animal. We will cover succession in more detail in Module 15.7.

In the 1920s, Charles Elton developed a more sophisticated view of communities, one that still persists today. He studied a tundra community on Bear Island in the North Atlantic. Elton's focus was on feeding. Which species feeds on which is one of the most important interactions in an ecosystem. Figure 15.1B shows some of the results from Elton's study. These feeding relationships also reveal a directional flow of energy. Moss captures energy from the sun. Energy in the mosses is then consumed by herbivorous rotifers that are ultimately eaten by ducks. Diagrams that show energy flows are called **food chains**.

The nature of an ecological community is not solely a function of the organisms that make up the community. The physical environment also influences the numbers and types of organisms in a community. Likewise, photosynthesis, respiration, and decomposition affect the physical environment. In 1935 the English plant ecologist A. G. Tansley coined the term **ecosystem** to describe ecological communities and their associated physical environment. In Module 15.15, we will discuss the interactions between biological communities and the physical environment.

Trophic Levels

In 1925 A. J. Lotka published his book *The Elements of Physical Biology*. Influenced by his training in chemistry, Lotka advocated the study of communities from a thermodynamic perspective, emphasizing the transfer of energy. This thermodynamic perspective and the importance of food chains were both embraced by Raymond Lindeman in 1942. For his Ph.D. thesis, Lindeman studied the feeding relationships in a bog community in Minnesota. He simplified the analysis of energy flow in this community by focusing on organisms that were at a similar position in the food chain. Such positions are referred to as **trophic levels**.

In most ecosystems, the lowermost or first trophic level is made up of the primary producers or plants, such as the mosses in Figure 15.1B. These organisms depend on sunlight for their energy. The next trophic level up consists of the herbivores, organisms that consume plants, such as the herbivorous rotifers in Figure 15.1B. The biomass or energy available to herbivores comes directly from the primary producers. It is also affected by the efficiency of conversion of energy. Consumers of herbivores—such as the ducks in Figure 15.1B—are at the next trophic level, and so on.

Lindeman noted that the dependence of each trophic level on the one below it suggests that the amount of energy contained in each level (for example, as plant or animal biomass) should decline as one moves from the lower to the higher trophic levels. Lindeman called this natural progression the Eltonian pyramid. In Modules 15.2 and 15.3, we will study in more detail what is known today about the energy relationships within communities and the factors that affect energy transfer from one trophic level to the next. ❖

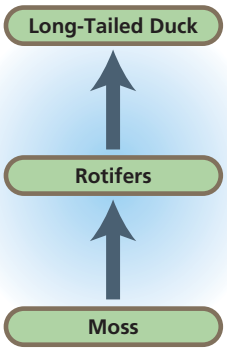

FIGURE 15.1B Some Feeding Relationships from Elton's study of Bear Island

Raymond Lindeman (1915–1942)

During his short life and even shorter academic career, Lindeman managed to write six scientific papers. One of these appeared in the journal *Ecology* after his death, with the title, "The Trophic-Dynamic Aspect of Ecology." This paper is credited with influencing many ecologists to look at the energy and feeding relationships among organisms as an important aspect of community structure. Lindeman received his Ph.D. from the University of Minnesota in 1941. Shortly afterward he moved to Yale University, where he began postdoctoral work with G. Evelyn Huchinson. The original version of Lindeman's trophic-dynamic paper was rejected by the journal *Ecology.* It was only after an appeal by Hutchinson that the editor of *Ecology,* Thomas Park, agreed to publish the paper.

FIGURE 15.1C Raymond Lindeman

15.2 In most biological communities, all energy comes from the sun

Biological systems are complicated, but they must follow the same laws of thermodynamics that physical systems obey. The first law of thermodynamics tells us that energy can be neither created nor destroyed. Energy can be changed, however, from one form into another. In biological communities, almost all energy originates from the sun. Green plants capture solar energy and turn it into chemical energy. Because of this special function, green plants are called **primary producers**. The chemical energy is stored by plants as bonds holding organic molecules together. Not all the captured energy from the sun is stored as chemical energy. Plants use some energy for metabolic maintenance, and some is lost as heat.

All trophic levels above plants gain energy by feeding on members of other trophic levels. Herbivores feed on plants and derive their energy from the energy stored in plant tissue. The flow of energy goes in one direction, from plants to herbivores—not the other way. Consequently, the energy content of all the herbivores in a community cannot exceed the energy contained in the primary producers. In fact, it will often be much less, for at least two reasons. (1) The herbivores cannot consume all the plants, or there would be no future source of energy for the herbivores. (2) The conversion of chemical energy in the plants to chemical energy in herbivores is not perfect. Energy is lost as heat or is unused due to incomplete digestion. Thus the total amount of energy in an ecosystem is determined by the primary producers, though much will be lost to the biological community.

A rough indication of the amount of energy in the primary producer level is their **biomass**. Figure 15.2C shows the Earth's **biomes** (major communities classified according to their predominant vegetation) and gives an indication of their typical biomass. As we can see, the amount of energy located at the level of the primary producers varies substantially from one type of community to the next.

What causes this variation? The variation seen in Figure 15.2A is a function of environmental factors. Tundra has low primary productivity due to the short growing season near the Earth's North Pole. On the other hand, severe water shortage keeps the productivity of deserts low. The open ocean has plenty of light near the surface and mostly benign temperatures, but nutrients such as phosphorus are in short supply, limiting plant growth. Plants and animals on the ocean surface die and settle to the bottom of the ocean, where their decomposition does not immediately return nutrients to the surface. In some parts of the ocean, currents carry water from great depths up to the surface. These upwelling currents (see Module 11.4) are important for supplying the surface waters of the oceans with nutrients.

Given the dependence of higher trophic levels on lower trophic levels, we expect that the biomass of herbivores would be positively correlated with the plant biomass. For freshwater lakes, this predicted relationship is generally obeyed (Figure 15.2A). When the biomass or the number of species in a community is controlled by the amount of primary production, the community is **bottom-up** regulated. Conversely, if species biomass at most trophic levels is controlled by predation, the community is regulated **top-down**. There is nothing that prevents a single community from experiencing both bottom-up and top-down effects.

In lakes, the effects of top-down regulation by predation can be studied by artificially increasing the numbers of fish that feed on lake zooplankton. In Figure 15.2B, we see that increases in fish numbers lead to a decrease in zooplankton biomass and an increase in plant biomass. Because many zooplankton species feed on plants, reductions in their numbers benefit plants. ❖

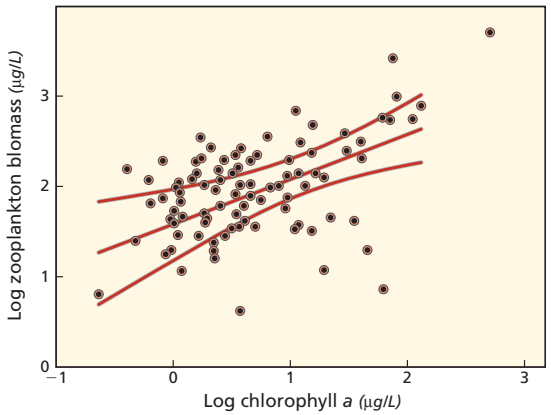

FIGURE 15.2A Biomass of Herbivores (zooplankton) versus Biomass of Plants (chlorophyll *a*) from Several Different Freshwater Lakes

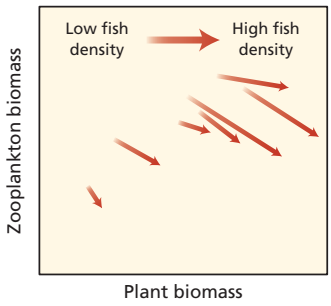

FIGURE 15.2B Changes in Zooplankton and Plant Biomass Following Manipulation of Fish Numbers The arrows show how zooplankton and plant biomass changes in going from low to high fish numbers.

Tropical Rainforest

Swamp and Marsh

Boreal Forest

Temperate Grassland

Tundra and Alpine

Desert

Open Ocean

Lakes and Streams

FIGURE 15.2C Primary Productivity in Major Biomes (grams per square meter per year)

15.3 The efficiency of energy transfer from one trophic level to the next varies among communities

What happens to the energy that is captured by primary producers? Some of the energy that is present in the plants is transferred to the next higher trophic level by herbivory and thus the conversion of plant biomass into herbivore biomass. This process continues up the energetic pyramid, as herbivores are eaten by carnivores, and so on.

Insights into community processes can be gained by analyzing such energy flows from one trophic level to the next. No chemical or physical process of energy conversion can be 100 percent efficient. Energy is lost in a variety of ways. In Figure 15.3A, we show how energy is lost as it flows from lower trophic levels to higher trophic levels.

The green arrows in Figure 15.3A represent the energy that successfully makes it from one stage to the next. The red arrows represent the energy that is lost in these transfers. At each of these steps, we can compute the efficiency of energy transfer if we know how much energy from one stage makes it into the next stage. In our example, a fox feeds on birds. Not all birds will be captured and eaten by the foxes, so not all the energy present in the bird trophic level can be converted to fox biomass, for this reason alone. The efficiency of this part of the energy transfer is called the **exploitation efficiency**.

Once a bird is eaten, the fox must convert the energy of its prey to energy it can use. Plants and animals consist in part of materials, such as cellulose and bone, that contain energy but cannot be digested and assimilated by most of the consumers that eat them. Thus, only a portion of the total energy devoured is chemically assimilated. The fraction of consumed energy that is assimilated is referred to as the **assimilation efficiency**.

Some of this assimilated energy will be used for work and maintenance. The rest will be used for growth and reproduction, adding to the energy level of the foxes. The fraction of the assimilated energy that is made into new biomass by foxes determines the **net production efficiency**.

The efficiency of the entire process of energy transfer between trophic levels is called the **ecological efficiency**. Ecological efficiency is the energy content of the higher trophic level divided by the energy content of the lower trophic level, as Figure 15.3A shows.

Energetic efficiencies vary across communities, depending on the lifestyles of the organisms that make up these communities. Figure 15.3B shows the net production and assimilation efficiencies of three categories of organisms. There is no general pattern of assimilation efficiency, with ectotherms and endotherms showing a mixture of high and low values. But the net production efficiency of ectotherms is consistently higher than that of the endotherms. This makes sense, because endotherms must spend a larger fraction of their energy budget maintaining their body temperature and thus have less energy to devote to growth.

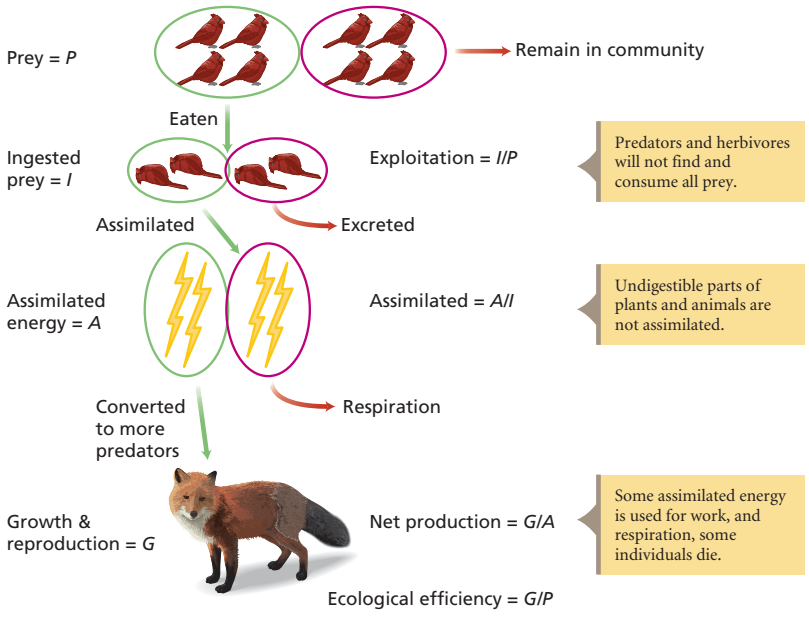

FIGURE 15.3A This figure shows the flow of energy from one trophic level (prey) to a second (predator). The amount of energy is represented by symbols in the leftmost column. The fraction of energy that passes through each step in this process is called efficiency and is shown in the middle column.

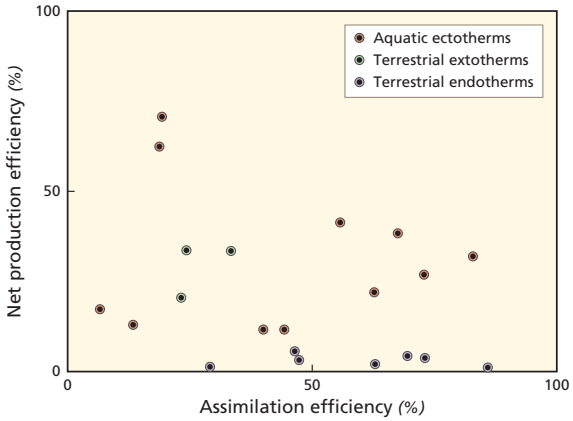

FIGURE 15.3B **Net Productivity Efficiency versus Assimilation Efficiency of Several Groups of Animals**

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Equilibrium and Nonequilibrium Communities

15.4 Community stability can be disrupted by sudden changes in the physical environment

What Is an Equilibrium? Populations in **ecological equilibrium** maintain relatively constant numbers of individuals, and if displaced from these numbers, will return back to their equilibrium levels. Density-dependent population growth is a mechanism that can help maintain equilibrium, as we saw in Chapter 10. Communities of competing species may also achieve equilibrium.

One concept of a community in equilibrium is much like the concept of an evolutionary equilibrium of species numbers, maintained by extinction and speciation, introduced in Chapter 6. The metaphor used there was of water dripping into a plugged sink from a faucet, counterbalanced by water dripping over the side of the sink. At an equilibrium population level, some factors tend to increase population size, while others tend to decrease it. If an equilibrium is stable, any change in the numbers of one or more species will be followed by a return to population sizes from before the perturbation. When the community ecology maintains equilibrium, the number of species in a community depends on the strength of competition between close competitors and the food-chain structure. Populations of all species reach a stable equilibrium size in a stable community.

FIGURE 15.4A Mount St. Helens, Washington, during Its Most Recent Eruption

A different view of community structure is that it does not produce equilibrium. **Nonequilibrium** theory proposes that natural disturbances prevent populations from reaching an equilibrium. Unfortunately, it is hard to choose between these alternative theories. Just to determine if natural populations are at a stable equilibrium or not is time consuming. One must get accurate census data from populations over many generations. Even then, a community may maintain roughly constant population densities only because of a lack of perturbations. This would be like the "stability" of a tall boulder that would roll or fall over if it were pushed, but has not yet been pushed.

Population Disturbance Populations can be prevented from reaching an equilibrium due to environmental disturbances. These disturbances can come in many forms: storms, fires, drought, floods, even volcanoes. The disturbance may cause relatively small changes in the population size or resource levels or, as in the case of the Mount St. Helens volcano (Figures 15.4A through 15.4C), it may wipe out entire communities over large areas. Large disturbances, like the Mount St. Helens volcano, effectively sterilize an area and then open it to the process of succession that we will review in Module 15.7. The community structure during succession is in constant change. Depending on the community, it can take many years for an equilibrium to be reached after disturbance. In some instances, an equilibrium may never be reached before the next major disturbance, or before the habitat and its resources are consumed.

FIGURE 15.4B Area Surrounding Mount St. Helens Immediately After the Volcano Erupted All signs of life are gone, and the ground is covered with ash.

FIGURE 15.4C Destruction of Vegetation Following the Eruption of Mount St. Helens

Other disturbances are less dramatic and may be important determinants of the species diversity in the community. For instance, forest fires have been a regular disturbance in some ecosystems well before humans arrived (Figure 15.4D). As humans began to manage forests, they naturally tried to avoid the destruction of forests by fires, including fires of human origin and those due to natural factors, such as lightning. It was soon realized that the health and composition of some forests actually required occasional fires and that human intervention to stop all fires was ill advised. We will see in Module 15.5 that, for some communities, moderate levels of disturbance can actually increase species diversity compared to communities with no disturbance.

Island Biogeography Islands are very special communities that rely on colonization from distant locations to populate communities with plants and animals. Some of the basic forces determining species diversity on islands were first described more than 30 years ago in a book by Robert MacArthur and Edward Wilson. Their keen insights have proven to be generally accurate and form the core of present-day theory in island biogeography. We will review some of these important ideas in Module 15.6.

Succession We have already introduced the concept of biological succession in Module 15.1. There are several circumstances that create opportunities for biological succession. Organisms die, snakes shed their skin, and large mammals leave substantial amounts of organic matter in their feces. In all these examples, the sudden appearance of organic matter creates a new habitat that can be colonized through a serial replacement of organisms that we call **degradative succession**. Of course this succession process ends once the organic material has been consumed. We will consider this process in detail in this module and examine how this process of succession is used to produce forensic evidence in criminal cases.

FIGURE 15.4D Destruction of Forest from Fire Although fires can be man-made, they are a regular disturbance in many ecosystems.

There are also natural processes that rapidly create unoccupied habitat for colonization and succession. The volcanic eruptions already mentioned are one such example. Glaciers may retreat and expose bare soil. Fires and tree falls may create conditions for succession to begin. These processes are referred to as **autogenic succession**. Unlike degradative succession, autogenic succession usually culminates in a mature community, referred to as the climax community. Oftentimes the species that appear early in the successional process may alter environmental conditions in a way that will permit the later successional species to invade and survive. For instance, when the glaciers in Alaska retreat, the exposed soil is first colonized by mosses and shallow-rooted herbs. A little later, alder plants invade. Both the herbs and alder have the ability to fix nitrogen. In time they will increase the nitrogen content of the soil substantially. Alder also acidifies the soil. The result is that the soil then becomes suitable for larger trees, like Sitka spruce.

In some places there may be a gradual change in the species composition as a result of externally changing physical or chemical conditions. These types of changes are sometimes referred to as **allogenic succession**. An example would be the changes that occur as silt accumulates at the mouth of a river system. This is a gradual process that transforms brackish water to soil. As a result, terrestrial species may gradually colonize this new land and displace species adapted to the brackish water conditions. ❖

15.5 The diversity of species in a community may depend on environmental disturbance

In 1961 the ideas of competitive exclusion (see Chapter 12) presented a problem for G. E. Hutchinson. His work with marine and freshwater plankton demonstrated that many species of phytoplankton can coexist in the same top layers of water. However, in these top waters, several resources, such as nitrogen and phosphorus, were often in limited supply. Why didn't competition drive all but one species of phytoplankton to extinction?

In a paper entitled "The Paradox of the Plankton," Hutchinson suggested an answer. He argued that the competitive relationships among plankton species were specific to a particular set of environmental conditions. If these environmental conditions changed before the superior competitor could achieve numerical dominance, then many species might persist in a locality for some time.

The role of environmental variation in determining species diversity has been important in ecological thought. In the intertidal zone, for example, many plants and animals compete for space. In an undisturbed environment, species diversity will decrease as the competitively dominant species eliminates other species. However, the intertidal zone is subject to disturbance. Waves or storms may turn over rocks. When this happens, some of the plants or animals on these rocks may be displaced or killed. As the graph in Figure 15.5A shows, when disturbance is very low, we have little displacement of species (green line) and high levels of competition (red line). The result is low species diversity, with the competitively dominant species being most numerous. On the other hand, when disturbance levels are high, there is little competition (red line), but species are constantly displaced (green line), so only a few good colonizing species are found on the rocks. Therefore, ecologists expect the highest levels of species diversity on intertidal surfaces with intermediate levels of disturbance. This idea is known as the **intermediate disturbance hypothesis** of species diversity.

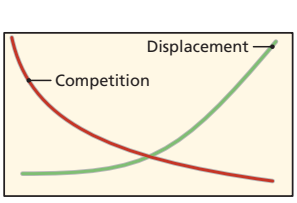

FIGURE 15.5A As environmental disturbance increases, displacement of organisms from rocks increases. However, competition is greatest when there is little disturbance.

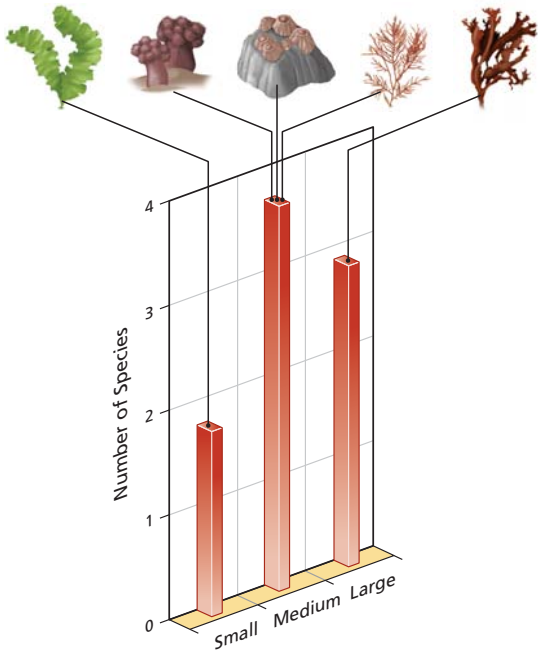

FIGURE 15.5B Small rocks tend to be dominated by the green alga *Ulva*. Large rocks are dominated by the red alga *Gigartina*. The medium-sized rocks have a much larger array of species including *Ulva*, barnacles (*Cthamalus*), sea anemones (*Anthopleura*), and additional species of algae (*Gelidium* and *Rhodoglossum*).

The intermediate disturbance hypothesis was tested in the intertidal zone by Wayne Sousa. Sousa studied the species diversity on intertidal rocks of different sizes. He reasoned that large rocks would be moved only by greater forces, so plants or animals on these rocks would be displaced less often than those on small rocks. The number of species of plants and animals on rocks in three size categories were measured. As Figure 15.5B shows, the most species were found on rocks of intermediate size. Thus, species diversity on intertidal rocks is consistent with the intermediate disturbance hypothesis.

Similar forms of disturbance can be found in other communities. For instance, in forests strong winds or attacks by insects may result in large trees falling (Figure 15.5C). The fallen tree no longer shades the soil surface, and many new plants may find opportunities to grow in these types of open areas. ❖

FIGURE 15.5C A gap in a forest is occupied by new growth. Gaps like this may be caused by mature trees being blown down during storms or falling down after being attacked by insect pests.

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15.6 The number of species on islands represents a balance between extinction and immigration

Biogeographers study the distribution of species. Their point of view is that "islands" may be small parcels of land surrounded by water, or they may be mountain peaks surrounded by valleys. The important requirement is that suitable habitat is surrounded by inhospitable habitat. Plants and animals will occupy the "island" only if they travel from some "mainland" location to the island, or from another island. When a new plant or animal species successfully establishes itself on the "island," we say it has successfully immigrated. The persistence of species on an island requires its successful reproduction and the growth of its population to substantial numbers. In general, the larger the population, the longer its persistence. Eventually all populations go extinct. On an island, the only way for an extinct species to become reestablished is by immigration. Ultimately the number of species on an island will represent a balance between immigrations and extinctions (Figure 15.6A).

What factors affect immigration and extinction? The number of species already on an island is one factor. Rates of successful immigration are high when species numbers on an island are low, for several reasons. When species numbers are low, most newly arrived plants and animals represent species not currently on the island, so there will be fewer competitors. Extinction rates will be low when species numbers are low. The reasons for these low extinction rates are basically the opposite of the reasons for high immigration rates: Few species are at risk of going extinct, because there is little competition.

Rates of extinction and immigration also depend on factors other than species numbers. Immigration rates are affected by proximity to mainland sources of plants and animals. Islands that are near the mainland have higher immigration rates than do more distant islands (Figure 15.6B). Extinction rates should be sensitive to island size. All other things being equal, small islands should support smaller populations of any particular species, making them more vulnerable to extinction (Figure 15.6C).

These theoretical expectations can be put together to make predictions about the relative number of species on islands as a function of their size and distance from mainland. For instance, if the useful habitat of a particular island were substantially reduced, extinction rates should increase. However, immigration rates should remain the same, so the number of species on the island would be expected to fall.

Daniel Simberloff conducted an experiment to test this prediction on mangrove islands. Over a period of three years, species counts were made on these small islands and then portions of the habitat were cleared and removed from the island (Figure 15.6D). In all cases, reductions in habitat area resulted in observable reductions in the numbers of species.

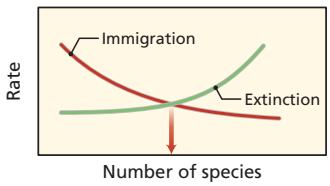

FIGURE 15.6A The number of species on an island will represent the balance between immigration and extinction. The arrow shows this equilibrium.

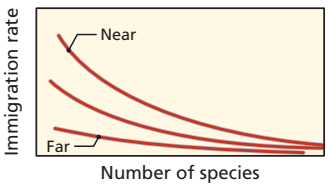

FIGURE 15.6B Immigrants from the mainland are more likely to reach nearby islands than distant islands.

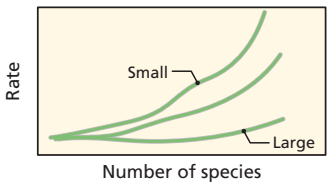

FIGURE 15.6C Extinctions will be less likely in large populations than in small populations. Small islands will generally support smaller populations and thus have higher extinction rates than large islands will.

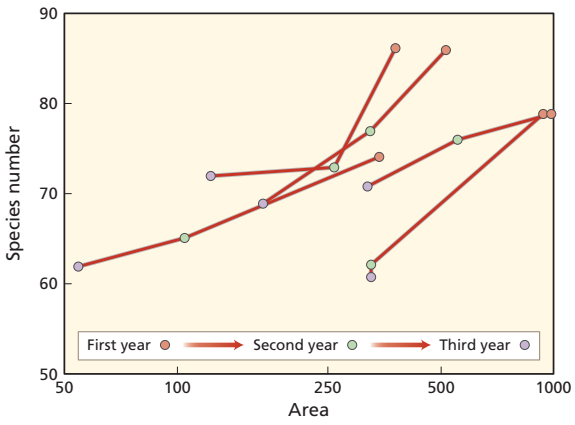

FIGURE 15.6D Changes in Species Numbers on Small Islands Each island was followed for three years. The occupied part of the island was reduced, usually in years two and three. The reduction in island area should be accompanied by increased extinction rates and lower numbers of species on the island. This general expectation was observed in each case.

15.7 Habitats go through predictable changes in species composition over time

Most of us have observed the biological changes that occur when a new piece of habitat becomes available for species to occupy. This can happen when a wooded area is cleared for construction or farming, or when fruit falls to the ground and is then left undisturbed. In each case, we see certain organisms making use of the new resources in these habitats. For instance, cleared land might first be occupied by small weedy plants. If the land is left undisturbed for a sufficiently long time, these weeds are displaced by larger bushes. And after very long periods of time, the species of tree that originally occupied the land takes over as the dominant species.

These transitions in community structure over time are called ecological **succession**. Geologic events such as volcanoes and glaciers may leave areas with no existing vegetation. The development of communities on these sites is called **primary succession**. Other places may already have established vegetation and leave seeds and well-developed soil after a disturbance. The changes in these habitats are called **secondary succession**. The end of succession often yields a community of stable species composition. This community is called a **climax community**. As we mentioned earlier, degradative succession does not produce a climax community, because it ends with the exhaustion of some resource. We consider an application of this successional process next.

The sequences of species that characterize degradative succession depend on the habitat available. These species sequences are sufficiently reliable that they can be used in criminal investigations to determine the time of death of corpses. The field of forensic entomology uses the principle of ecological succession to determine when a dead body began to decompose. As a body decays, the moisture content and pH change in such a way that the types of insect species living on the corpse go through a predictable sequence of changes or succession (Figure 15.7A). Bodies that are found within the first day or so of death can have the time of death estimated by the change in the temperature of the body. However, once a body has reached ambient temperature, other techniques must be used. The identification of the insects on the decaying body is one means of making these estimates. The application of these techniques to forensics was developed by Pierre Mégnin in 1894. There have since been many useful applications of these techniques.

Dr. Buck Ruxton, a London physician, had a stormy relationship with his wife, Isabella. On September 15, 1935, Ruxton's wife and their housekeeper, Mary Rogerson, were seen for the last time. Dr. Ruxton said they had gone on holiday to Scotland. On September 29, the parts of two female bodies were found floating in the River Annon. Fingerprints identified one body as Mary Rogerson. The presence of third instar larvae of the blowfly *Calliphora vicina* (Figure 15.7A) was used to determine that the two

Time	State of Corpse	Insect Fauna
First 3 months	Initially fresh the corpse is subject to bacteria decay and the bloating from gasses. Larval forms of these insects feed on blood and tissues, first focusing on the heart and digestive system	*Calliphora vicina* *Sarcophaga carnaria*
3–6 months	After fermentation of fats corpse continues to dry	*Piophilia casei*
4–8 months	Remaining body fluids are now absorbed	*Ophyra leucostyoma*
1–3 years	The corpse is completely dry	*Derestes lardarius* *Tineola biselliella*

FIGURE 15.7A Forensic Entomology

women had been dead for 12–14 days. Based on this and other evidence, Dr. Ruxton was convicted of murder and executed on May 12, 1936.

Much of the scientific study of insect succession in decaying corpses has been done not with humans, but with other vertebrates such as pigs and dogs. Because it is not clear if the results on these smaller animals would be similar to those on a human corpse, Dr. William Bass has created an experimental site to study this problem (Figure 15.7B). On a three-acre wooded lot near the University of Tennessee campus, he has established an outdoor laboratory known informally as the "Body Farm." At this location, human cadavers have been placed under different conditions to monitor their progressive change over time. Some bodies are embalmed, others not. Some are buried under a carpet of leaves, while others lie on the surface, exposed to the elements. This research will help law enforcement officials determine date of death, often the most important piece of information in determining guilt or innocence in murder cases.

FIGURE 15.7B **The Body Farm at the University of Tennessee**

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COMMUNITY ORGANIZATION

15.8 The diversity of a community may be affected by competition, predation, or primary productivity

We have already seen how the members of a community depend on each other for energy. This dependence structures their ecological relationships. The most obvious pattern is reduced biomass at higher trophic levels.

Communities can also be understood based on the diversity of the species of which they are composed. **Species diversity** is the number and relative abundance of species in a community. Among the factors that shape species diversity are competition and predation, which we reviewed in Chapters 12 and 13. These processes can affect the number of species coexisting on the same trophic level or on different trophic levels.

Interspecific Competition

In Chapter 12, we examined the conditions for the coexistence of competing species. We saw that if intraspecific competition is stronger than interspecific competition, two species can coexist. The most detailed examination of the Lotka-Volterra competition equations (see Module 12.7) was carried out by Vandemeer.

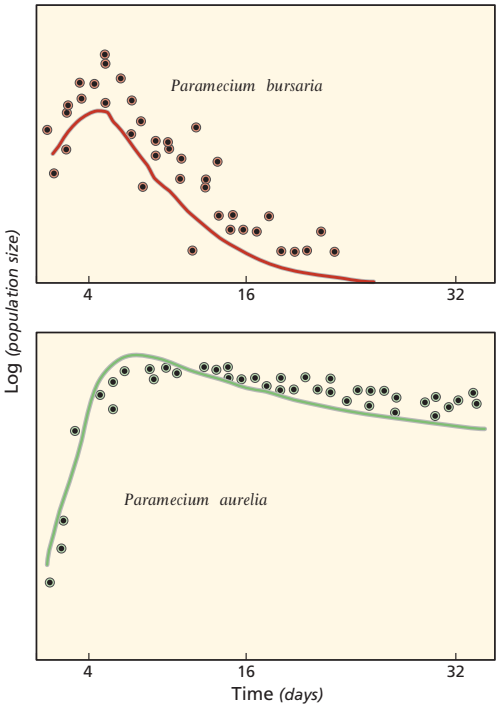


FIGURE 15.8A The numbers of *P. aurelia* and *P. bursaria* when these species are in competition with themselves and *P. caudatum* and *Blepharisma*. Solid lines are the predictions from the Lotka-Volterra equations; circles are the observed numbers.

In his experiment, three species of *Paramecium* and a species of *Blepharisma* were raised separately to estimate their carrying capacity and intrinsic rates of increase, when growing on their own (see Module 10.6). Then pairs of species were raised together to estimate their competition coefficients (see Module 12.7). Finally, all four species were placed together and allowed to grow. Figure 15.8A shows the observed numbers of *P. aurelia* and *P. bursaria*. The population sizes predicted from the Lotka-Volterra equations are also shown as a solid line. The Lotka-Volterra theory not only correctly predicted the extinction of *P. bursaria,* but it also did reasonably well at predicting the actual numbers of *Paramecium*.

Interspecific competitors usually occupy the same trophic level. In some communities, however, an important limiting resource may affect species at several trophic levels. For example, space in the intertidal zone is a limiting resource for species at many different trophic levels, as described in Chapter 7.

Predation

Predation and herbivory involve feeding relationships between species on different trophic levels. However, the ecological factor controlling the numbers of predators or herbivores is not necessarily their food source, as we will see in Module 15.9. For instance, most terrestrial herbivores live in environments with an enormous amount of available plant material. This suggests that the numbers of herbivores in a biological community is not related to the amount of food in any simple way. In 1960 Hairston, Smith, and Slobodkin suggested that it is more likely that the numbers of herbivores are regulated by predators that reduce herbivore numbers well below what can be supported by the primary production. This hypothesis is sometimes called "why the earth is green." It is an example of top-down regulation. However, not all herbivores and predators have this type of top-down regulation. Later in the module, we consider additional possibilities.

Food Webs

Food webs show the feeding relationships between organisms. A species or group of species is represented by a **node** (point) in the food web. A **link** (line) connects two nodes, indicating a predator-prey or plant-herbivore relationship. Links may be either undirected or directed, as Figure 15.8B shows. A **directed link** shows the flow of energy between two species, while an **undirected link** only indicates that a feeding relationship exists (Figure 15.8B). A **cycle** exists when two nodes feed on each other. When two or more species make a closed circuit, this is called a **loop**. A **chain** is a series of directed links starting from a species that feeds on no other species and ending in a species that is not fed on by any other species. The number of links in a chain is called its **length**.

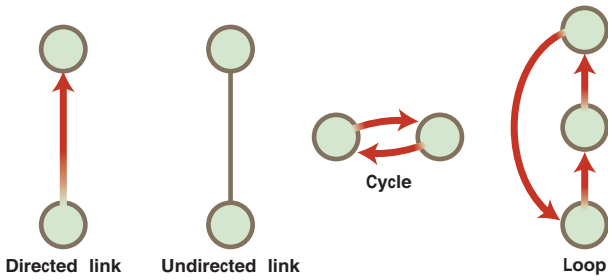


FIGURE 15.8B Components of Food Chains See text for details.

There are several types of food webs. A **source web** arises when a group of species derive all their energy from a single food source. A **sink web** arises when the feeding relationships direct all energy ultimately to a common top carnivore. A **community web** shows the feeding relationships of all members of a community. The mean chain length of a web is the arithmetic average of the lengths of all its component chains.

Understanding the factors that affect the mean chain length of food webs has been an active area of research in ecology. Several hypotheses have been proposed, and we will review evidence for some of them in this module. The **energetic** or **productivity hypothesis** suggests that the mean chain length will be proportional to the amount of energy at the primary producer level. Because energy will be lost with each link in the chain, the total number of links should depend on the amount of energy at the base level.

The **dynamical stability hypothesis** suggests that long chains will be inherently less stable. Thus, longer chains are more likely to be found in benign environments where populations are not subject to large fluctuations in population size.

The **ecosystem-size hypothesis** suggests that chain lengths will be greater in ecosystems with greater physical volume, all other things being equal. This is a complicated theory, but basically a greater number of different species can be supported in larger areas. It happens that average chain length increases with increasing species numbers and thus average chain length also increases with increasing ecosystem size.

15.9 The number of species in a community may depend on predation

Some of the most spectacular examples of the effects of predators involve *biological control.* In Chapter 14 we learned about the explosive growth of rabbits introduced to Australia at the end of the nineteenth century. The introduction of a viral parasite was effective at reducing the numbers of rabbits. A similar example is the aquatic fern, *Salvinia molesta,* that is native to waterways in Brazil. This fern has become a pest in much of the tropics. Its dense populations block waterways and prevent fishing. Effective control has been achieved using a small weevil, *Cyrtobagus singularis.* The adult weevil feeds on the buds of the fern, while the larvae feed on the plant's roots and rhizomes. The specificity of this interaction was demonstrated by the failure of the first control efforts. A weevil from a closely related fern, *Salvinia auriculata,* was tried but failed to control *S. molesta,* even though these two species were thought to be the same for some time.

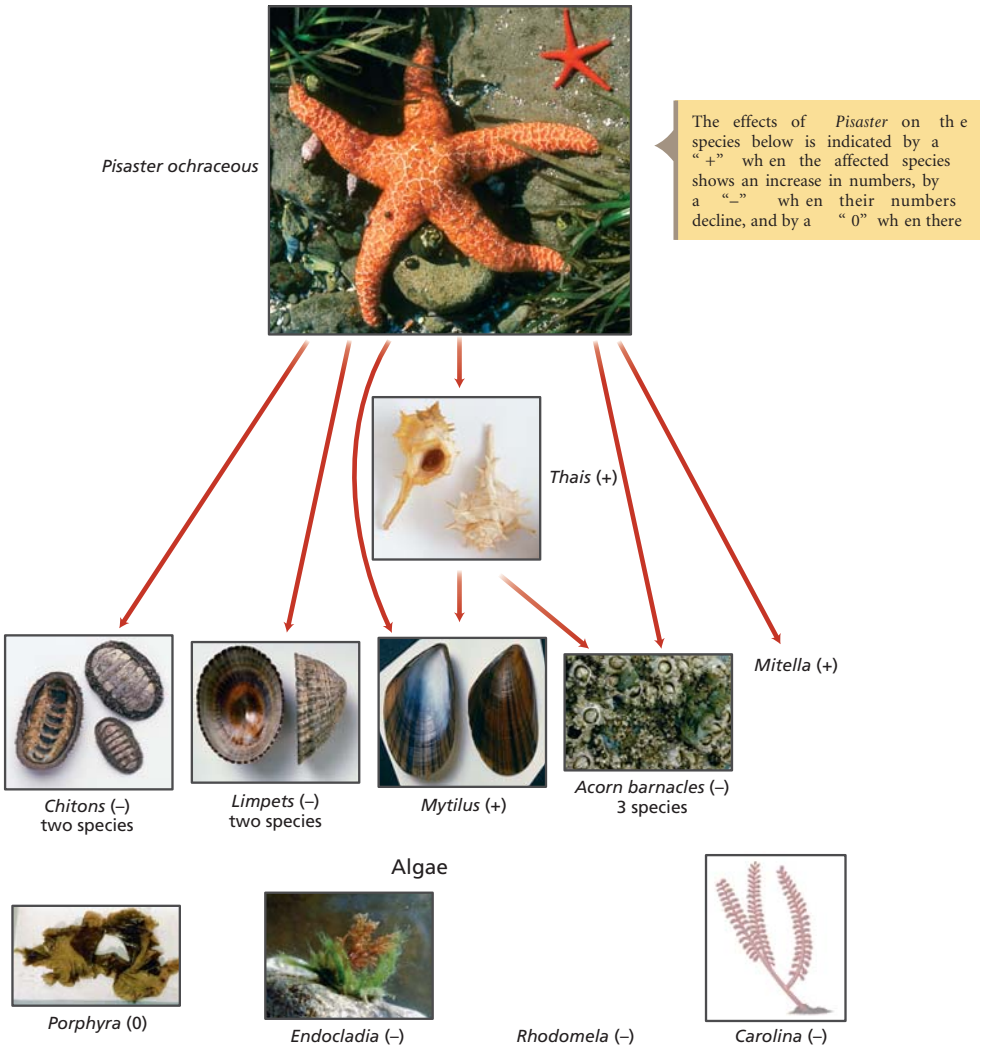


FIGURE 15.9A *Pisaster*, a Keystone Predator in the Intertidal Zone

These examples demonstrate the potential for predation and herbivory to affect the numbers of a prey species, but not the numbers of species. One of the earliest and most influential demonstrations of the importance of predation on species composition was a study by Robert Paine on an intertidal marine invertebrate community. In this study, the ecology of a carnivorous starfish (*Pisaster ochraceous*) was observed at two different research sites. In the experimental site, the starfish was removed and kept out of the area. In the control site, the starfish were allowed to forage as usual. A total of 15 different species were monitored. In the experimental site, the **species richness,** or number of species, dropped from 15 to 8, while in the control area it remained unchanged.

What explains these results? The decline in species numbers in the experimental area was due to increased numbers of the competitively dominant mussel *Mytilus.* Other species of animals and plants were eliminated because the removal of the starfish led to the explosive growth of *Mytilus.* In Figure 15.9B, the species that were negatively affected by the removal of starfish have a negative sign next to their names. A positive sign indicates a benefit to the species due to starfish removal, whereas a 0 indicates no effect. Paine called the starfish a **keystone predator**, because of its central role in maintaining species diversity in this community.

Species numbers in terrestrial communities may also be affected by keystone predators. Wade Worthen studied three species of mushroom-feeding *Drosophila.* These fruit flies serve as food for the predatory rove beetle *Ontholestes cingulatus,* which eats adult *Drosophila*. In the absence of the beetle, there is strong interspecific competition between the three species of *Drosophila,* with *D. tripunctata* often eliminating the other two species. However, when the beetle was added to experimental cultures, the level of competition among *Drosophila* larvae was reduced, and all three species coexisted. As Figure 15.9A shows, beetle predation affected the competitively dominant species *D. tripunctata* most. With fewer *D. tripunctata,* the other two species were able to increase their numbers and so stably coexist.

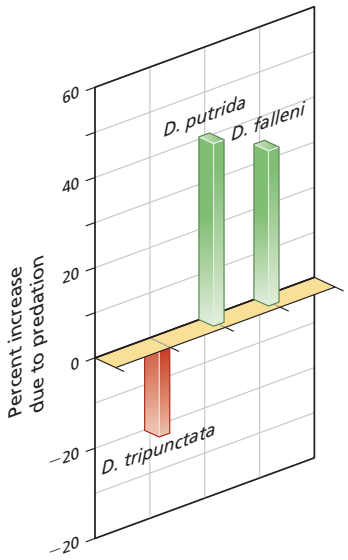


FIGURE 15.9B Effects of a Predatory Beetle on the Composition of a *Drosophila* Community In the absence of the beetle, *D. tripunctata* is competitively superior to *D. putrida* and *D. falleni*, often eliminating them. When the beetle—which feeds on all three species—is added to the community, the numbers of *D. tripunctata* fall and the numbers of the other two species increase. All three species coexist at similar population sizes in the presence of the predator.

15.10 River communities show a top-down structure

The starfish study by Paine demonstrates the potential for predation to shape the diversity of species in the trophic level directly below it. The theory of food webs also predicts that in long food chains the qualitative effects of removing top predators should alternate as one goes down to lower trophic levels. Thus, this theory would predict that in a community with four trophic levels (producers-herbivores-small carnivores-top carnivores) removal of the top predator would have a beneficial effect on the small carnivores. However, once the number of small carnivores increased, that would cause a negative effect on the herbivores. The reduction in herbivore numbers would then have a positive effect on the primary producers. This predicted series of positive and negative effects is sometimes called a **trophic cascade**.

To investigate whether communities showed such cascades, Mary Power undertook a study of a river community (Figure 15.10A). This community also has four trophic levels, as does the example used in the previous paragraph. At the bottom are green algae, *Cladophora* and *Nostoc*. These are consumed by herbivorous insect larvae called chironomids. Chironomids are related to mosquitoes. The chironomids are eaten by predatory insects and juvenile fish, like the stickleback. The rivers that Power studied in northern California also have large fish, steelhead and roach, that feed on the small predators (Figure 15.10A).

Power introduced replicate cages covered with a small mesh that permitted small insects to pass through freely, but not fish. At random, some cages were designated as enclosures and others as exclosures. Each enclosure was stocked with 20 steelhead and 40 roach fish. The exclosures were kept free of large fish. After five weeks, samples were made of all the enclosures to determine the numbers of predators and the biomass of algae. The results were consistent with the predictions of a trophic cascade. The small predators all showed increased numbers in the exclosures relative to the enclosures. However, the next lower level in the food web, chironomids, showed a dramatic decline in the exclosures. This decline of chironomids was accompanied by an increase in algal biomass. Thus, the change in numbers of top carnivores was followed by a series of changes that were alternatively positive and negative at different trophic levels. ❖

Are Aquatic Food Webs Different from Terrestrial Food Webs?

The two examples we have just considered show how strong the effects of top predators in a marine and freshwater community can be. The evidence for such effects in terrestrial communities is less compelling, however. This finding has led some to suggest that there may be a difference between aquatic and terrestrial communities that will naturally give rise to aquatic communities experiencing more top-down regulation. Possible reasons for such differences include the following: (1) Terrestrial food webs are more complex than aquatic food webs. This complexity might make it less likely that the effects of top predators would work their way down to primary producers. Terrestrial plants are also more likely to protect themselves from herbivores by producing toxic secondary chemical compounds. This would also make such plants insensitive to changes in numbers of herbivores. (2) Timescales and turnover rates are faster in aquatic systems. Because the plankton at the top layer of the water column contain many small algae, their growth rates are rapid. This may lead to fundamental differences between terrestrial and aquatic systems, or it may simply make it easier to detect strong food-web interactions in aquatic ecosystems.

However, other scientists have argued that an examination of large numbers of studies, not just a few prominent ones, suggests that terrestrial interactions are not substantially different from aquatic communities. There is a lot of heterogeneity within aquatic and terrestrial communities, making it difficult to reach general conclusions about the average behavior. At this time, more work is needed before these questions can be settled.

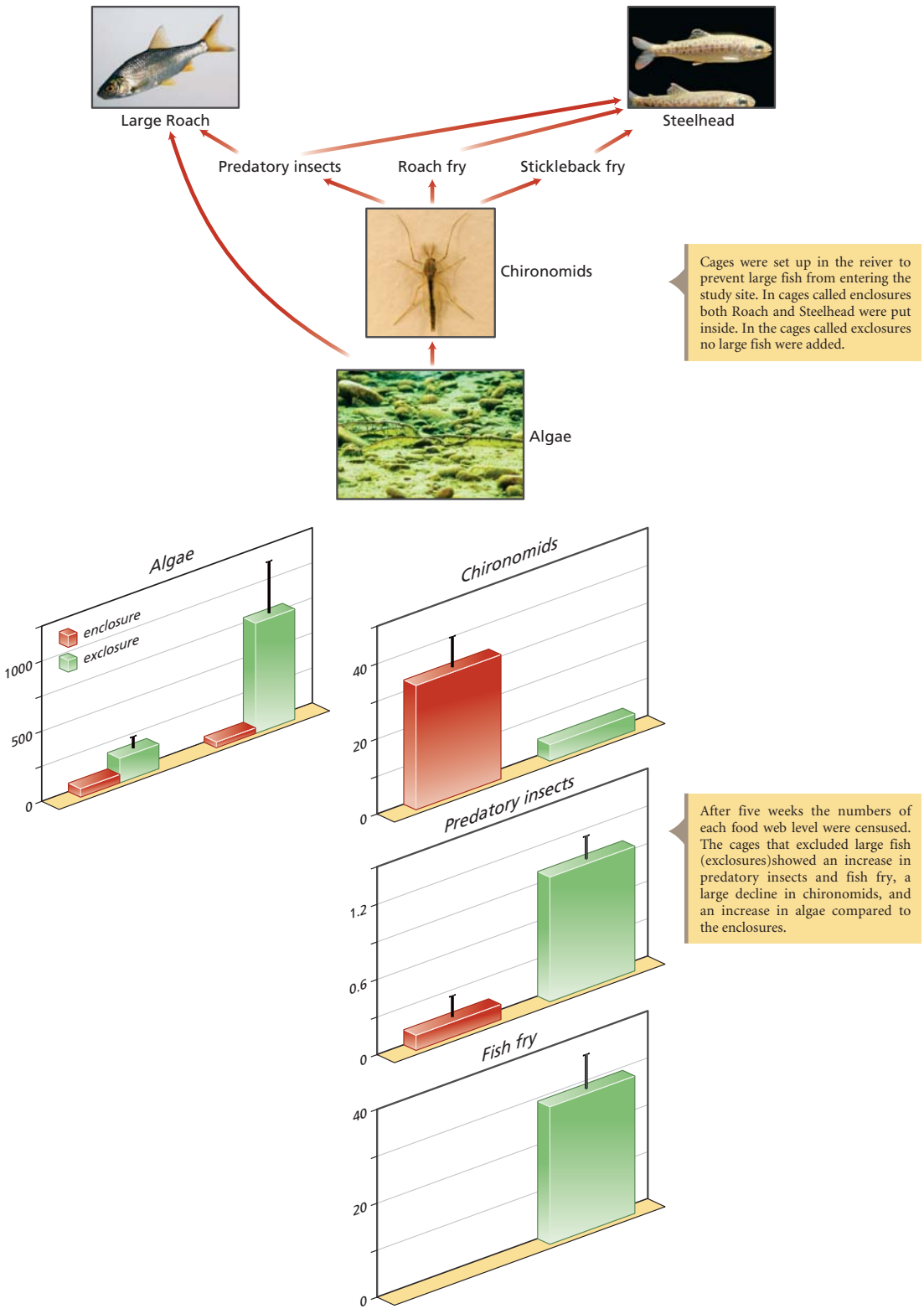


FIGURE 15.10A **Effects of Predation in River Food Webs**

15.11 Many features of food webs can be described by the cascade model

Several theories have been proposed concerning the properties of food webs, such as the mean chain length, maximum chain length, and total number of links. One simple theory, called the cascade model, provides numerical estimates of all these quantities. Before describing this model, let's look at how food web data are summarized.

In Figure 15.11A, the food web for the river community considered earlier is shown. A community food web matrix lists the trophic species that are prey as row entries (bold numbers) and those that act as predators in the column entries (bold numbers). If a 1 appears in the matrix, it indicates that the species in that column feeds on the species of that row. A zero means no feeding relationship exists. Quantitatively this is an easier way to summarize a food web than the pictures that show connections between species. A basal species is one that is prey for one or more species and does not eat any other species. In the food web matrix, a basal species will have a column of zeros under its number. In Figure 15.11A, the algae are the only trophic species meeting this definition. A top species is one that feeds on one or more species but is not itself prey for any other species. A top species should have a row of zeros next to its number in the food web matrix. Both the steelhead and large roach are top species in Figure 15.11A. The diagonal elements in this matrix are the cells where the same-numbered row and column intersect. A 1 at these positions would imply that the species can eat itself. In this food web none of the species are cannibals, because all diagonal elements are zero.

Predators

Prey	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0	1	0	0	0	1	0
2	0	0	1	1	1	0	0
3	0	0	0	0	0	1	1
4	0	0	0	0	0	0	1
5	0	0	0	0	0	0	1
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0

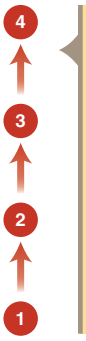
A number 1 in the matrix indicates a feeding relationship that

1. Algae
2. Chironomids
3. Predatory insects
4. Roach fry
5. Stickleback fry
6. Large roach
7. Steelhead

FIGURE 15.11A A Food-Web Matrix

Joel Cohen and Charles Newman have developed a simple model to study the properties of food webs. We review the assumptions of the model in Figure 15.11B. It is assumed that there are no loops or cycles in the food web. So no species are cannibals. This assumption means that all the diagonal elements will be zero and all the elements below the diagonal will also be zero. This also means that the species in the community can be organized as a cascade (see Figure 15.11B). Trophic species may feed on species with lower numbers, but are never fed on by species with lower numbers.

The model then assumes that feeding relationships are created at random and that the chance of any allowable relationship forming is determined by a common probability, p. From this simple formulation, the model predicts with some accuracy the mean chain length in many different communities (see Figure 15.11B). This may seem surprising, because community food webs are not put

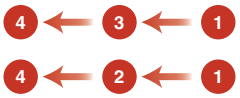


The trophic species within a community are assumed to form as a cascade. That is, species are ordered so that those with the highest number can feed on any species below them; however, a trophic species cannot feed on a species above them.

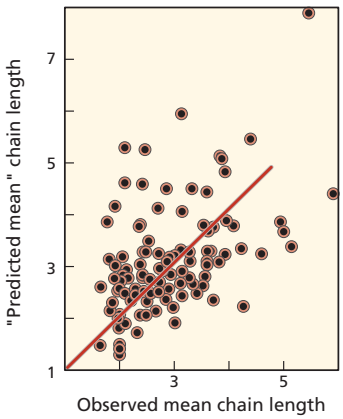
In the figure on the left the arrows indicate the direction of energy flow. Trophic species 3 can potentially feed on species 2 and 1, but not on species 4.

The properties of food webs are studied by assuming that they are constructed at random. Thus, using the rules in the paragraphs above, the chance that any pair of trophic species will form a feeding relationship is a constant, p. This

Consider a community with the four trophic species illustrated above. All possible food chains having two links with species 1 as the basal species and species 4 as th top species are shown below.



Because each of these food webs has two links, the probability of each forming would be p^2.



The cascade model can be used to predict the mean chain length of a food web. The figure on the right shows the predicted mean length versus the observed length for 113 different community food webs. The solid line indicates prec ise agreement between the predictions and the observations.

FIGURE 15.11B The Cascade Model of Food Webs

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together at random. The ability of the cascade model to do such a good job of predicting mean chain length suggests that while food webs are not created randomly, the details of how they are created are not needed to make accurate theoretical predictions.

This is not unusual in science. It is possible to create a detailed theory of the kinetics of a coin placed in motion by the flip of our finger. We could take into account the forces that our finger generates and the atmospheric conditions—particularly the presence of wind—as well as the position at which the coin is typically caught, and then predict how often we should get a head or tails. If we do this calculation correctly, we would see that the coin will come up heads about 50 percent of the time. Or we can, and often do, use a simple statistical model to predict the chances of getting heads without worrying about all the details of the forces that affect the trajectory of coins. One such model is simply heads half the time, tails the rest.

One interesting result from the theoretical cascade model is that the mean chain length increases slowly with total number of species in the food web. This result can be combined with the theory of island biogeography to arrive at a prediction about the mean chain length and size of the habitat. From the theory of island biogeography, we know that the rate of extinction decreases with island size. If all other variables remain constant, then the equilibrium number of species should increase on larger islands. This result, in combination with the conclusions that mean chain length increases with species numbers, suggests that mean chain length increases as community size or volume increases. ❖

15.12 Food-web chain length is proportional to ecosystem size in lakes

In the last module we noted that the cascade model and the theory of island biogeography predict increasing chain length in larger communities. To test this idea requires samples from many communities that vary in size. There would also have to be some way to rapidly collect information on the mean chain length of each community. David Post and his colleagues (2000) have been able to collect this sort of information for lake ecosystems. They also collected information on the productivity so that they could simultaneously compare mean food-chain length to productivity.

If mean chain length depends only on ecosystem size, we would expect the data collected by Post to look something like Figure 15.12A. Mean chain length would increase with the size of the ecosystem independently of the productivity. Likewise, ecosystems that varied in productivity would show no consistent trend in mean chain length. So what did the results look like?

In Figure 15.12B, we summarize the results of Post's study. Ecosystem size was estimated from the volume of the lake, which is fairly easy to do. The lakes studied were in the northeastern United States. In these lakes, primary productivity is limited by the amount of available phosphorus. Levels of total phosphorus (TP) are highly correlated with the primary productivity and may be used as an estimate of primary productivity. A detailed study of the feeding relationships of the entire community of each lake would take an enormous amount of time. To estimate the mean chain length of each lake, an ingenious method that utilizes radioisotopes of nitrogen was used (Figure 15.12C). This technique is objective and allows information to be collected on a large number of communities.

When the data are analyzed, we can see that there is a very strong positive relationship between ecosystem size and mean chain length (see Figure 15.12B). This relationship holds for

The ecosystem size hypothesis predicts that the food-chain length of a community will increase with increasing ecosystem size, no matter what the productivity.

If productivity was unimportant, then there should be no change in food-chain length with increasing productivity, no mater how large the ecosystem.

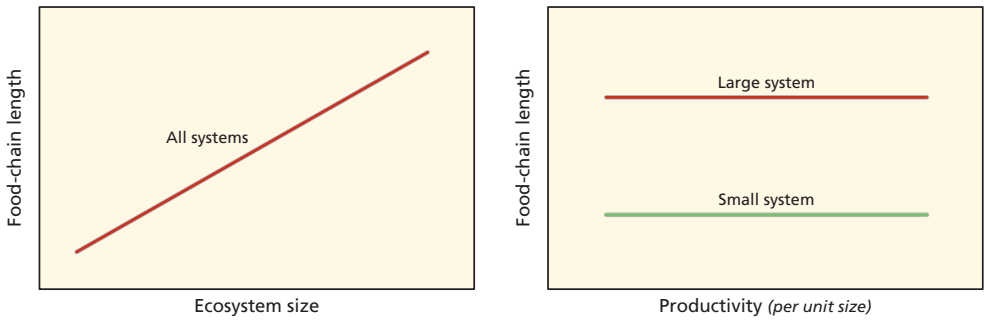

FIGURE 15.12A Ecosystem Size and Food-Chain Length

The mean chain length was estimated by the stable isotope technique (Figure 15.12C) in several lakes that varied in size and productivity.
The mean chain length increases in direct porportion to size, no matter what the productivity of the lake is.

For these same lakes examined above, there was no consistent relationship between mean chain length and productivity.

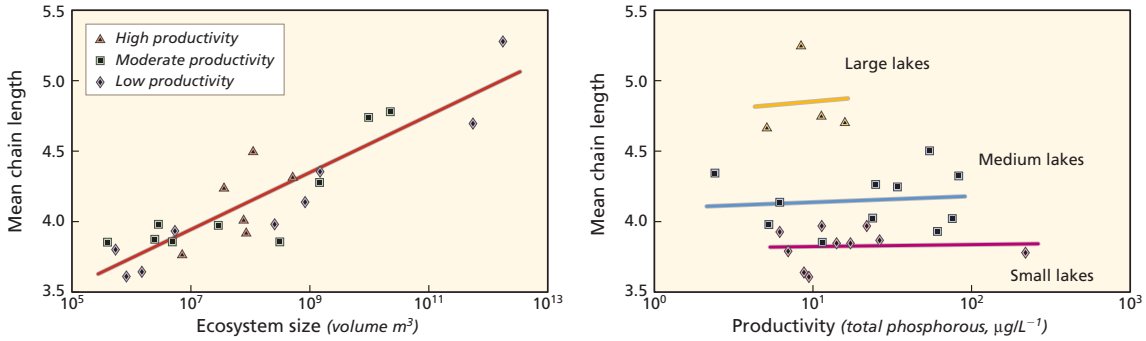

FIGURE 15.12B Tests of the Ecosystem Size Hypothesis

lakes that varied in productivity. On the other hand, there is either no relationship or a very weak relationship between productivity and mean chain length. These observations provide strong empirical support for the importance of ecosystem size in the structure of food webs.

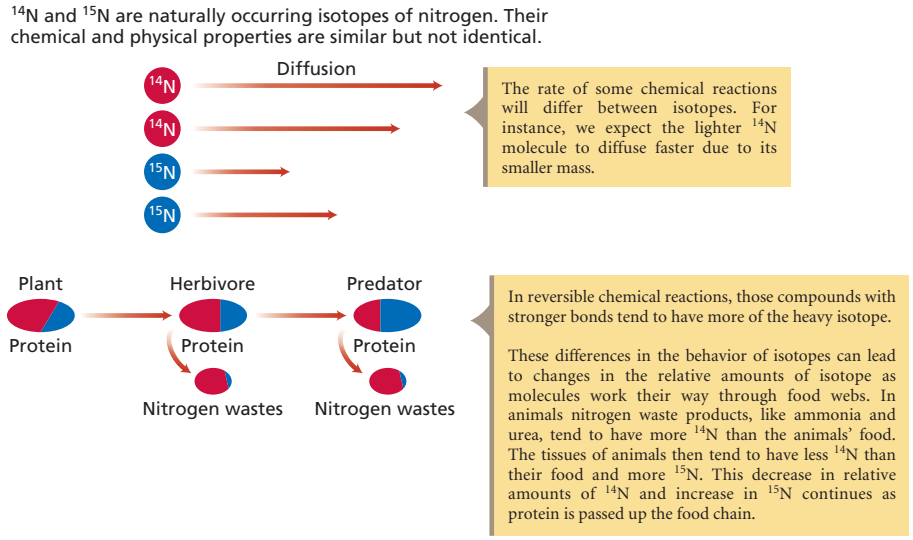

FIGURE 15.12C Radioisotope Measurement of Food-Chain Length

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15.13 Increased productivity can increase food-chain length but decrease stability

In this chapter, we have already seen evidence that increases in primary productivity lead to increases in the biomass of herbivores. This observation leads naturally to the hypothesis that increases in primary productivity might also lead to increases in the biomass of predators that feed on herbivores, and so on. Furthermore, it is conceivable that the total number of trophic levels—that is, food-chain length—might respond to changes in primary productivity.

This idea has been investigated experimentally by Jenkins and his colleagues (1992). They studied communities of bacteria and insects that live in treeholes in the Australian tropics. These communities can be found in a variety of plants that collect water, like bromeliads (Figure 15.13A). Decaying leaves and animals provide the primary energy supply to these communities. Jenkins was able to replicate these communities artificially by placing plastic containers under trees. Each container initially started with some water and decaying leaves. The amount of decaying leaves was varied over three levels: high, medium, and low. The numbers of species and their feeding relationships were determined at regular intervals over a 48-week period. Figure 15.13B shows the results. As the levels of primary energy to the community were increased, the food-web structure became more complex. That is, there were more species in the community and more trophic links. On average, the maximum food-chain length was greatest at the highest productivity. Thus, this study supports the idea that food-chain length is positively correlated with primary productivity.

FIGURE 15.13A The leaves and central tank of the bromeliad support a community of bacteria and insects.

Are there other factors that might limit the length of food chains? Is it reasonable to suppose that food chains will become longer and longer as primary productivity is increased? One problem that must be

considered is the stability of long food chains. If small changes in the numbers of primary producers cause large changes in the numbers of top carnivores, then even modest variation may cause top predators to go extinct.

Lawler and Morin (1993) examined the stability of small communities of protists (Figure 15.13C). In the simplest community there were two species, a bacteria and a bacterivore (bacteria-eating) protist, *Colpidium*. In this simple community, *Colpidium* rapidly reaches its carrying capacity and then changes little in population size over time (panel I). When an additional *Actinosphaerium* carnivore is added, *Colpidium* persists, but its numbers fluctuate (panel II). In a second community with bacteria, *Colpidium*, and the omnivore *Blepharisma*, the numbers of *Colpidium* fluctuate wildly (panel III), and in one replicate the *Colpidium* population goes extinct (panel IV).

Together these two studies show that food-chain length may depend on both primary productivity and the ecological stability of top carnivores. Increasing primary productivity may increase food-chain length up to a point. Very high levels of primary productivity may not result in longer food chains due to the extinction of top carnivores.

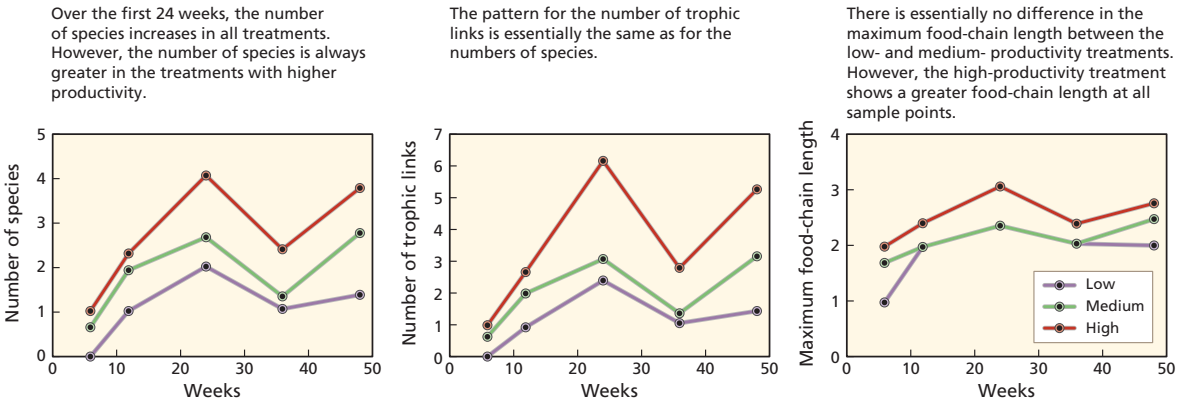


FIGURE 15.13B Community Structure as a Function of Primary Productivity

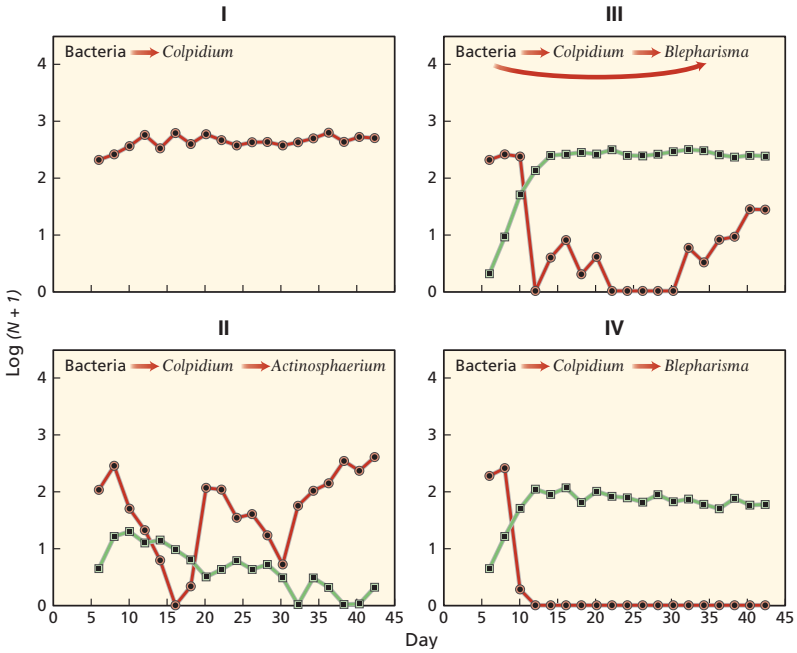


FIGURE 15.13C The Numbers of *Colpidium* (squares) Over Time In each panel, the food chain of the introduced species is shown. Panel I—a two-species community. II—three species, two links. III and IV—the same three species are shown in both these panels but in different replicate cultures. In III, *Colpidium* persists but fluctuates wildly. In IV, *Colpidium* goes extinct by day 12.

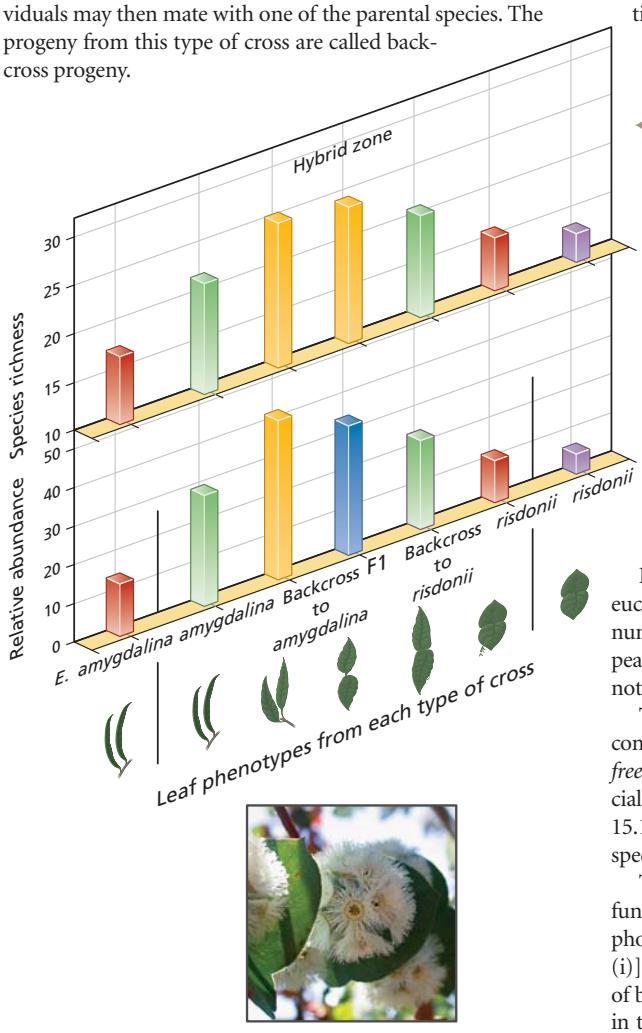
15.14 The structure of communities is also affected by the genetic structure of its members

We have already seen that many predator-prey and host-parasite relationships can be species specific. It is not unreasonable to think that some interactions may even depend on the genotypes within a population. Certainly, for some parasites we have already considered the idea that some genotypes may be susceptible to parasites while others are resistant. Although most species consist of many genotypes, plants possess the ability to generate large levels of genetic variability in a small area by hybridization with other species. It is not unusual to find closely related species of plants that can form viable hybrids. In fact, 30 to 80 percent of all plant species may arise through hybridization.

The areas where different species meet and form hybrids is called a hybrid zone. The progeny that result from the cross of two different species are called the F_1 generation. The F_1 individuals may then mate with one of the parental species. The progeny from this type of cross are called backcross progeny.

In Australia, two different species of eucalyptus trees (*E. amygdalina* and *E. risdonii*) hybridize. These hybrids have very different leaf morphologies than those seen in either parent (Figure 15.14A), and different physiology. These trees harbor a number of insect and fungal species. Thomas Whitham and his colleagues have examined the insect and fungal communities of each parental species of eucalyptus and of trees found in the hybrid zone. They measured the species richness of these insect and fungal communities, which is a measure of the number of different species and their relative abundance. In general for a community, the more species there are and the more even their distribution, the greater that community's species richness will be.

This study revealed that the species richness and relative abundance of insects and fungi was much greater in the hybrid community than in either of the parental eucalyptus populations (see Figure 15.14A). This effect is seen in natural populations as well as in controlled conditions. These observations show that the genetic structure of an important member of a community can have a profound effect on the species composition.



Two species of Eucalyptus (*E. amygdalina, E.risdonii*) intermate and form hybrids in parts of Australia. In these hybrid zones the characteristics of the plants range from mostly *amygdalina* to mostly *risdonii*, and the F_1 hybrids have intermediate traits.
The species richness and relative abundance of 40 different insect and fungal taxa increase dramatically in comparing the parental strands of Eucalyptus to those consisting of mostly hybrids (F_1s). A backcross is a cross between a hybrid and one of the parental species.
The bars of the same color have statistically the same values of either species richness or relative abundance.

FIGURE 15.14A Biodiversity in a Eucalyptus Hybrid Zone

It is not entirely clear what is causing this effect among the eucalyptus populations. However, these plants produce a large number of oils that deter attacks by insects. The hybrids appear to make intermediate levels of these oils. Thus, they may not have sufficient levels of chemical protection from insects.

These findings are not peculiar to eucalyptus. Cottonwood communities in Utah also form hybrids between *Populus freemontii* and *P. angustifolia.* The bud gall mite appears to specialize on the F_1 hybrids of these two cottonwoods [Figure 15.14B, part (i)]. It is almost never found on the parental species or even on backcrosses.

The effects of these hybrids are not limited to insects and fungi. The hybrid cottonwoods also have a very different morphology than either of these parents [see Figure 15.14B, part (i)]. These hybrids are apparently more attractive to a variety of bird species and, as a result, many more bird nests are found in the hybrid zone than in either of the parental populations [Figure 15.14B, part (ii)]. ❖

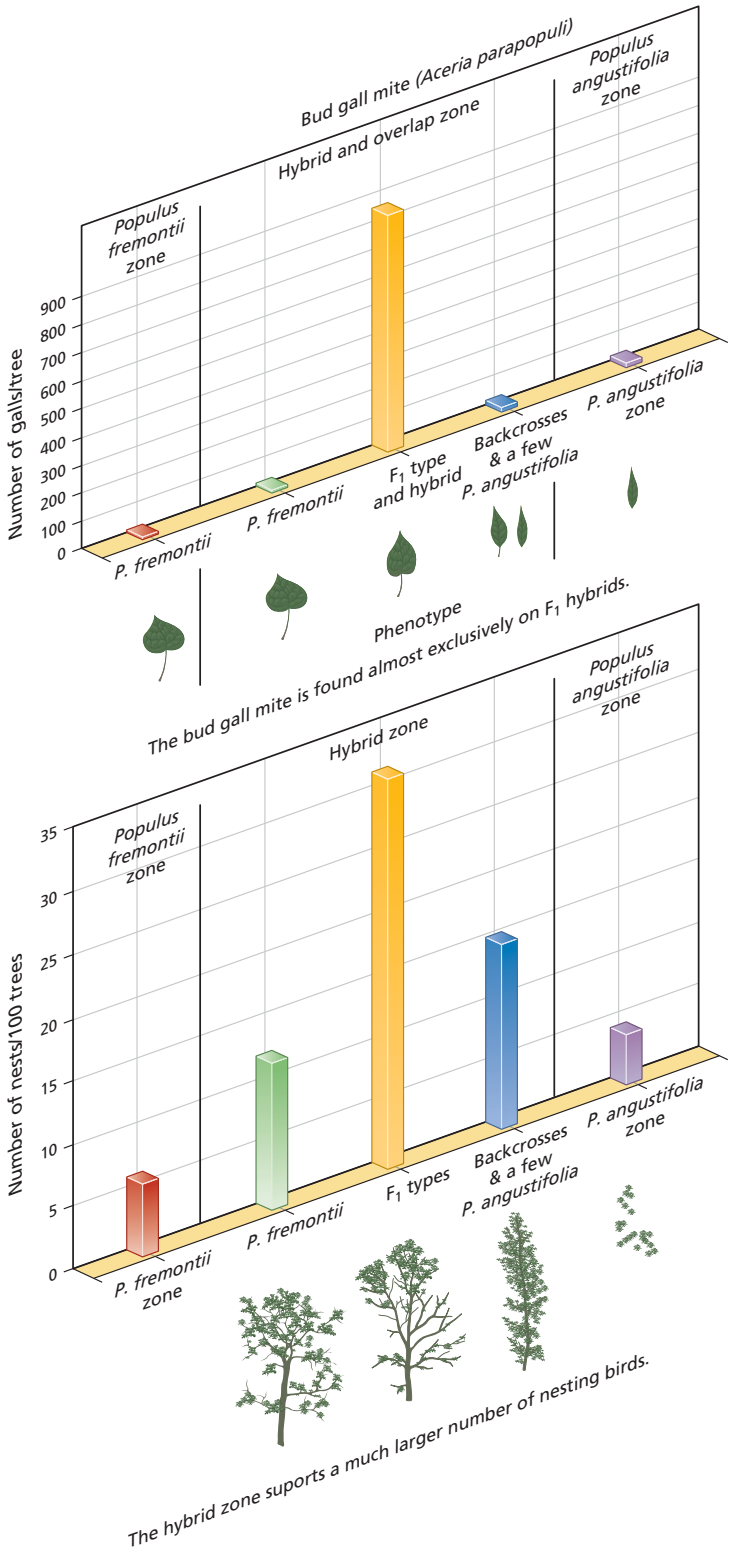


FIGURE 15.14B ***Populus*** **Hybrid Zones**

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ECOSYSTEMS

15.15 An important feature of ecosystems and their biological communities is their interaction with the physical environment

Life on Earth is almost entirely sustained by energy from the sun. Plants form the essential link between the sun's energy and the energy that is used by virtually all biological life. The Earth is an open system with respect to energy. Energy comes from outside the boundaries of the Earth and its immediate atmosphere (Figure 15.15A).

One consequence of this dependence on the sun is that certain thermodynamic laws that apply specifically to closed systems are violated, because the Earth is an open system for energy. In closed thermodynamic systems, entropy (or disorder) should always increase. However, on Earth the organization of chemical elements into living organisms represents a decrease in entropy. This decrease in entropy is possible only because of the flow of energy into the Earth from the sun.

FIGURE 15.15A
The Earth is an open system for energy, but it is a closed system for nutrients essential to life.

Nutrient Cycles Life depends on other components in addition to energy. All organisms are composed of various essential elements, such as carbon, nitrogen, sulfur, phosphorus, and others. In addition to these essential elements, all life requires water. We will collectively refer to these required substances as **essential nutrients**. Because the Earth gets no significant amount of these nutrients from outside its boundaries, the Earth is a closed system with respect to these essential nutrients.

Does life use up these nutrients? Is it possible that we will run out of these essential nutrients just like we may one day run out of fossil fuels? The basic answer is no, because life on Earth recycles these essential nutrients between living organisms and nonliving components of the Earth such as the atmosphere and oceans. These cycles of nutrients are called **biogeochemical cycles**, since they depend on both living and nonliving components. We will review three important biogeochemical cycles in Module 15.16.

Large pools of nutrients reside in reservoirs on Earth. For nutrients that have a gaseous stage in their cycle, such as water, nitrogen, and oxygen, the atmosphere and oceans serve as important reservoirs. For nutrients with sedimentary cycles, such as phosphorus, rocks and soil serve as the main reservoirs.

The movement of nutrients from one component of the biogeochemical cycle to another is called **flux**. The flux is measured in the amount of nutrient per unit of time. The parts of the cycle with large fluxes are key to understanding the dynamics of the nutrient. These parts of the cycle, if perturbed, would be expected to have the greatest impact on the availability of the nutrient.

Ecosystem Function Understanding ecosystems requires that we understand the interaction be-tween biological communities and the physical environment. Indeed, it is impossible to understand some processes completely without looking at the interaction of the environment and organisms. Many biogeochemical cycles have important biological components. The cycling of nutrients such as nitrogen depends critically on the ability of microorganisms to carry out important chemical reactions. Physical processes such as weather also depend on the activities of living organisms. Plants and animals have played an important role in the cycling of CO_2 in the atmosphere. However, over the last century humans have significantly increased atmospheric CO_2 through the burning of fossil fuels. This rise in CO_2 is continuing to this day (Figure 15.15B).

As we will see in Chapter 16, CO_2 plays an important role in the global climate, along with water vapor and nitrous oxide. A significant amount of heat energy that would otherwise radiate from the Earth back into space is captured by these molecules,

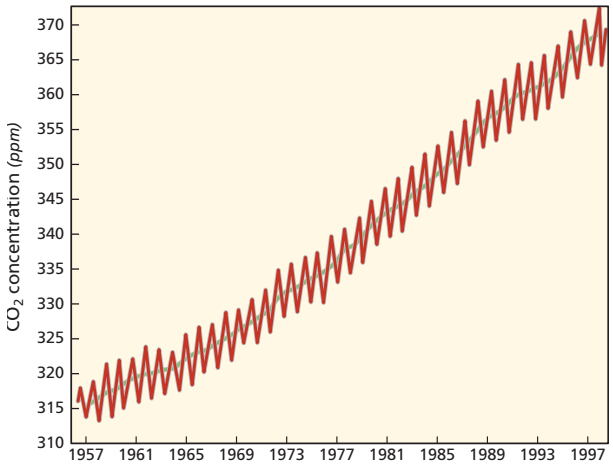

FIGURE 15.15B Change in Atmospheric CO_2 Concentration
These measurements, made in Hawaii, show a steady increase in the levels of CO_2 over a 20-year period. Within a single year there are also small rises in CO_2 concentrations during the winter months. This change corresponds to the decline in CO_2 uptake by plants during the dormant winter months.

keeping the Earth warm through the **greenhouse effect**. This effect refers to the action of our atmosphere that lets visible and ultraviolet light through to the Earth's surface but absorbs much of the heat energy that the Earth radiates back to the atmosphere. There is currently concern that human production of CO_2 may be leading to increases in global temperature. There may also be a positive feedback loop between temperature and atmospheric levels of CO_2. In the remaining modules we will consider evidence that elevated temperatures may accelerate the decomposition of soil carbon and its release into the atmosphere. If these changes were to continue, local climates could change in a significant fashion.

Atmospheric CO_2 levels also change as Earth's ecosystems change. In Module 15.18, we will see that changes in the diversity of biological communities may also affect a community's ability to take up CO_2. Thus, preservation of species diversity may ultimately be critical to preserving the physical environment on which all life depends.

15.16 Essential nutrients are recycled through biological systems

Here we review the cycles of three important nutrients: water (Figure 15.16A), carbon (Figure 15.16B) and nitrogen (Figure 15.16C). In the hydrologic cycle, the largest reservoir of water is the Earth's oceans. The oceans are also the components with greatest flux of water, through evaporation and rainfall, as the numbers in Figure 15.16A show. On land, water is lost by evaporation from the Earth and from plants and animals. This flux is called **evapotranspiration**.

The Earth's atmosphere is composed of 78 percent nitrogen, 21 percent oxygen, and only 0.03 percent carbon dioxide along with other trace gases. Nevertheless all plants depend on atmospheric CO_2 for the carbon used in photosynthesis (Figure 15.16B). In the oceans, carbon dioxide is dissolved in water, where it exists as carbonate ion (HCO_3^-). The carbon fixed by plants either stays in the plant or is consumed by animals. Ultimately, both plants and animals die, and then they decompose through the action of microorganisms. Much of the carbon content then returns to the atmosphere after decomposition.

Some of the carbon in dead organisms, however, is lost to the cycle in sediments. Most of these sediments have very low carbon concentrations, but occasionally there are high concentrations of carbon in fossil fuel deposits. Before the advent of human civilization, these reservoirs contributed little to atmospheric CO_2 concentrations. However, over the last 100 years these reservoirs have been returned to the carbon cycle through human burning of fossil fuels. Although this burning also consumes atmospheric oxygen, the net change in atmospheric oxygen levels has been very small, while the CO_2 levels in the atmosphere have significantly increased over the last 100 years.

The nitrogen cycle is more complicated than the other two (Figure 15.16C). This cycle depends critically on the action of numerous microorganisms that convert nitrogen from one form to another. Composed of 78 percent nitrogen, the atmosphere represents a tremendous reservoir of nitrogen; but relatively few organisms are able to take atmospheric nitrogen (N_2) and convert it to a biologically useful form. This conversion is accomplished for plants by nitrogen-fixing bacteria that live in the soil or in close association with the roots of certain plants. Both aerobic bacteria such as *Azotobacter* and anaerobic bacteria such as *Clostridium* fix nitrogen. Animals get their nitrogen from the consumption of plant or animal proteins. As plants or animals die, their proteins and amino acids are converted to ammonium ions by microorganisms that derive energy from this process. Ammonium can be taken up by plants for their nitrogen needs, or it can be oxidized to nitrate by a process known as **nitrification**. The first step in nitrification is the conversion of ammonia to nitrite (NO_2^-) by the bacteria *Nitrosomonas*. Nitrite is then oxidized to nitrate (NO_3^-) by another group of bacteria, the *Nitrobacter*. Nitrate can then be taken up by plants or returned to the atmosphere as nitrogen (N_2) by the process of **denitrification**. This last process is carried out by bacteria of the genus *Pseudomonas*. ❖

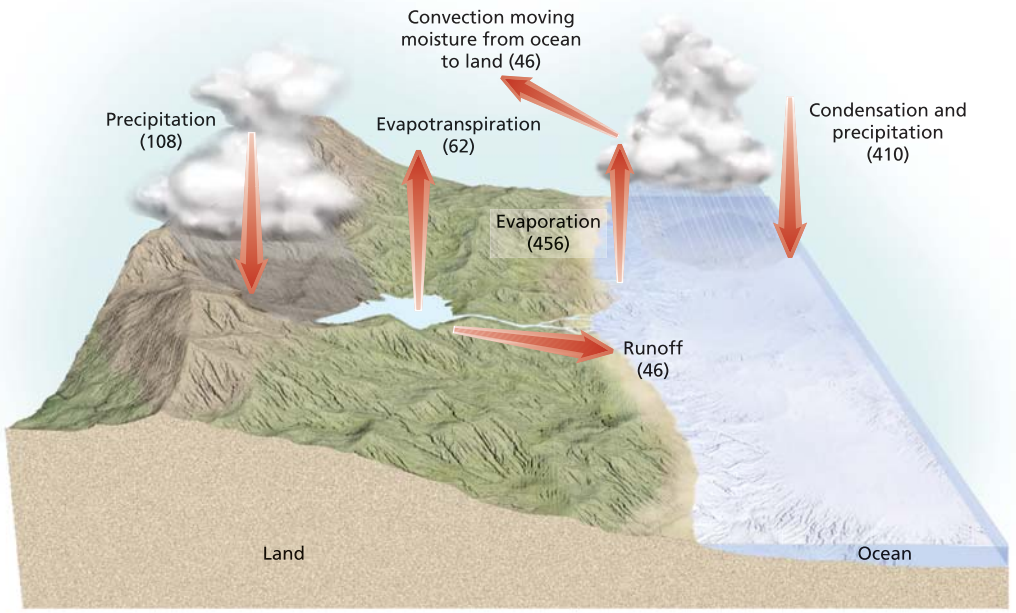

FIGURE 15.16A The Hydrologic Cycle All numbers are in units 1000 km^3/yr.

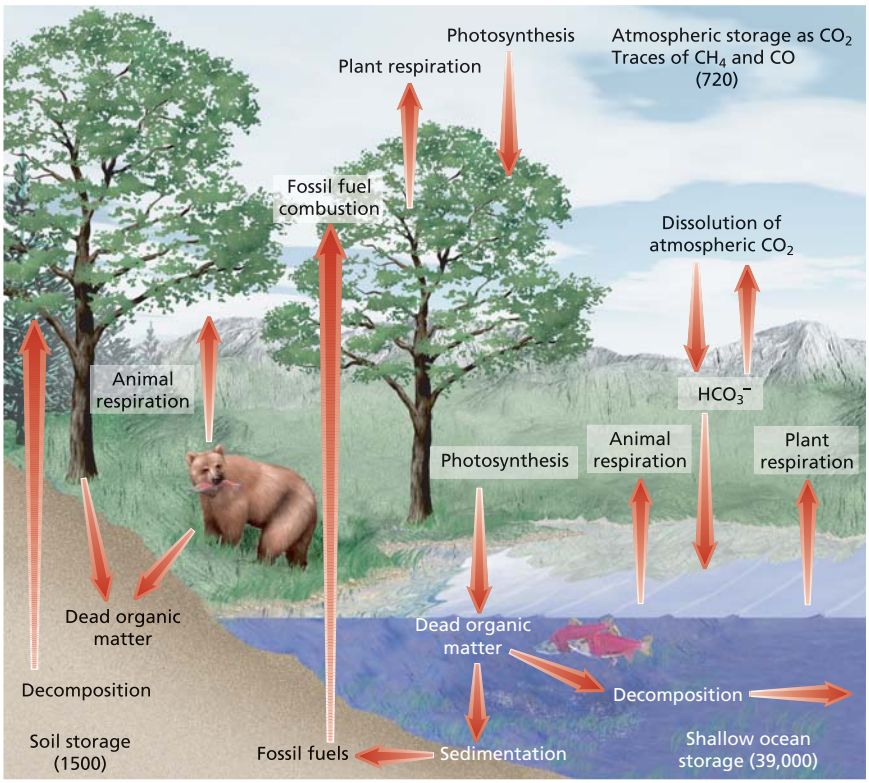

FIGURE 15.16B The Carbon Cycle Storage units are in billions of metric tons of carbon.

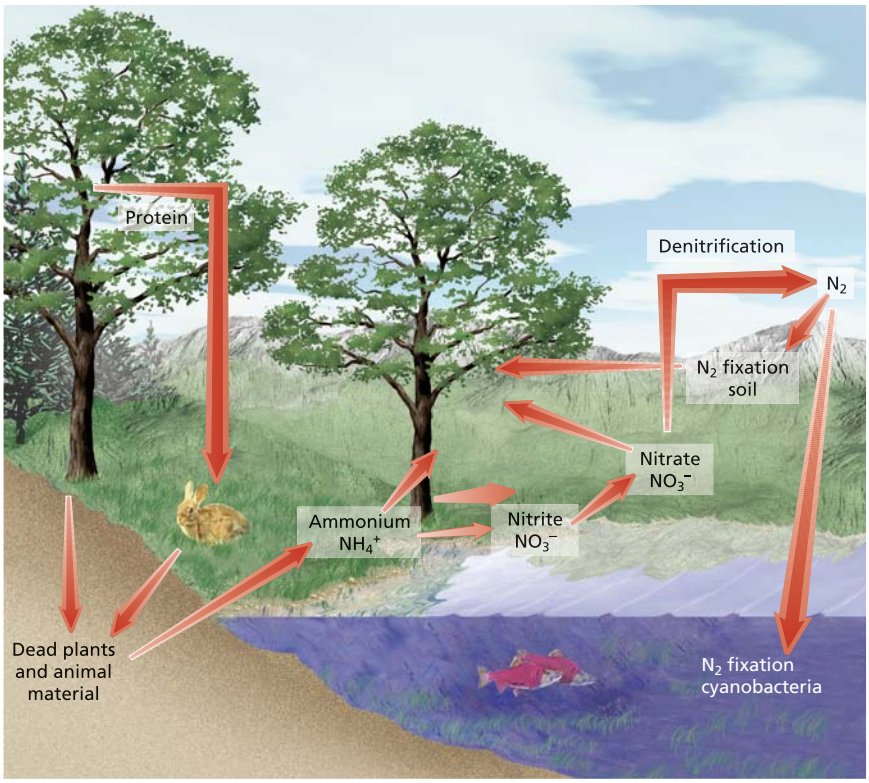

FIGURE 15.16C The Nitrogen Cycle

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15.17 Soil carbon levels are affected by temperature

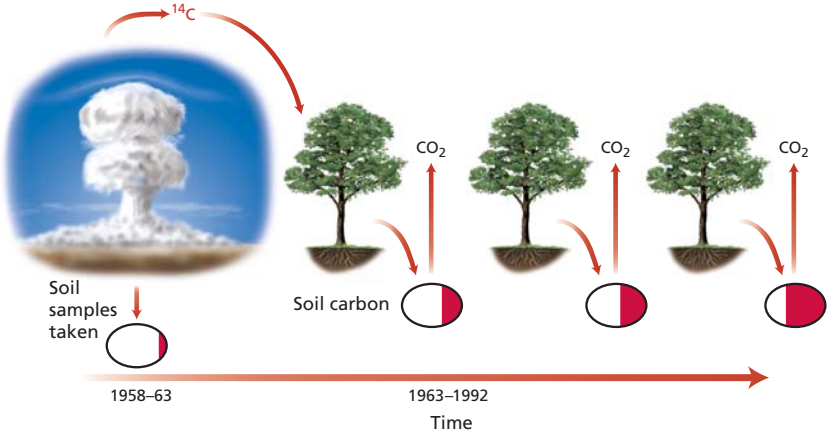
The levels of atmospheric carbon dioxide are important for their greenhouse effects. The amount of carbon that is stored in soils is two to three times greater than the amounts in the atmosphere. Much of this carbon is in the form of soil organic matter. Because soil organic matter can be decomposed and its carbon released as CO_2, it is a potentially important dynamic source of atmospheric carbon dioxide.

Factors that affect the decomposition of organic matter may also affect the levels of atmospheric carbon. One obvious factor is temperature. Because the metabolic rates of decomposing organisms will increase with increasing temperature, the rates at which soil organic matter is recycled into the atmosphere may also depend on temperature.

In an odd twist of fate, nuclear testing in the western United States has provided an opportunity to explore the important ecological relationship between temperature and soil carbon levels. Nuclear testing between 1958 and 1963 roughly doubled the levels of carbon-14 near the Sierra Nevada mountain range. About the same time, soil samples from the Sierra Nevada were taken and stored as archive samples for later testing.

After 1963, the organic matter in the soils of the Sierria Neveda would be expected to start showing elevated levels of carbon-14 as this isotope became incorporated into plants, and these plants died or shed leaves into the soil (Figure 15.17A). Of course the relative amounts of carbon-14 in the organic matter of the soil would depend on how fast the old organic matter was decomposing and moving out of the soil carbon reservoir.

The Sierra Nevada range is also an interesting study site because the mean annual temperature declines steadily and substantially as one moves from the base of the range to the summits. Using soil samples taken in 1992, Susan Trumbore and her colleagues were able to compare these soils to the archive samples. From these comparisons, the rates of turnover of soil carbon could be estimated at many different elevations



After nuclear testing, the levels of ^{14}C from these tests will increase in the soil carbon at a rate that depends on the rate of carbon turnover in the soil. The red indicates the level of soil carbon-14 at different times. This increase can be documented by coparing soil samples in the 1990s with those taken in the period of 1958–1963.

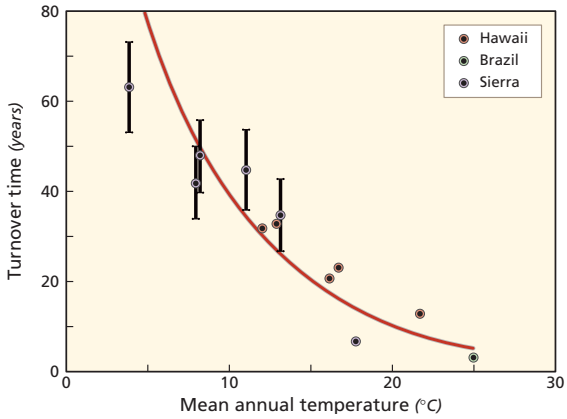


FIGURE 15.17A Soil Carbon Levels and Temperature

(temperatures). Their study showed dramatically that soil carbon turnover is much higher at higher temperatures (see Figure 15.17A). These findings suggest that global warming will increase atmospheric carbon dioxide levels still further.

Based on their studies, Trumbore and colleagues estimated the effects of a 0.5°C increase in temperature on carbon levels in various ecosystems (Figure 15.17B). The effects are greatest in the tropics. In just a single year, all forests would release nearly 1.4×10^{15} grams of carbon, which is nearly 25 percent of the amount released by all fossil fuel consumption in a year. These findings show the complicated dependence of global nutrient cycles on many factors.

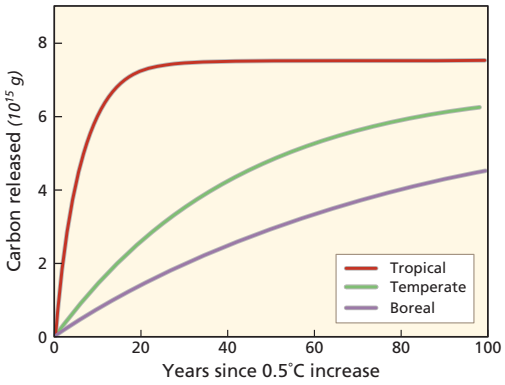


FIGURE 15.17B Global Warming and Carbon Release

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15.18 Species diversity affects ecosystem performance

We have just seen how ecosystems function to recycle essential nutrients. Does the ability to recycle nutrients depend on properties of the community? Many have suggested that species diversity may have multiple effects on ecosystems, including increased productivity and lower loss of nutrients.

This problem has been examined by Shahid Naeem and colleagues with replicated artificial communities. A large environmental chamber called the *ecotron* was used to create replicate communities with four trophic levels and different numbers of species (Figure 15.18A). The high-diversity community had 31 species, while the low-diversity community had 9 species. These communities were followed for a total of 206 days.

As the plants in each community grew, researchers recorded the fraction of surface area covered by them. The largest changes in percentage of cover were observed in the more diverse community (see Figure 15.18A). This result is not an unavoidable consequence of having more plant species. However, in the more diverse communities, the available space was filled more densely than in the low-diversity communities.

The net consumption of CO_2 was used as a measure of overall photosynthetic rates. These rates were also higher in diverse communities (Figure 15.18B). Given these results, it is perhaps not surprising that the primary productivity was also greater in the high-diversity communities (Figure 15.18C). One possible explanation for these results is that the diverse communities of plants include species that vary in height and leaf shape. This variety may result in the community more effectively making use of the available energy from sunlight.

More diverse communities also reduce available nitrates to lower levels (Figure 15.18D). This means that less nitrogen is leached from the soil. Ultimately this would have a positive effect on sustaining nutrient cycling and soil fertility.

An important implication of these studies is that reductions in species diversity might have a negative impact on ecosystem function. Consequently, we have additional reasons for being concerned about the loss of species due to human activity. The ecosystems that humans rely on for recycling the nutrients that we need may be impaired by the loss of species.

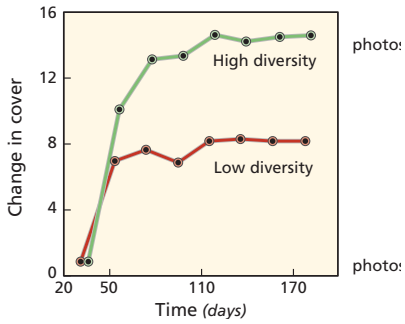

FIGURE 15.18A Replicate communities with either 9 (low diversity) or 31 (high diversity) species were followed over time. In the more diverse communities, there was greater plant coverage of the soil surface.

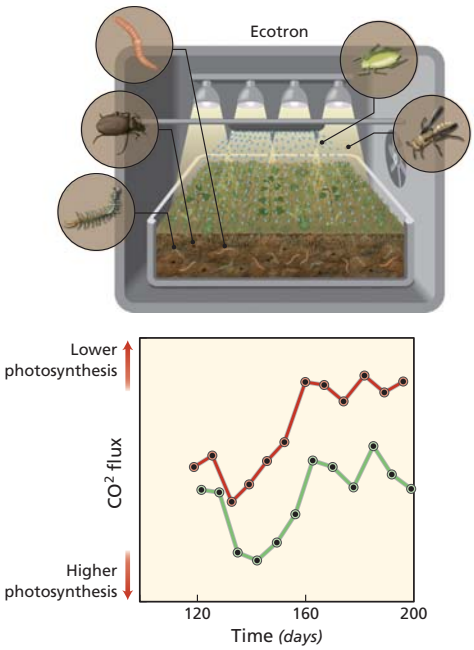

FIGURE 15.18B Overall rates of photosynthesis were also greater in the more diverse communities.

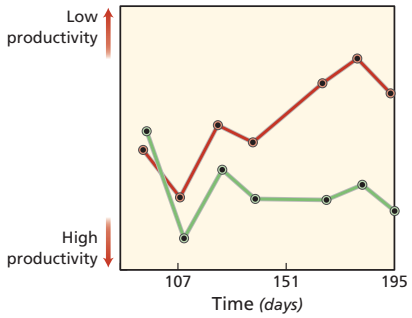

FIGURE 15.18C The amount of plant material (productivity) was greatest in the more diverse communities

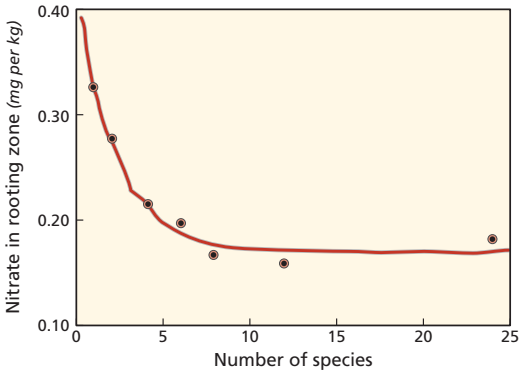

FIGURE 15.18D Diversity vs. Nitrate Concentration

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SUMMARY

1. Ecological communities are bound to follow the other laws of science, including the law of thermodynamics.
   - **a.** Because energy cannot be created or destroyed, important insights about communities can be gained by following the transfer of energy from one trophic level to the next.
   - **b.** This transfer of energy is not very efficient, although some communities do better than others.
2. Communities in change are quite common.
   - **a.** Some of the earliest ecological work was motivated by the process of ecological succession.
   - **b.** There is enough regularity in the succession process that it has been used to date the time of death of decaying human bodies.
3. The number of species and the number of trophic levels in a community depend on many factors.
   - **a.** Predators may prevent a superior competitor from eliminating less-effective competitors.
   - **b.** Occasional environmental disturbances can also have a similar effect.
   - **c.** The numbers of species in a community may also have positive effects on the functioning of the entire ecosystem.
4. The cascade model predicts many features of real food webs while making few assumptions.
   - **a.** This model can also be used in conjunction with the theory of island biogeography to predict that the average chain length in food webs will increase with ecosystem size.
   - **b.** Lake communities show increases in food-chain length with ecosystem size.
5. Ecosystems perform many functions that are essential for all life on Earth.
   - **a.** The recycling of important nutrients is one of these functions.
   - **b.** Atmospheric gases like carbon dioxide are produced by ecosystems, and these in turn have effects on global climates.
   - **c.** Ecosystem function appears to be improved by increasing species diversity.

REVIEW QUESTIONS

1. Why does Figure 15.1B support the conclusion that lake communities are top-down regulated?
2. For each of the following terms, explain how energy is lost, making the measure of efficiency less than 100 percent: (i) exploitation efficiency, (ii) assimilation efficiency, (iii) net production efficiency.
3. What did G. E. Hutchinson find paradoxical about plankton communities? How did he explain this paradox?
4. Would you expect the equilibrium number of species on an island far from the mainland to be greater, smaller, or equal to the number on a nearby island? Draw a graph to show how you reached your conclusion.
5. What is a trophic cascade? Are the results in Figure 15.1B consistent with a trophic cascade?
6. In this food-web matrix, indicate which species are primary producers, herbivores, and top carnivores:

	1	**2**	**3**	**4**
1	0	0	1	0
2	0	0	1	0
3	0	0	0	1
4	0	0	0	0

7. Review the roles of different species of bacteria in the nitrogen cycle.

KEY TERMS

allogenic succession
assimilation efficiency
autogenic succession
biogeochemical cycles
biomass
biome
bottom-up regulation
climax community
community
community web
degradative succession
denitrification
directed link
dynamical stability hypothesis
ecological efficiency
ecological equilibrium
ecosystem
ecosystem-size hypothesis
essential nutrients
evapotranspiration
exploitation efficiency
flux
food chains
food web
food-web chain
food-web cycle
food-web length
food-web link
food-web loop
greenhouse effect
intermediate disturbance hypothesis
keystone predator
net production efficiency
nitrification
node
nonequilibrium
primary producers
primary succession
productivity hypothesis
secondary succession
sink web
source web
species diversity
species richness
succession
top-down regulation
trophic cascade
trophic levels
undirected link

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