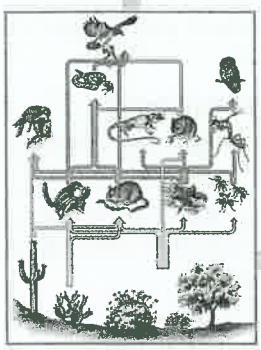
CHAPTER

37

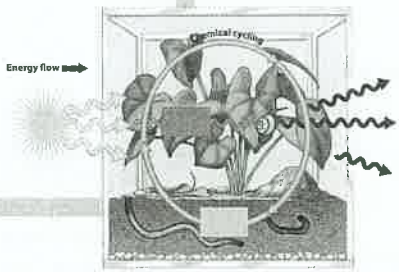
Communities and Ecosystems

BIG IDEAS



Community Structure and Dynamics (37.1–37.13)

Community ecologists examine factors that influence the species composition and distribution of communities and factors that affect community stability.



Ecosystem Structure and Dynamics (37.14–37.23)

Ecosystem ecology emphasizes energy flow and chemical cycling.

As the human population has expanded, we have changed natural ecosystems to serve our needs. Only about a quarter of Earth's land surfaces remain untouched by human alterations, and our activities have also had an enormous impact on aquatic biomes.

What is the value of natural ecosystems? Most people appreciate the direct benefits provided by certain ecosystems. For example, some of the resources we use, including water and food such as fish and shellfish, come from natural or near-natural ecosystems. Many people enjoy outdoor recreation such as hiking or whitewater rafting in pristine ecosystems, while others appreciate nature in less strenuous ways. As the 2010 oil spill in the Gulf of Mexico dramatically demonstrated, some ecosystems have obvious economic value. Billions of dollars were lost by fishing, recreation, and other industries as a result of the disaster.

But human well-being also depends on less obvious services that healthy ecosystems provide. The coastal wetlands affected by the Gulf oil spill normally act as a buffer against hurricanes, reduce the impact of flooding, and filter pollutants. The wetlands also furnish nesting sites for birds and marine turtles, and breeding areas and nurseries for a wide variety of fish and shellfish. Other services provided by natural ecosystems include recycling nutrients, preventing erosion and mudslides, and controlling agricultural pests and pollinating crops.

In this chapter, you'll examine the interactions among organisms and how those relationships determine the features of communities. On a larger scale, you'll explore the dynamics of ecosystems. And throughout the chapter, you'll learn how an understanding of these ecological relationships can help us manage Earth's resources wisely.

Community Structure and Dynamics

37.1 A community includes all the organisms inhabiting a particular area

In the previous chapter, we saw that a population is a group of interacting individuals of a particular species. We now move one step up the hierarchy of nature to the level of the community. A biological **community** is an assemblage of all the populations of organisms living close enough together for potential interaction. Ecologists define the boundaries of the community according to the research questions they want to investigate. For example, one ecologist interested in wetland communities might study the shoreline plants and animals of a particular marsh, while another might investigate only the benthic (bottom-dwelling) microbes.

A community can be described by its species composition. Community ecologists seek to understand how abiotic factors and interactions between populations affect the composition and distribution of communities. For example, a community ecologist might compare the benthic microbes of a marsh located in the temperate zone with those of a tundra marsh.

Community ecologists also investigate community dynamics, the variability or stability in the species composition of a community caused by biotic and abiotic factors. For example, a community ecologist might study changes in the species composition of a wetlands community in Louisiana after a hurricane.

Community ecology is necessary for the conservation of endangered species and the management of wildlife, game, and fisheries. It is vital for controlling diseases, such as malaria, bird flu, and Lyme disease, that are carried by animals. Community ecology also has applications in agriculture, where people attempt to control the species composition of communities they have established.

? What is the relationship between a community and a population?

A community is a group of populations that interact with each other.

37.2 Interspecific interactions are fundamental to community structure

In Chapters 35 and 36, we discussed interactions between members of the same species. Organisms also engage in **interspecific interactions**—relationships with individuals of other species in the community—that greatly affect population structure and dynamics. In **Table 37.2**, interspecific interactions are classified according to the effect on the populations concerned, which may be helpful (+) or harmful (−).

Recall from Module 36.5 that members of a population may compete for limited resources such as food or space. **Interspecific competition** occurs when populations of two different species compete for the same limited resource. For example, desert plants compete for water, while plants in a tropical rain forest compete for light. Squirrels and black bears are among the animals that feed on acorns in a temperate broadleaf forest in autumn. When acorn production is low, the nut is a limited resource for which squirrels and bears compete. In general, the effect of interspecific competition is negative for both populations (−/−). However, it may be far more harmful for one population than the other. Interspecific competition is responsible for some of the disastrous effects of introducing non-native species into a community, a topic we will explore further in Module 37.13.

TABLE 37.2 | INTERSPECIFIC INTERACTIONS

Interspecific Interaction	Effect on Species 1	Effect on Species 2	Example
Competition	−	−	Squirrels/ black bears
Mutualism	+	+	Plants/ mycorrhizae
Predation	+	−	Crocodiles/fish
Herbivory	+	−	Caterpillars/ leaves
Parasites and pathogens	+	−	Heartworm/dogs; *Salmonella*/ humans

In **mutualism**, both populations benefit (+/+). Plants and mycorrhizae (see Module 17.14) and herbivores and the cellulose-digesting microbes that inhabit their digestive tracts (see Module 21.13) are examples of mutualism between symbiotic species. Mutualism can also occur between species that are not symbiotic. For example, flowers and their pollinators are mutualists (see Figure 17.12C).

There are three categories of interactions in which one species exploits another species (+/−). In **predation**, one species (the predator) kills and eats another species (the prey). **Herbivory** is consumption of plant parts or algae by an animal. Both plants and animals may be victimized by parasites (see Module 16.13) or pathogens (see Module 16.1). Thus, parasite-host and pathogen-host interactions are also +/−.

In the next several modules, you will learn more about these interspecific interactions and how they affect communities. You will also discover how interspecific interactions can act as powerful agents of natural selection.

? Populations of eastern bluebirds declined after the introduction of non-native house sparrows and European starlings. All three species nest in tree cavities. Suggest how an interspecific interaction could explain the bluebird's decline.

Based on the information given, interspecific competition for nest sites is a plausible explanation.

37.3 Competition may occur when a shared resource is limited

Each species in a community has an **ecological niche**, defined as the sum of its use of the biotic and abiotic resources in its environment. For example, the ecological niche of a small bird called the Virginia's warbler **(Figure 37.3A)** includes its nest sites and nest-building materials, the insects it eats, and climatic conditions such as the amount of precipitation and the temperature and humidity that enable it to survive. In other words, the ecological niche encompasses everything the Virginia's warbler needs for its existence.

▲ Figure 37.3A A Virginia's warbler (*Vermivora virginiae*)

Interspecific competition occurs when the niches of two populations overlap and both populations need a resource that is in short supply. Ecologists can study the effects of competition by removing all the members of one species from a study site. For example, in central Arizona, the niche of the orange-crowned warbler **(Figure 37.3B)** overlaps in some respects with the niche of the Virginia's warbler. When researchers removed either species, the remaining species was significantly more successful in raising their offspring. Thus, interspecific competition has a direct effect on reproductive fitness in these birds.

▲ Figure 37.3B An orange-crowned warbler (*Vermivora celata*)

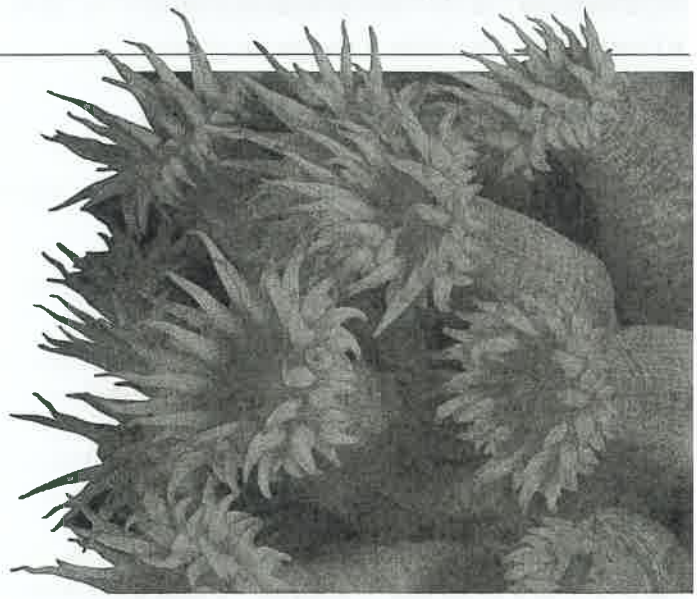
In general, competition lowers the carrying capacity (see Module 36.4) for competing populations because the resources used by one population are not available to the other population. In 1934, Russian ecologist G. F. Gause demonstrated the effects of interspecific competition using three closely related species of ciliates (see Module 16.15): *Paramecium caudatum*, *P. aurelia*, and *P. bursaria*. He first determined the carrying capacity for each species under laboratory conditions. Then he grew cultures of the two species together. In a mixed culture of *P. caudatum* and *P. bursaria*, population sizes stabilized at lower numbers than each achieved in the absence of a competing species—competition lowered the carrying capacity of the environment. On the other hand, in a mixed culture of *P. caudatum* and *P. aurelia*, only *P. aurelia* survived. Gause concluded that the requirements of these two species were so similar that they could not coexist under those conditions; *P. aurelia* outcompeted *P. caudatum* for essential resources.

? Which do you think has more severe effects, competition between members of the same species or competition between members of different species? Explain why.

Competition between members of the same species is more severe because members of the same species have exactly the same niche. Thus, they compete for exactly the same resources.

37.4 Mutualism benefits both partners

Reef-building corals and photosynthetic dinoflagellates (unicellular algae; see Module 16.15) provide a good example of how mutualists benefit from their relationship. As you learned in Module 34.6, coral reefs are constructed by successive generations of colonial coral animals that secrete an external calcium carbonate ($CaCO_3$) skeleton. Deposition of the skeleton must outpace erosion and competition for space from fast-growing seaweeds. Corals could not build and sustain the massive reefs that provide the food, living space, and shelter to support the splendid diversity of the reef community without the millions of dinoflagellates that live in the cells of each coral polyp **(Figure 37.4)**. The sugars that the dinoflagellates produce by photosynthesis provide at least half of the energy used by the coral animals. In return, the dinoflagellates gain a secure shelter that provides access to light. They also use the coral's waste products, including CO_2 and ammonia (NH_3), a valuable source of nitrogen for making proteins. Unicellular algae have similar mutually beneficial relationships with a wide variety of other marine invertebrates, including sponges, flatworms, and molluscs.



▲ Figure 37.4 Coral polyps

? When corals are stressed by environmental conditions, they expel their dinoflagellates in a process called bleaching. How is widespread bleaching likely to affect coral reefs?

Without their dinoflagellate mutualists, corals do not have enough energy to maintain the reef structure. Bleached reefs will die.

EVOLUTION CONNECTION

37.5 Predation leads to diverse adaptations in prey species

+/−

Predation benefits the predator but kills the prey. Because predation has such a negative impact on reproductive success, numerous adaptations for predator avoidance have evolved in prey populations through natural selection.

In Module 18.12, you learned how insect color patterns, including camouflage, provide protection against predators. Camouflage is also common in other animals. As **Figure 37.5A** shows, the gray tree frog (*Hyla arenicolor*), an inhabitant of the southwestern United States, becomes almost invisible on a gray tree trunk.

Other protective devices include mechanical defenses, such as the sharp quills of a porcupine (see Figure 35.9) or the hard shells of clams and oysters. Chemical defenses are also widespread. Animals with effective chemical defenses usually have bright color patterns, often yellow, orange, or red in combination with black. Predators learn to associate these color patterns with undesirable consequences, such as noxious taste or a painful sting, and avoid potential prey with similar markings. The vivid orange and black pattern of monarch butterflies **(Figure 37.5B)** warns potential predators of a nasty taste. Monarchs acquire and store the unpalatable chemicals during the larval stage, when the caterpillars feed on milkweed plants.

? **Explain why predation is a powerful factor in the adaptive evolution of prey species.**

The prey that avoid being eaten will most likely survive and reproduce, passing alleles for antipredator adaptations on to their offspring.

▲ **Figure 37.5A** Camouflage: a gray tree frog on bark

▲ **Figure 37.5B** Chemical defenses: the monarch butterfly

EVOLUTION CONNECTION

37.6 Herbivory leads to diverse adaptations in plants

+/−

Although herbivory is not usually fatal, a plant whose body parts have been eaten by an animal must expend energy to replace the loss. Consequently, numerous defenses against herbivores have evolved in plants. Thorns and spines are obvious anti-herbivore devices, as anyone who has plucked a rose from a thorny rosebush or brushed against a spiky cactus knows. Chemical toxins are also very common in plants. Like the chemical defenses of animals, toxins in plants tend to be distasteful, and herbivores learn to avoid them. Among such chemical weapons are the poison strychnine, produced by a tropical vine called *Strychnos toxifera*; morphine, from the opium poppy; nicotine, produced by the tobacco plant; mescaline, from peyote cactus; and tannins, from a variety of plant species. A variety of sulfur compounds, including those that give Brussels sprouts and cabbage their distinctive taste, are also toxic to herbivorous insects and mammals such as cattle. (The vegetables we eat are not toxic because the amount of chemicals in them has been reduced by crop breeders.) Some plants even produce chemicals that cause abnormal development in insects that eat them. Chemical companies have taken advantage of the poisonous properties of certain plants to produce the pesticides called pyrethrin and rotenone. Nicotine is also used as an insecticide.

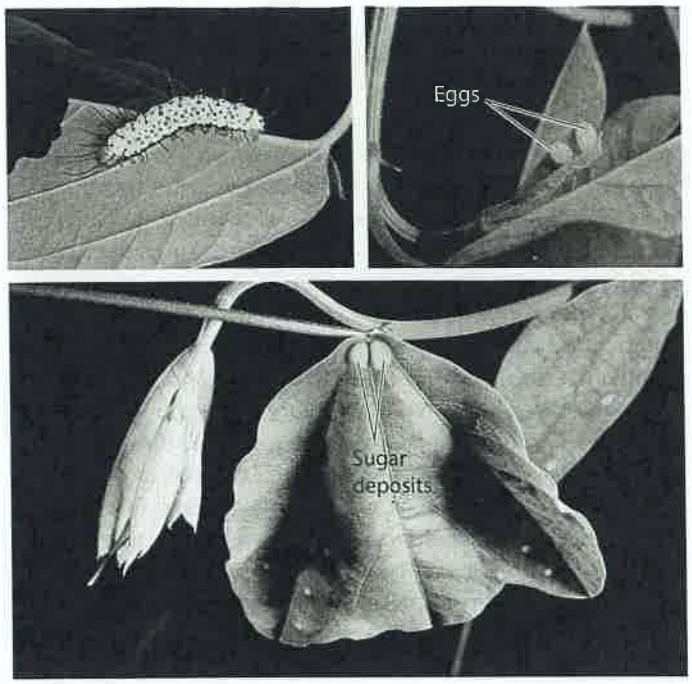
Some herbivore-plant interactions illustrate the concept of **coevolution**, a series of reciprocal evolutionary adaptations in two species. Coevolution occurs when a change in one species acts as a new selective force on another species, and the resulting adaptations of the second species in turn affect the selection of individuals in the first species. **Figure 37.6** (top right of next page) illustrates an example of coevolution between an herbivorous insect (the caterpillar of the butterfly *Heliconius*, top left) and a plant (the passionflower, *Passiflora*, a tropical vine). *Passiflora* produces toxic chemicals that protect its leaves from most insects, but *Heliconius* caterpillars have digestive enzymes that break down the toxins. As a result, *Heliconius* gains access to a food source that few other insects can eat.

These poison-resistant caterpillars seem to be a strong selective force for *Passiflora* plants, and defenses have evolved in some species. For instance, the leaves of some *Passiflora* species produce yellow sugar deposits that look like *Heliconius* eggs. You can see two eggs in the top right photograph of Figure 37.6 and two egg-like sugar deposits in the bottom photo. Female butterflies avoid laying their eggs on leaves that already have eggs, presumably ensuring that only a few caterpillars will hatch and feed on any one leaf. Because the butterfly often mistakes the yellow sugar deposits for eggs, *Passiflora* species with the yellow deposits are less likely to be eaten.

The story of *Passiflora* is even more complicated, however. The egg-like sugar deposits, as well as smaller ones scattered over the leaf, attract ants and wasps that prey on *Heliconius* eggs and larvae. Thus, adaptations that appear to be coevolutionary responses between just two species may in fact involve interactions among many species in a community.

? People find most bitter-tasting foods objectionable. Why do you suppose we have taste receptors for bitter-tasting chemicals?

Individuals having bitter taste receptors presumably survived better because they could identify potentially toxic food when they foraged.



▲ **Figure 37.6** Coevolution: *Heliconius* and the passionflower vine (*Passiflora*)

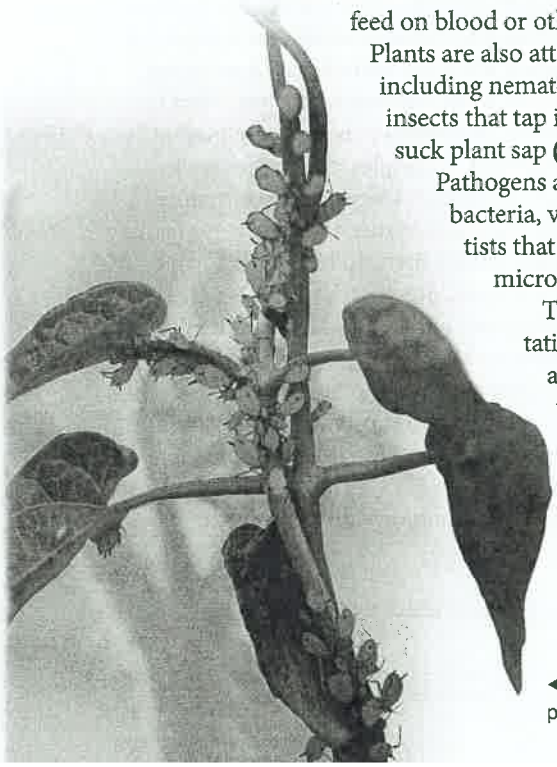
37.7 Parasites and pathogens can affect community composition

A parasite lives on or in a host from which it obtains nourishment. You may recall learning about several invertebrate parasites, including flukes and tapeworms in Module 18.7 and a variety of nematodes in Module 18.8 that live inside a host organism's body.

External parasites include arthropods such as ticks, lice, mites, and mosquitoes (see Module 18.11), which attach to their victims temporarily to feed on blood or other body fluids. Plants are also attacked by parasites, including nematodes and aphids, tiny insects that tap into the phloem and suck plant sap **(Figure 37.7)**.

Pathogens are disease-causing bacteria, viruses, fungi, or protists that can be thought of as microscopic parasites.

The potentially devastating effects of parasites and pathogens on cultivated plants, livestock, and humans are well known, but ecologists know little about how these interactions affect natural communities. Non-native pathogens, whose impact is rapid and often dramatic, have provided some opportunities to study the effects of pathogens on communities. In one example, ecologists studied the consequences of an epidemic of chestnut blight that wiped out virtually all American chestnut trees during the first half of the 20th century; the disease is caused by a protist. Chestnuts were massive canopy trees that dominated many forest communities in North America. Their loss had a significant impact on species composition and community structure. Overall, the diversity of tree species increased as trees that had formerly competed with chestnuts, such as oaks and hickories, became more prominent. The dead chestnut trees furnished niches for other organisms, such as insects, cavity-nesting birds, and eventually decomposers. On the other hand, populations of organisms that depended heavily on living chestnut trees for their food and shelter declined.



◀ **Figure 37.7** Aphids parasitizing a plant

A fungus-like protist that causes a disease called sudden oak death is currently spreading on the West Coast. More than a million oaks have been lost so far, causing the decline of bird populations. Despite its name, sudden oak death affects many other species as well, including the majestic redwood and Douglas fir trees and flowering shrubs such as rhododendron and camellia. Because the epidemic is in its early stages, its full effect on forest communities will not be known for some time.

? Use your knowledge of interspecific interactions to explain why tree diversity increased after all the chestnuts died.

Chestnuts had many of the same niche characteristics as other trees, but apparently chestnuts were superior competitors. After they died, the remaining species may have had fewer niche similarities, or they may have been more equal as competitors, allowing more species to coexist.

37.8 Trophic structure is a key factor in community dynamics

Every community has a trophic structure, a pattern of feeding relationships consisting of several different levels. The sequence of food transfer up the trophic levels is known as a **food chain**. This transfer of food moves chemical nutrients and energy from organism to organism up through the trophic levels in a community.

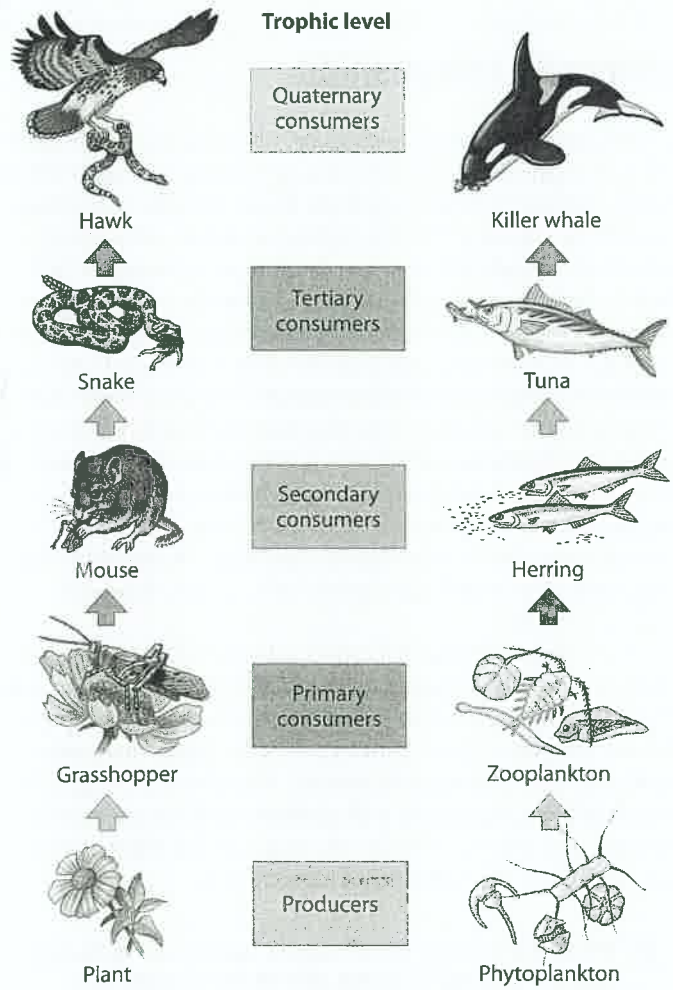
Figure 37.8 compares a terrestrial food chain and an aquatic food chain. In this figure, the trophic levels are arranged vertically, and the names of the levels appear in colored boxes. The arrows connecting the organisms point from the food to the consumer. Starting at the bottom, the trophic level that supports all others consists of autotrophs ("self-feeders"), which ecologists call **producers**. Photosynthetic producers use light energy to power the synthesis of organic compounds. Plants are the main producers on land. In water, the producers are mainly photosynthetic unicellular protists and cyanobacteria, collectively called phytoplankton. Multicellular algae and aquatic plants are also important producers in shallow waters. In a few communities, such as deep-sea hydrothermal vents, the producers are chemosynthetic prokaryotes.

All organisms in trophic levels above the producers are heterotrophs ("other-feeders"), or consumers, and all consumers are directly or indirectly dependent on the output of producers. Herbivores, which eat plants, algae, or phytoplankton, are **primary consumers**. Primary consumers on land include grasshoppers and many other insects, snails, and certain vertebrates, such as grazing mammals and birds that eat seeds and fruits. In aquatic environments, primary consumers include a variety of zooplankton (mainly protists and microscopic animals such as small shrimps) that eat phytoplankton.

Above primary consumers, the trophic levels are made up of carnivores and insectivores, which eat the consumers from the level below. On land, **secondary consumers** include many small mammals, such as the mouse shown here eating an herbivorous insect, and a great variety of birds, frogs, and spiders, as well as lions and other large carnivores that eat grazers. In aquatic ecosystems, secondary consumers are mainly small fishes that eat zooplankton.

Higher trophic levels include **tertiary** (third-level) **consumers**, such as snakes that eat mice and other secondary consumers. Most ecosystems have secondary and tertiary consumers. As the figure indicates, some also have a higher level, **quaternary** (fourth-level) **consumers**. These include hawks in terrestrial ecosystems and killer whales in the marine environment.

Not shown in Figure 37.8 is another trophic level—consumers that derive their energy from **detritus**, the dead material produced at all the trophic levels. Detritus includes animal wastes, plant litter, and the bodies of dead organisms. Different organisms consume detritus in different stages of decay. **Scavengers**, which are large animals, such as crows and vultures, feast on carcasses left behind by predators or speeding cars. The diet of **detritivores** is made up primarily of decaying organic material. Examples of detritivores include earthworms and millipedes. **Decomposers**, mainly prokaryotes and fungi, secrete enzymes that digest molecules in organic material and convert them to inorganic forms. Enormous numbers of microscopic decomposers in the soil and in the mud at the bottom of lakes and oceans break down most of the community's organic materials to inorganic compounds that plants or phytoplankton can use. The breakdown of organic materials to inorganic ones is called **decomposition**. By breaking down detritus, decomposers link all trophic levels. Their role is essential for all communities and, indeed, for the continuation of life on Earth.



▲ **Figure 37.8** Two food chains

? **I'm eating a cheese pizza. At which trophic level(s) am I feeding?**

Primary consumer (flour and tomato sauce) and secondary consumer (cheese, a product from cows, which are primary consumers)

37.9 Food chains interconnect, forming food webs

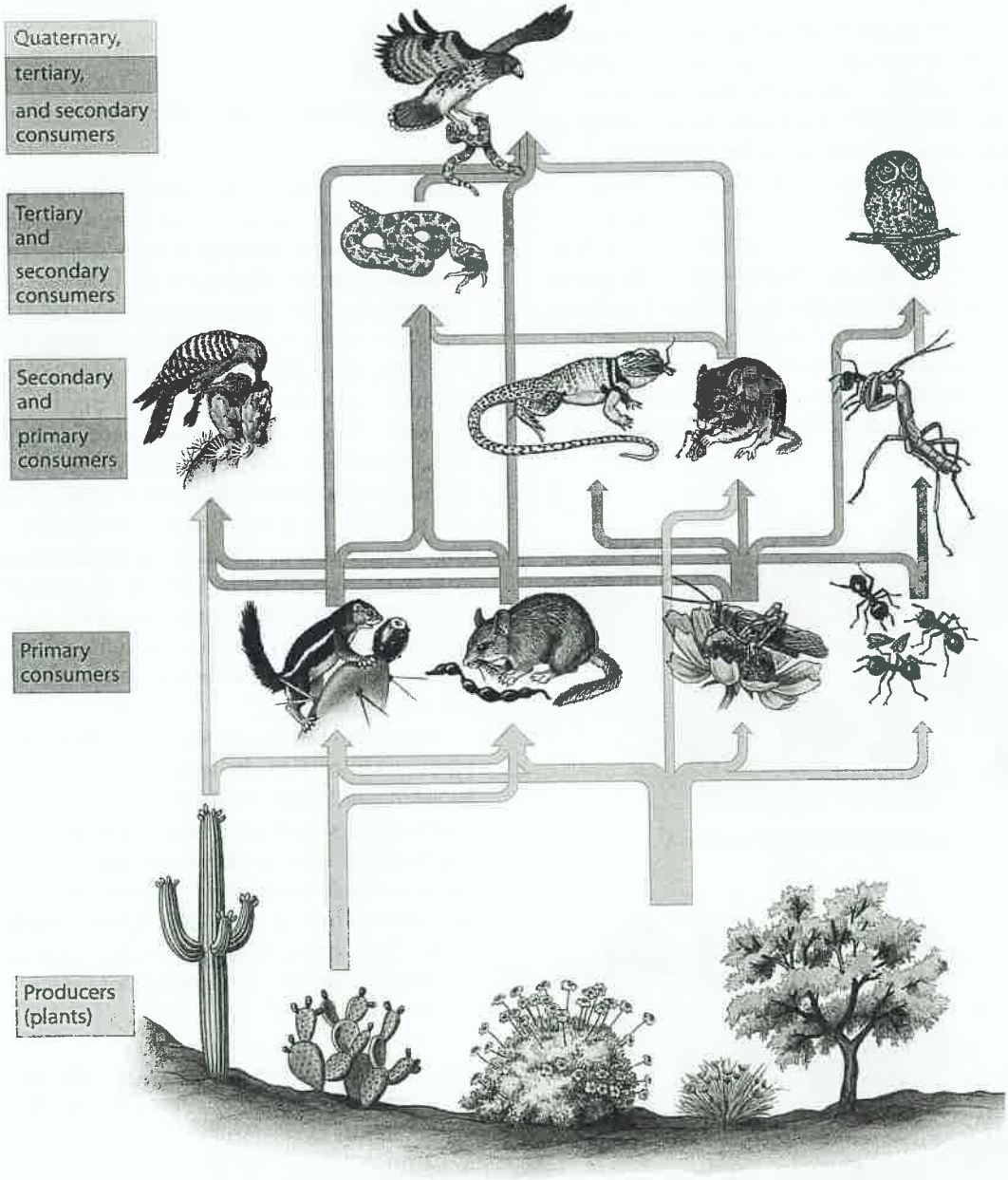
A more realistic view of the trophic structure of a community is a **food web**, a network of interconnecting food chains. **Figure 37.9** shows a simplified example of a food web in a Sonoran desert community. As in the food chains of Figure 37.8, the arrows indicate the direction of nutrient transfer ("who eats whom") and are color-coded by trophic level.

Notice that a consumer may eat more than one type of producer, and several species of primary consumers may feed on the same species of producer. Some animals weave into the web at more than one trophic level. The lizard and mantid are strictly secondary consumers, eating insects. The woodpecker on the left, however, is a primary consumer when it eats cactus seeds and a secondary consumer when it eats ants or grasshoppers. The hawk at the top of the web is a secondary, tertiary, or quaternary consumer, depending on its prey. Food webs, like food chains, do not typically show detritivores and decomposers, which obtain energy from dead organic material from all trophic levels.

We have now looked at how populations in a community interact with each other. In the next few modules, we consider factors that affect the community as a whole.

? **Even consumers at the highest level of a food web eventually become food for _____.**

detritivores and decomposers



▲ **Figure 37.9** A food web

37.10 Species diversity includes relative abundance and species richness

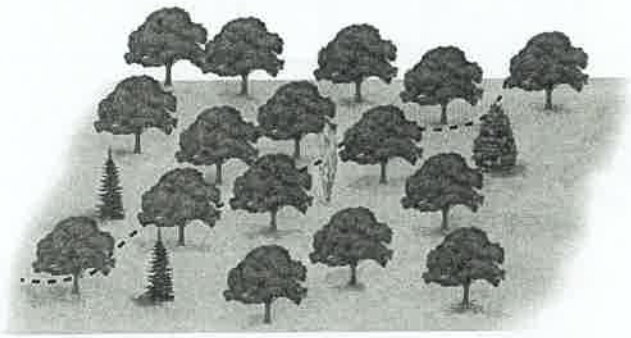
A community's **species diversity** is defined by two components: species richness, or the number of different species in a community, and relative abundance, the proportional representation of a species in a community. To understand why both components are important for describing species diversity, imagine walking through woodlot A on the path shown in **Figure 37.10A**. You would pass by four different species of trees, but most of the trees you encounter would be the same species. Now imagine walking on the path through woodlot B in **Figure 37.10B**. You would see the same four species of trees that you saw in woodlot A—the species richness of the two woodlots is the same. However, woodlot B would probably seem more diverse to you, because no single species predominates. As **Table 37.10** shows, the relative abundance of one species in woodlot A is much higher than the relative abundances of the other three species. In woodlot B, all four species are equally abundant. As a result, species diversity is greater in woodlot B.

Plant species diversity in a community often has consequences for the species diversity of animals in the community. For example, suppose a species of caterpillar only eats the leaves of a tree that makes up just 5% of woodlot A. If the caterpillar is present at all, its population may be small and scattered. Birds that depend on those caterpillars to feed their young may be absent. But the caterpillars would easily be able to locate their food source in woodlot B, and their abundance would attract birds as well. By providing a broader range of habitats, a diverse tree community promotes animal diversity.

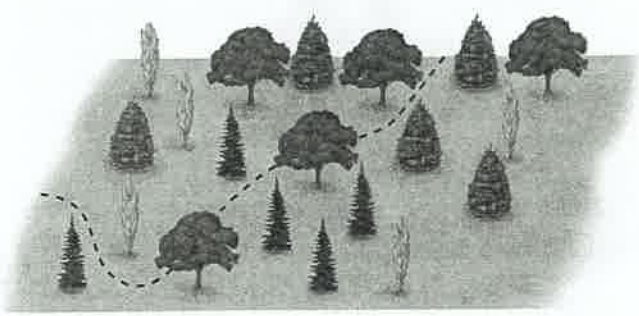
Species diversity also has consequences for pathogens. Most pathogens infect a limited range of host species or may even be restricted to a single host species. When many potential hosts are living close together, it is easy for a pathogen to spread from one to another. In woodlot A, for example, a pathogen that infects the most abundant tree would rapidly be transmitted through the entire forest. On the other hand, the more isolated trees in woodlot B are more likely to escape infection.

TABLE 37.10 RELATIVE ABUNDANCE OF TREE SPECIES IN WOODLOTS A AND B

Species	Relative Abundance in Woodlot A (%)	Relative Abundance in Woodlot B (%)
	80	25
	10	25
	5	25
	5	25



▲ **Figure 37.10A** Species composition of woodlot A



▲ **Figure 37.10B** Species composition of woodlot B

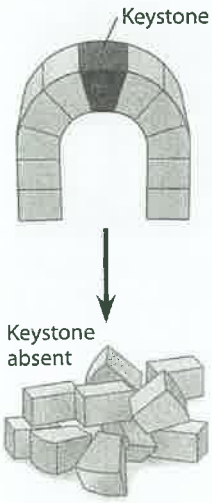
Low species diversity is characteristic of most modern agricultural ecosystems. For efficiency, crops and trees are often planted in monoculture—a single species grown over a wide area. Monocultures are especially vulnerable to attack by pathogens and herbivorous insects. Also, plants grown in monoculture have been bred for certain desirable characteristics, so their genetic variation is typically low, too. As a result, a pathogen can potentially devastate an entire field or more. Between 1845 and 1849, a pathogen wiped out a monoculture of genetically uniform potatoes throughout Ireland. As a result, thousands of people died of starvation, and thousands more left the country.

To combat potential losses, many farmers and forest managers rely heavily on chemical methods of controlling pests. Modern crop scientists have bred varieties of plants that are genetically resistant to common pathogens, but these varieties can suddenly become vulnerable, too. In 1970, pathogen evolution led to an epidemic of a disease called corn leaf blight that resulted in a billion dollars of crop damage in the United States. Some researchers are now investigating the use of more diverse agricultural ecosystems—polyculture—as an alternative to monoculture.

? **Which would you expect to have higher species diversity, a well-maintained lawn or one that is poorly maintained? Explain.**

A lawn that is poorly maintained would have higher species diversity. A well-maintained lawn should have low species diversity. While a lawn that is cared for may not be a perfect monoculture, any weeds that are present would have low relative abundance. The opposite is true if the lawn is not cared for.

37.11 Keystone species have a disproportionate impact on diversity

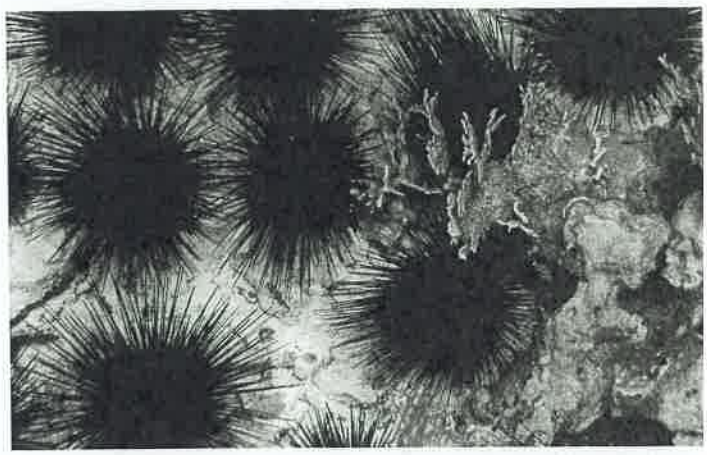


▲ **Figure 37.11A** Arch collapse with removal of keystone

In Module 37.10, you saw that the abundance of dominant species such as a forest tree can have an impact on the diversity of other species in the community. But less abundant species may also exert control over community composition. A **keystone species** is a species whose impact on its community is much larger than its biomass or abundance would indicate. The word "keystone" comes from the wedge-shaped stone at the top of an arch that locks the other pieces in place. If the keystone is removed, the arch collapses **(Figure 37.11A)**. A keystone species occupies a niche that holds the rest of its community in place.

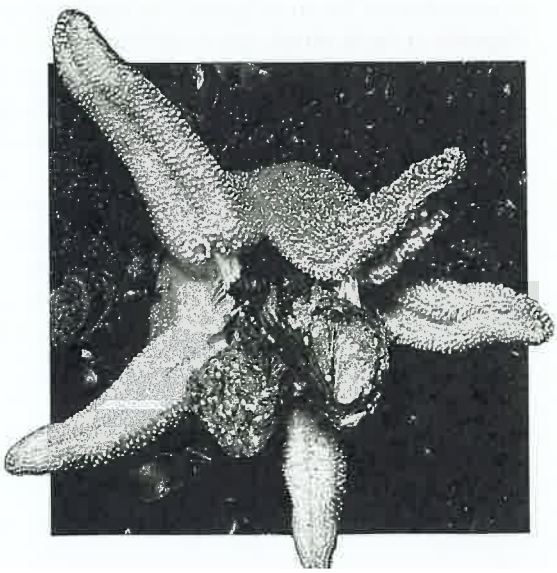
To investigate the role of a potential keystone species in a community, ecologists compare diversity when the species is present and when it is absent. Experiments by Robert Paine in the 1960s were among the first to provide evidence of the keystone species effect. Paine manually removed a predator, a sea star of the genus *Pisaster* **(Figure 37.11B)**, from experimental areas within the intertidal zone of the Washington coast. The result was that *Pisaster*'s main prey, a mussel of the genus *Mytilus*, outcompeted many of the other shoreline organisms (algae, barnacles, and snails, for instance) for the important resource of space on the rocks. The number of different organisms present in experimental areas dropped from more than 15 species to fewer than 5 species.

The keystone concept has practical application in efforts to restore or rehabilitate damaged ecosystems. In 1983, a disease swept through the coral reefs of the Caribbean, killing huge numbers of the long-spined sea urchin, *Diadema antillarum* **(Figure 37.11C)**. In the following decade, the area of reef covered by living coral animals plummeted, along with overall species diversity. Fleshy seaweeds replaced the low turf of encrusted red algae that is vital to reef building **(Figure 37.11D)**. The thick growth of seaweed also prevented light from reaching the symbiotic dinoflagellates that corals depend on for food. These dramatic changes in the reef community revealed that *Diadema* is a keystone species whose herbivorous habits have two major effects. First, its grazing suppresses the seaweed populations. (Because *Diadema* normally shares this role with herbivorous fishes, it is an especially important species on the many Caribbean reefs that have been overfished.) Second, the urchins scrape patches of substrate clear of algae, providing platforms for coral larvae to settle. *Diadema* populations have been slow to rebound from the catastrophic die-off. However, recognition of this organism's key role in the community has prompted conservationists to artificially replenish urchin populations in some areas to help restore damaged reefs.



▲ **Figure 37.11C** *Diadema* sea urchins grazing on a reef

▲ **Figure 37.11D** A reef overgrown by fleshy seaweeds



▶ **Figure 37.11B** A *Pisaster* sea star, a keystone species, eating a mussel

? Removing saguaro cacti from the Sonoran desert community (see Module 37.9) would have a drastic impact, and yet saguaro is not considered a keystone species. Why not?

Saguaro is abundant and makes up a large part of the community. Keystone species have a large effect relative to their representation in the community just as a keystone is a small but vital piece of the arch.

37.12 Disturbance is a prominent feature of most communities

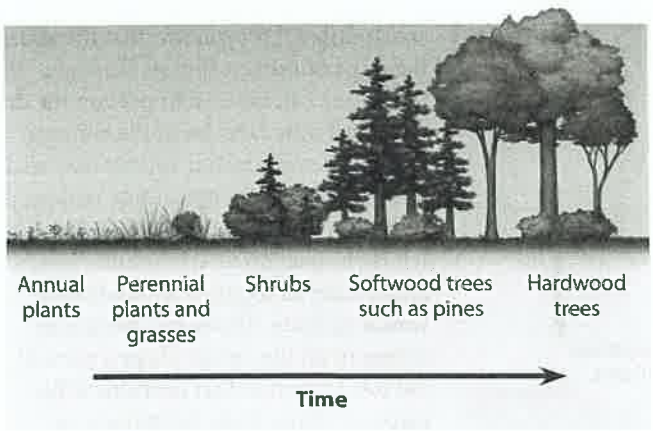
Early ecologists viewed biological communities as more or less stable in structure and species composition. But like many college campuses, where some construction or renovation project is always under way, many communities are frequently disrupted by sudden change. **Disturbances** are events such as storms, fires, floods, droughts, or human activities that damage biological communities and alter the availability of resources. The types of disturbances and their frequency and severity vary from community to community.

Although we tend to think of disturbances in negative terms, small-scale disturbances often have positive effects. For example, when a large tree falls in a windstorm, it creates new habitats. For instance, more light may now reach the forest floor, giving small seedlings the opportunity to grow; or the depression left by its roots may fill with water and be used as egg-laying sites by frogs, salamanders, and numerous insects.

Communities change drastically following a severe disturbance that strips away vegetation and even soil. The disturbed area may be colonized by a variety of species, which are gradually replaced by a succession of other species, in a process called **ecological succession**. When ecological succession begins in a virtually lifeless area with no soil, it is called **primary succession**. Examples of such areas are the rubble left by a retreating glacier or fresh volcanic lava flows **(Figure 37.12A)**. Often the only life-forms initially present are autotrophic bacteria. Lichens and mosses, which grow from windblown spores, are commonly the first large photosynthesizers to colonize the area. Soil develops gradually as rocks break down and organic matter accumulates from the decomposed remains of the early colonizers. Lichens and mosses are gradually overgrown by larger plants that sprout from seeds blown in from nearby areas or carried in by animals. Eventually, the area is colonized by plants that become the community's prevalent form of vegetation. Primary succession can take hundreds or thousands of years.

▲ **Figure 37.12A** Primary succession on a lava flow

Secondary succession occurs where a disturbance has cleared away an existing community but left the soil intact. For example, secondary succession occurs as areas recover from fires or floods. Some disturbances that lead to secondary succession are caused by human activities. Even before colonial times, people were clearing the forests of eastern North America for agriculture and settlements. Some of this land was later abandoned as the soil was depleted of its chemical nutrients or the residents moved west to new territories. Whenever human intervention stops, secondary succession begins.



▲ **Figure 37.12B** Stages in the secondary succession of an abandoned farm field

Numerous studies have documented the stages by which an abandoned farm field returns to forest **(Figure 37.12B)**. A recently disturbed site provides an environment that is favorable to *r*-selected species (see Module 36.7)—plants and animals that reach reproductive age rapidly, produce huge numbers of offspring, and provide little or no parental care. Interspecific competition is not a major factor during the very early stages of succession, which are dominated by weedy annual species such as crabgrass and ragweed. Within a few years, perennial grasses and small broadleaf plants cover the field. (An annual plant completes its life cycle in a single year. Perennial plants live for many years.) Softwood trees, especially pines, begin to invade within 5 years, turning the area into a pine forest in roughly 10 to 15 years. But pine seedlings, which need high levels of light to grow, don't do well in the understory. The seedlings of many hardwood species are more shade tolerant, and thus trees such as oak and maple begin to replace pine as competition becomes a significant force in determining the composition of the community. The final mixture of species depends on local abiotic factors such as soil and topography. Because animals depend on plants for food and shelter, the animal community undergoes successional changes, too. The diversity of bird species, for example, increases dramatically as trees replace herbaceous plants.

Understanding the effects of disturbance in communities is especially important today; as we discuss in Chapter 38, people are the most widespread and significant agents of disturbance. Disturbances may also create opportunities for undesirable plants and animals that people transport to new habitats, which is the topic of the next module.

? **What is the main abiotic factor that distinguishes primary from secondary succession?**

Absence (primary) versus presence (secondary) of soil at the onset of succession

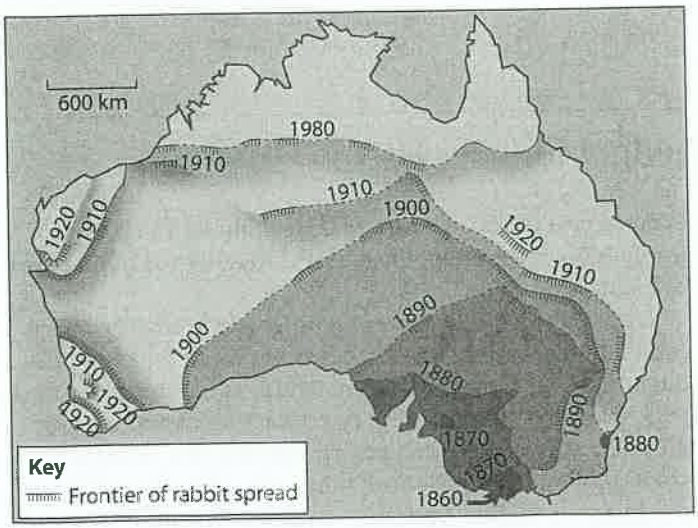
CONNECTION

37.13 Invasive species can devastate communities

For as long as people have traveled from one region to another, they have carried organisms along, sometimes intentionally and sometimes by accident. Many of these non-native species have established themselves firmly in their new locations. Furthermore, many have become **invasive species**, spreading far beyond the original point of introduction and causing environmental or economic damage by colonizing and dominating wherever they find a suitable habitat. In the United States alone, there are hundreds of invasive species, including plants, mammals, birds, fishes, arthropods, and molluscs. Worldwide, there are thousands more. Invasive species are a leading cause of local extinctions, a topic we'll return to in Chapter 38. The economic costs of invasive species are enormous—an estimated $120 billion a year in the United States. Regardless of where you live, an invasive plant or animal is probably living nearby.

Not every organism that is introduced to a new habitat is successful, and not every species that is able to survive in its new habitat becomes invasive. There is no single explanation for why any non-native species turns into a destructive pest, but community ecology offers some insight. Interspecific interactions act as a system of checks and balances on the populations in a community. Every population is subject to multiple negative effects, whether from competitors, predators, herbivores, or pathogens, that curb its growth rate. Without biotic factors such as these to check population growth, a population will continue to expand until limited by abiotic factors.

In Module 36.4, we illustrated exponential population growth with rabbits, which are notoriously prolific breeders. In 1859, 12 pairs of European rabbits (*Oryctolagus cuniculus*) were released on a ranch in southern Australia by a European who wanted to hunt familiar game. The animals quickly became a nuisance. In 1865, 20,000 rabbits were killed on the ranch. By 1900, *several hundred million* rabbits were distributed over much of the continent **(Figure 37.13A)**. The rabbit invasion was a catastrophe in several ways. Their activities destroyed farm and grazing land by eating vegetation down to, and sometimes including, the roots



▲ **Figure 37.13A** The spread of rabbits in Australia

▲ **Figure 37.13B** A familiar sight in early 20th-century Australia

(Figure 37.13B). Especially in arid regions, the loss of plant cover led to soil erosion. In addition, rabbits dug extensive underground burrows that made grazing treacherous for cattle and sheep. They also competed directly with native herbivorous marsupials. After many fruitless attempts to control the rabbit population, in 1950 the Australian government turned to **biological control**, the intentional release of a natural enemy to attack a pest population. A virus lethal to rabbits was introduced into the environment. The rabbits and virus then underwent several coevolutionary cycles as the rabbits became more resistant to the disease and the virus became less lethal. The government managed to stave off a complete resurgence of the rabbit population by introducing new viral strains, but in 1995, they had to switch to a different pathogen to maintain control.

Coevolution is just one potential pitfall of biological control. The imported enemy may not be as successful in the new environment as the target species. It may not disperse widely enough, or its population growth rate may not be high enough to overtake a rapidly expanding population. Caution is especially warranted because the control agent may turn out to be as invasive as its target. For example, cane toads **(Figure 37.13C)** imported to control an agricultural pest in Australia became a widespread threat to native wildlife.

▲ **Figure 37.13C** A cane toad (*Bufo ma*

In the next modules, we broaden our scope to look at ecosystems, the highest level of ecological complexity.

? **What is the ecological basis for biological control of pests?**

By having a negative effect on population growth rate, a natural enemy keeps the target population in check.

Ecosystem Structure and Dynamics

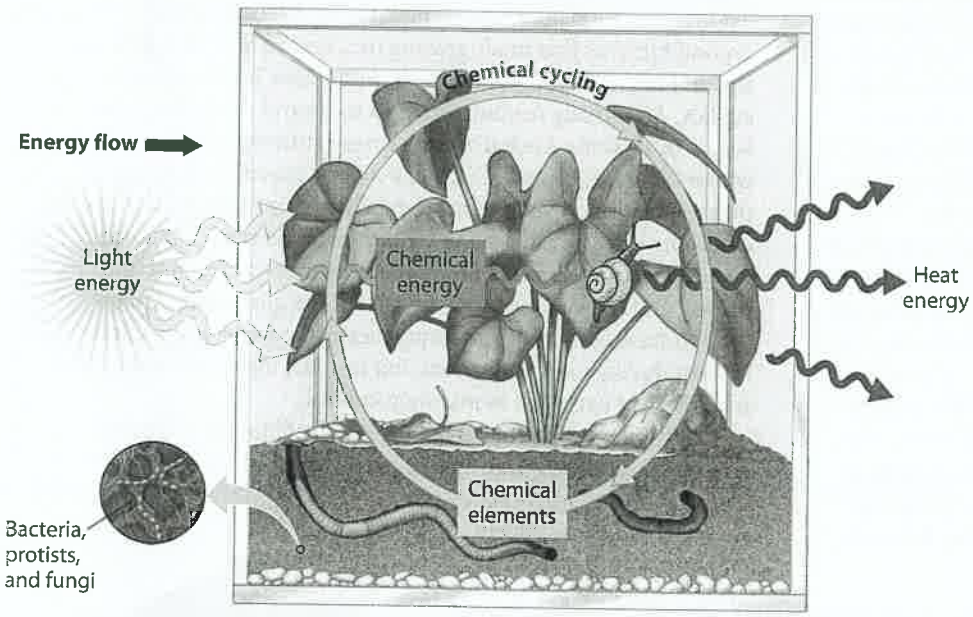
37.14 Ecosystem ecology emphasizes energy flow and chemical cycling

An **ecosystem** consists of all the organisms in a community as well as the abiotic environment with which the organisms interact. Ecosystem ecologists are especially interested in **energy flow**, the passage of energy *through* the components of the ecosystem, and **chemical cycling**, the transfer of materials *within* the ecosystem.

The terrarium in **Figure 37.14** represents a familiar type of ecosystem and illustrates the fundamentals of energy flow. Energy enters the terrarium in the form of sunlight (〰). Plants (producers) convert light energy to chemical energy (〰➤) through the process of photosynthesis. Animals (consumers) take in some of this chemical energy in the form of organic compounds when they eat the plants. Decomposers, such as bacteria and fungi in the soil, obtain chemical energy when they decompose the dead remains of plants and animals. Every use of chemical energy by organisms involves a loss of some energy to the surroundings in the form of heat (〰➤; see Module 6.1). Because so much of the energy captured by photosynthesis is lost as heat, the ecosystem would run out of energy if it were not powered by a continuous inflow of energy from the sun. A few ecosystems—for example, hydrothermal vents—are powered by chemical energy obtained from inorganic compounds.

In contrast to energy flow, chemical cycling (⟹) involves the transfer of materials *within* the ecosystem. While most ecosystems have a constant input of energy from sunlight, the supply of the chemical elements used to construct molecules is limited. Chemical elements such as carbon and nitrogen are cycled between the abiotic component of the ecosystem, including air, water, and soil, and the biotic component of the ecosystem (the community). Plants acquire these chemical elements in inorganic form from the air and soil and use them to build organic molecules. Animals, such as the snail in Figure 37.14, consume some of these organic molecules. When the plants and animals become detritus, decomposers return most of the elements to the soil and air in inorganic form. Some elements are also returned to the soil as the by-products of plant and animal metabolism.

In summary, both energy flow and chemical cycling involve the transfer of substances through the trophic levels of the ecosystem. However, energy flows through, and ultimately out of, ecosystems, whereas chemicals are recycled within ecosystems. We explore these fundamental ecosystem dynamics in the rest of the chapter.



▲ **Figure 37.14** A terrarium ecosystem

? How do chemical cycles in an ecosystem differ from food chains in a community?

Chemicals pass through one or more abiotic components of an ecosystem as well as passing through the biotic components (food chain).

37.15 Primary production sets the energy budget for ecosystems

Each day, Earth receives about 10^{19} kcal of solar energy, the energy equivalent of about 100 million atomic bombs. Most of this energy is absorbed, scattered, or reflected by the atmosphere or by Earth's surface. Of the visible light that reaches plants, algae, and cyanobacteria, only about 1% is converted to chemical energy by photosynthesis.

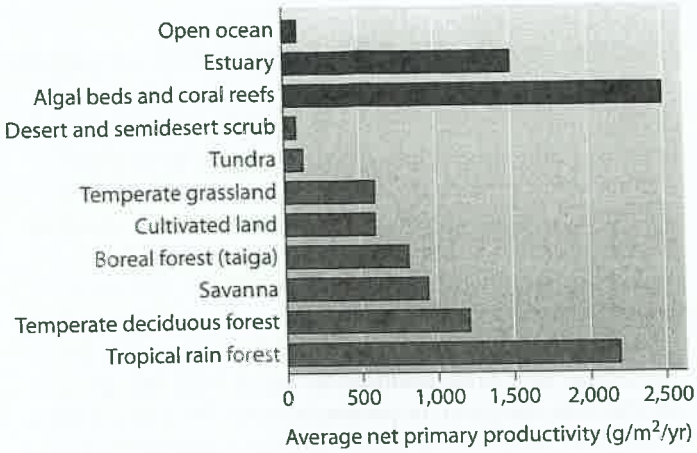
Ecologists call the amount, or mass, of living organic material in an ecosystem the **biomass**. The amount of solar energy converted to chemical energy (in organic compounds) by an ecosystem's producers for a given area and during a given time period is called **primary production**. It can be expressed in units of energy or units of mass. The primary production of the entire biosphere is roughly 165 billion tons of biomass per year.

Different ecosystems vary considerably in their primary production as well as in their contribution to the total production of the biosphere. **Figure 37.15**, at the top of the next page, contrasts the net primary production of a number of different ecosystems. (Net primary production refers to the amount of biomass produced minus the amount used by producers as fuel for their own cellular respiration.) Tropical rain forests are among the most productive terrestrial

ecosystems and contribute a large portion of the planet's overall production of biomass. Coral reefs also have very high production, but their contribution to global production is small because they cover such a small area. Interestingly, even though the open ocean has very low production, it contributes the most to Earth's total net primary production because of its huge size—it covers 65% of Earth's surface area.

? Deserts and semidesert scrub cover about the same amount of surface area as tropical forests but contribute less than 1% of Earth's net primary production, while rain forests contribute 22%. Explain this difference.

The primary production of tropical rain forests is over 20 times greater than that of desert and semidesert scrub ecosystems.

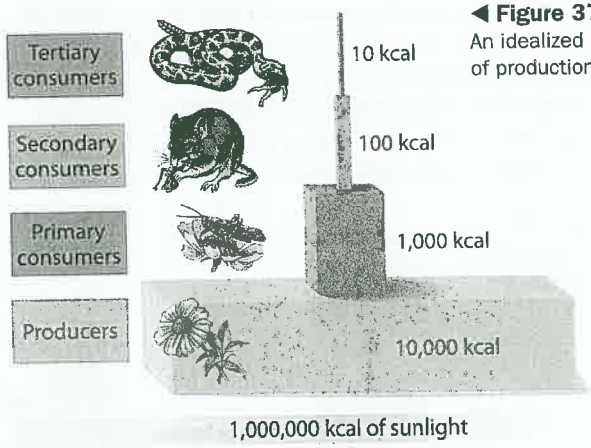


▲ **Figure 37.15** Net primary production of various ecosystems

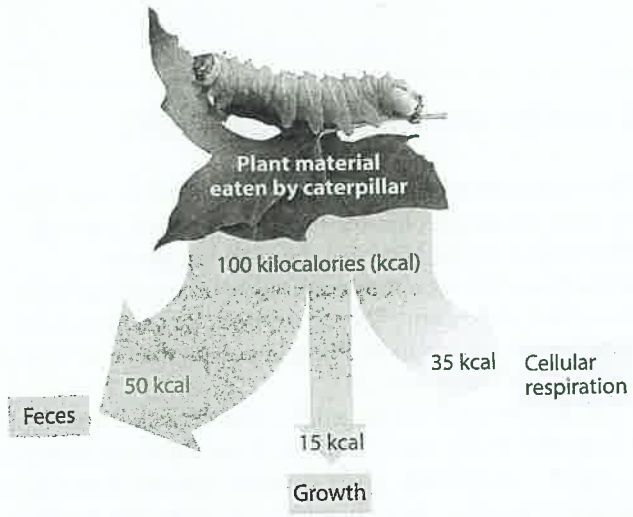
37.16 Energy supply limits the length of food chains

When energy flows as organic matter through the trophic levels of an ecosystem, much of it is lost at each link in a food chain. Consider the transfer of organic matter from a producer to a primary consumer, such as the caterpillar shown in **Figure 37.16A**. The caterpillar might digest and absorb only about half the organic material it eats, passing the indigestible wastes as feces. Of the organic compounds it does absorb, the caterpillar typically uses two-thirds as fuel for cellular respiration. Only the chemical energy left over after respiration—15% of the organic material the caterpillar consumed—can be converted to caterpillar biomass. Thus, a secondary consumer that eats the caterpillar only gets 15% of the biomass (and the energy it contains) that was in the leaves the caterpillar ate.

Figure 37.16B, called a *pyramid of production*, illustrates the cumulative loss of energy with each transfer in a food chain. Each tier of the pyramid represents the chemical energy present in all of the organisms at one trophic level of a food chain. The width of each tier indicates how much of the chemical energy of the tier below is actually incorporated into the organic matter of that trophic level. Note that producers convert only about 1% of the energy in the sunlight available to them to primary production. In this idealized pyramid, 10% of the energy available at each trophic level becomes incorporated into the next higher level. The efficiencies of energy transfer usually range from 5 to 20%. In other words, 80–95% of the energy at one trophic level never transfers to the next.



◀ **Figure 37.16B** An idealized pyramid of production



▲ **Figure 37.16A** The fate of leaf biomass consumed by a caterpillar

An important implication of this stepwise decline of energy in a trophic structure is that the amount of energy available to top-level consumers is small compared with that available to lower-level consumers. Only a tiny fraction of the energy stored by photosynthesis flows through a food chain all the way to a tertiary consumer. This explains why top-level consumers such as lions and hawks require so much geographic territory; it takes a lot of vegetation to support trophic levels so many steps removed from photosynthetic production. Pyramids of production help us understand why most food chains are limited to three to five levels; there is simply not enough energy at the very top of an ecological pyramid to support another trophic level.

? Approximately what proportion of the energy produced by photosynthesis makes it to the snake in Figure 37.16B?

1/1,000 of the 10,000 kcal produced by photosynthesis $(0.1 \times 0.1 \times 0.1)(10{,}000 \text{ kcal}) = 10 \text{ kcal}$

CONNECTION

37.17 A pyramid of production explains the ecological cost of meat

The dynamics of energy flow apply to the human population as much as to other organisms. As omnivores, people eat both plant material and meat. When we eat grain or fruit, we are primary consumers; when we eat beef or other meat from herbivores, we are secondary consumers. When we eat fish like trout and salmon (which eat insects and other small animals), we are tertiary or quaternary consumers.

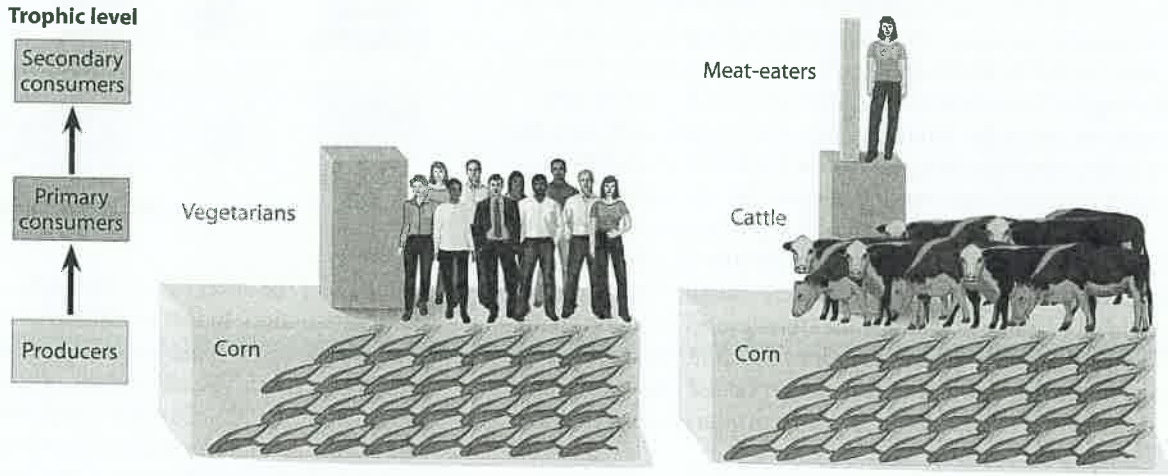
The pyramid of production on the left in **Figure 37.17** indicates energy flow from producers to vegetarians (primary consumers). The energy in the producer trophic level comes from a corn crop. The pyramid on the right illustrates energy flow from the same corn crop, with people as secondary consumers, eating beef. These two pyramids are generalized models, based on the rough estimate that about 10% of the chemical energy available in a trophic level appears at the next higher trophic level. Thus, the pyramids indicate that the human population has about 10 times more energy available to it when people eat corn than when they process the same amount of corn through another trophic level and eat corn-fed beef.

Eating meat of any kind is both economically and environmentally expensive. Compared with growing plants for direct human consumption, producing meat usually requires that more land be cultivated, more water be used for irrigation, more fossil fuels be burned, and more chemical fertilizers and pesticides be applied to croplands used for growing grain. In many countries, people cannot afford to buy much meat and are vegetarians by necessity. Sometimes religion also plays a role in the decision. In India, for example, about 80% of the population practice Hinduism, a religion that discourages meat-eating. India's meat consumption was roughly 5.2 kg (11.5 pounds) per person annually in 2002 (the most recent year for which statistics are available). In Mexico, where many people are too poor to eat meat daily, per capita consumption in 2002 was 58.6 kg (129 pounds) per year. That is a large amount compared with India, but less than half that of the United States, where the per capita rate was 124.8 kg (275 pounds) in 2002.

We turn next to the subject of chemical nutrients. Unlike energy, which is ultimately lost from an ecosystem, all chemical nutrients cycle within ecosystems.

? Why does demand for meat also tend to drive up prices of grains such as wheat and rice, fruits, and vegetables?

The potential supply of plants for direct consumption as food for humans is diminished by the use of agricultural land to grow feed for cattle, chickens, and other meat sources.



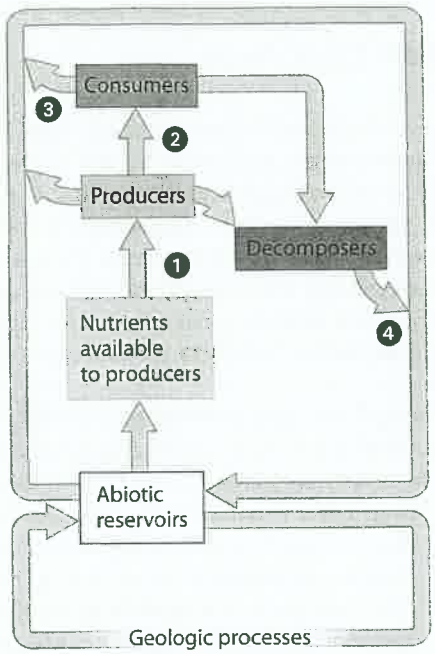
▶ **Figure 37.17** Food energy available to people eating at different trophic levels

37.18 Chemicals are cycled between organic matter and abiotic reservoirs

The sun (or in some cases Earth's interior) supplies ecosystems with a continual influx of energy, but aside from an occasional meteorite, there are no extraterrestrial sources of chemical elements. Life, therefore, depends on the recycling of chemicals. While an organism is alive, much of its chemical stock changes continuously as nutrients are acquired and waste products are released. Atoms present in the complex molecules of an organism at the time of its death are returned to the environment by the action of decomposers, replenishing the pool of inorganic nutrients that plants and other producers use to build new organic matter.

Because chemical cycles in an ecosystem include both biotic and abiotic (geologic and atmospheric) components, they are called **biogeochemical cycles**. **Figure 37.18**, at the top of the next page, is a general scheme for the cycling of a nutrient within an ecosystem. Note that the cycle has **abiotic reservoirs**, where chemicals accumulate or are stockpiled outside of living organisms. The atmosphere, for example, is an abiotic reservoir for carbon. Phosphorus, on the other hand, is available only from the soil.

Let's trace the general biogeochemical cycle in Figure 37.18. ❶ Producers incorporate chemicals from the abiotic reservoirs into organic compounds. ❷ Consumers feed on the producers, incorporating some of the chemicals into their own bodies. ❸ Both producers and consumers release some chemicals



▶ **Figure 37.18** A general model of the biogeochemical cycling of nutrients

back to the environment in waste products (CO_2 and nitrogenous wastes of animals). ❹ Decomposers play a central role by breaking down the complex organic molecules in detritus such as plant litter, animal wastes, and dead organisms. The products of this metabolism are inorganic compounds such as nitrates (NO_3^-), phosphates (PO_4^{3-}), and CO_2, which replenish the abiotic reservoirs. Geologic processes such as erosion and the weathering of rock also contribute to the abiotic reservoirs. Producers use the inorganic molecules from abiotic reservoirs as raw materials for synthesizing new organic molecules (carbohydrates and proteins, for example), and the cycle continues.

Biogeochemical cycles can be local or global. Soil is the main reservoir for nutrients in a local cycle, such as phosphorus. In contrast, for those chemicals that exist primarily in gaseous form—carbon and nitrogen are examples—the cycling is essentially global. For instance, some of the carbon a plant acquires from the air may have been released into the atmosphere by the respiration of an organism on another continent.

In the next three modules, we look at the cyclic movements of carbon, phosphorus, and nitrogen. As you study the cycles, look for the four basic steps we have cited, as well as the geologic processes that may move chemicals around and between ecosystems. In the diagrams, the main abiotic reservoirs are highlighted in white boxes.

? **Which boxes in Figure 37.18 represent biotic components of an ecosystem?**

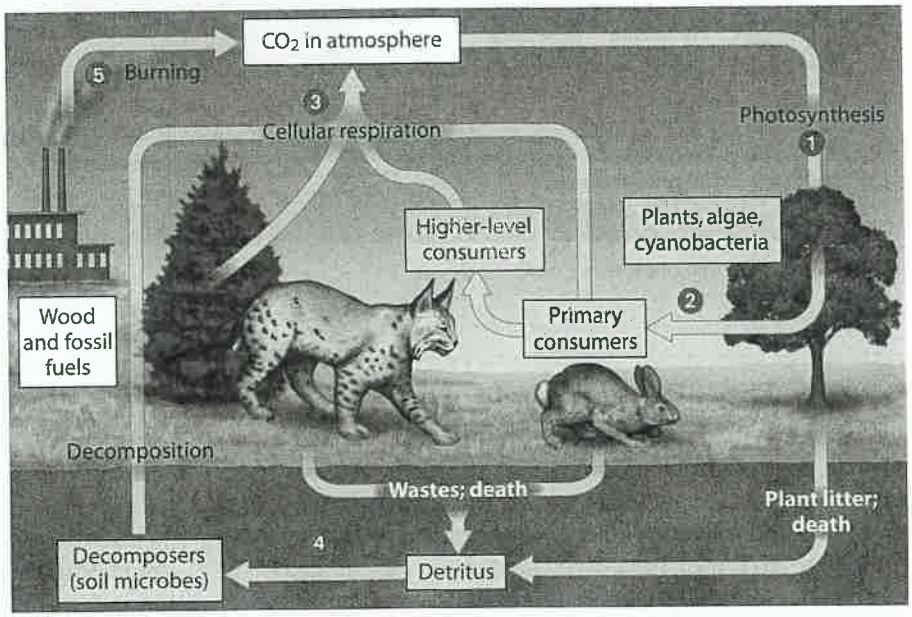
Consumers, producers, and decomposers

37.19 The carbon cycle depends on photosynthesis and respiration

Carbon, the major ingredient of all organic molecules, has an atmospheric reservoir and cycles globally. Carbon also resides in fossil fuels and sedimentary rocks, such as limestone ($CaCO_3$), and as dissolved carbon compounds in the oceans.

As shown in **Figure 37.19**, the reciprocal metabolic processes of photosynthesis and cellular respiration are mainly responsible for the cycling of carbon between the biotic and abiotic worlds. ❶ Photosynthesis removes CO_2 from the atmosphere and incorporates it into organic molecules, which are ❷ passed along the food chain by consumers. ❸ Cellular respiration by producers and consumers returns CO_2 to the atmosphere. ❹ Decomposers break down the carbon compounds in detritus; that carbon, too, is eventually released as CO_2.

On a global scale, the return of CO_2 to the atmosphere by cellular respiration closely balances its removal by photosynthesis. However, ❺ the increased burning of wood and fossil fuels (coal and petroleum) is raising the level of CO_2 in the atmosphere. As we will discuss in Module 38.5, this increase in CO_2 is leading to significant global warming.



▲ **Figure 37.19** The carbon cycle

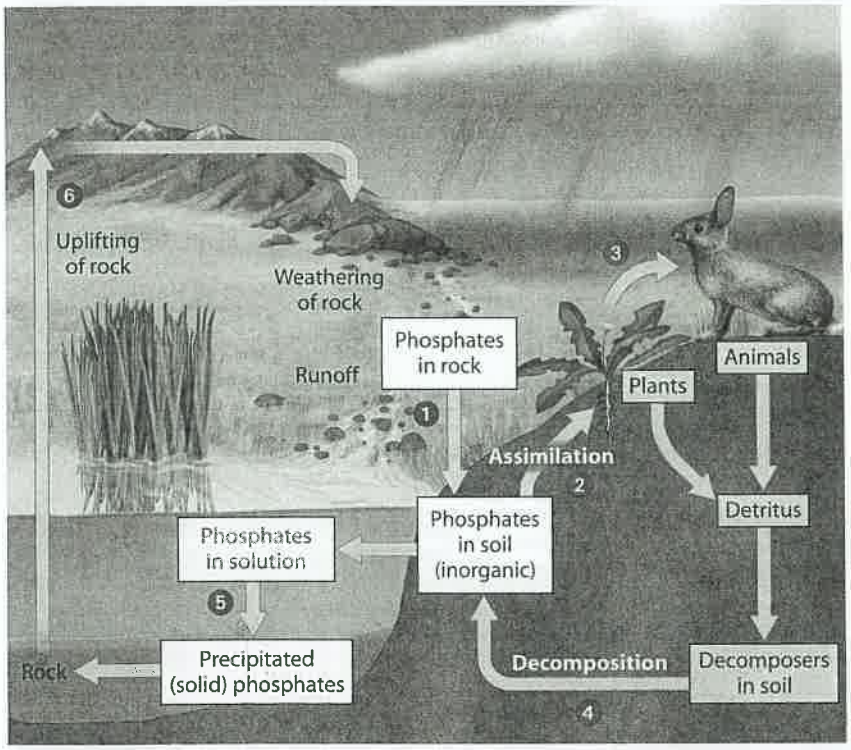
? **What would happen to the carbon cycle if all the decomposers suddenly went on "strike" and stopped working?**

Carbon would accumulate in organic mass, the atmospheric reservoir of carbon would decline, and plants would eventually be starved for CO_2.

37.20 The phosphorus cycle depends on the weathering of rock

Organisms require phosphorus—usually in the form of the phosphate ion (PO_4^{3-})—as an ingredient of nucleic acids, phospholipids, and ATP and (in vertebrates) as a mineral component of bones and teeth. In contrast to the carbon cycle and the other major biogeochemical cycles, the phosphorus cycle does not have an atmospheric component. Rocks are the only source of phosphorus for terrestrial ecosystems; in fact, rocks that have high phosphorus content are mined for agricultural fertilizer.

At the center of **Figure 37.20**, ❶ the weathering (breakdown) of rock gradually adds inorganic phosphate (PO_4^{3-}) to the soil. ❷ Plants assimilate the dissolved phosphate ions in the soil and build them into organic compounds.



▲ **Figure 37.20** The phosphorus cycle

❸ Consumers obtain phosphorus in organic form by eating plants. ❹ Phosphates are returned to the soil by the action of decomposers on animal waste and the remains of dead plants and animals. ❺ Some phosphate drains from terrestrial ecosystems into the sea, where it may settle and eventually become part of new rocks. This phosphorus will not cycle back into living organisms until ❻ geologic processes uplift the rocks and expose them to weathering, a process that takes millions of years.

Because phosphates are transferred from terrestrial to aquatic ecosystems much more rapidly than they are replaced, the amount in terrestrial ecosystems gradually diminishes over time. Furthermore, much of the soluble phosphate released by weathering quickly binds to soil particles, rendering it inaccessible to plants. As a result, the phosphate availability is often quite low and commonly a limiting factor. Mycorrhizal fungi (see Module 17.14) that facilitate phosphorus uptake are essential to many plants, especially those living in older, highly weathered soils. Soil erosion from land cleared for agriculture or development accelerates the loss of phosphates.

Farmers and gardeners often use crushed phosphate rock, bone meal (finely ground bones from slaughtered livestock), or guano to add phosphorus to the soil. Guano, the droppings of seabirds and bats, is mined from densely populated colonies or caves, where meters-deep deposits have accumulated. As you'll learn in Module 37.22, however, runoff of large amounts of phosphate fertilizer pollutes aquatic ecosystems.

? **Over the short term, why does phosphorus cycling tend to be more localized than either carbon or nitrogen cycling?**

Because phosphorus is cycled almost entirely within the soil rather than transferred over long distances via the atmosphere

37.21 The nitrogen cycle depends on bacteria

As an ingredient of proteins and nucleic acids, nitrogen is essential to the structure and functioning of all organisms. In particular, it is a crucial and often limiting plant nutrient. Nitrogen has two abiotic reservoirs, the atmosphere and the soil. The atmospheric reservoir is huge; almost 80% of the atmosphere is nitrogen gas (N_2). However, plants cannot absorb nitrogen in the form of N_2. The process of **nitrogen fixation**, which is performed by some bacteria, converts N_2 to compounds of nitrogen that can be used by plants. Without these organisms, the natural reservoir of usable soil nitrogen would be extremely limited.

Figure 37.21, on the facing page, illustrates the actions of two types of nitrogen-fixing bacteria. Starting at the far right in the figure, ❶ some bacteria live symbiotically in the roots of certain species of plants, supplying their hosts with a direct source of usable nitrogen. The largest group of plants with this mutualistic relationship is the legumes, a family that includes peanuts, soybeans, and alfalfa (see Module 32.13). A number of non-legume plants that live in nitrogen-poor soils have a similar relationship with bacteria. ❷ Free-living nitrogen-fixing bacteria in soil or water convert N_2 to ammonia (NH_3), which then picks up another H^+ to become ammonium (NH_4^+).

❸ After nitrogen is "fixed," some of the NH_4^+ is taken up and used by plants. ❹ Nitrifying bacteria in the soil also convert some of the NH_4^+ to nitrate (NO_3^-), which is more readily

❺ absorbed by plants. Plants use the nitrogen they assimilate to synthesize molecules such as amino acids, which are then incorporated into proteins.

❻ When an herbivore (represented by the rabbit in Figure 37.21) eats a plant, it digests the proteins into amino acids, then uses the amino acids to build the proteins it needs. Higher-order consumers gain nitrogen from their prey. Recall from Module 25.5 that nitrogen-containing waste products are formed during protein metabolism; consumers excrete some nitrogen as well as incorporate some into their body tissues. Mammals, such as the rabbit, excrete nitrogen as urea, a substance that is widely used as an agricultural fertilizer.

Organisms that are not consumed eventually die and become detritus, which is decomposed by prokaryotes and fungi. ❼ Decomposition releases NH_4^+ from organic compounds back into the soil, replenishing the soil reservoir of NH_4^+ and, with the help of nitrifying bacteria (step 4), NO_3^-. Under low-oxygen conditions, however, ❽ soil bacteria known as denitrifiers strip the oxygens from NO_3^-, releasing N_2 back into the atmosphere and depleting the soil reservoir of usable nitrogen. Aerobic denitrification produces a different gas, N_2O.

Although not shown in the figure, some NH_4^+ and NO_3^- are made in the atmosphere by chemical reactions involving N_2 and ammonia gas (NH_3). The ions produced by these chemical reactions reach the soil in precipitation and dust, which are crucial sources of nitrogen for plants in some ecosystems.

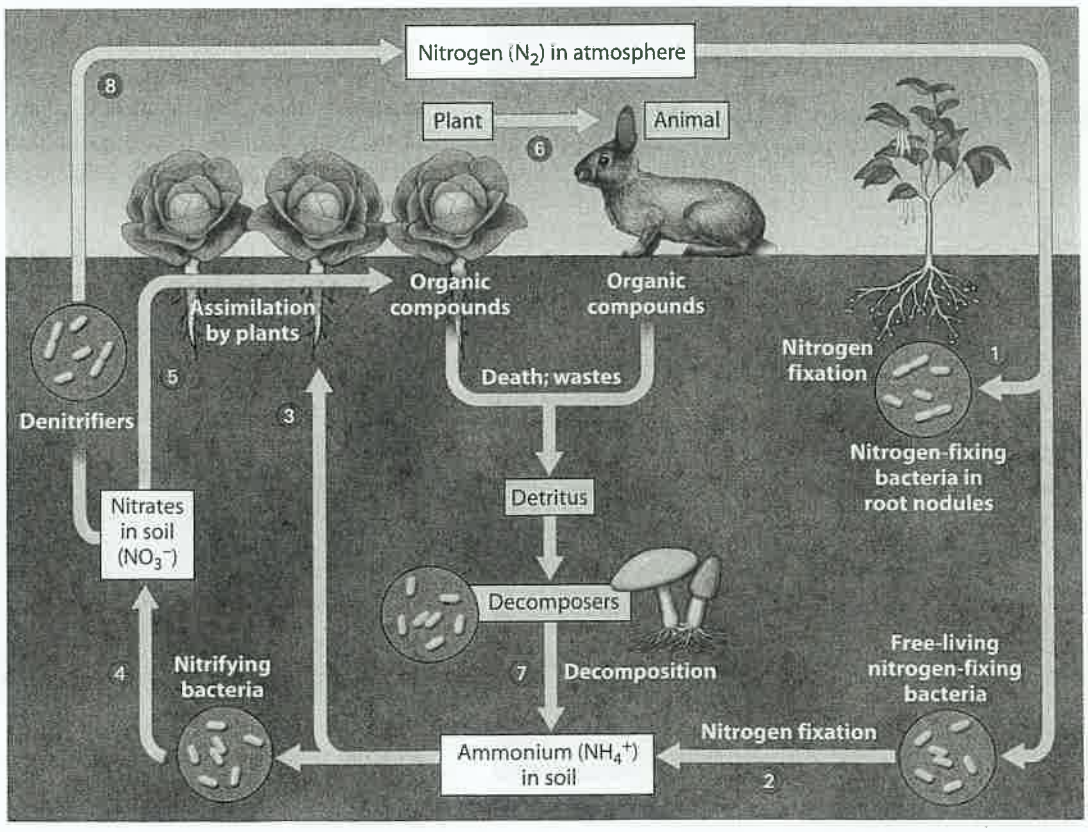
Human activities are disrupting the nitrogen cycle by adding more nitrogen to the biosphere each year than natural processes. Combustion of fossil fuels in motor vehicles and coal-fired power plants produces nitrogen oxides (NO and NO_2). Nitrogen oxides react with other gases in the lower atmosphere to increase the production of ozone. Unlike the protective ozone layer in the upper atmosphere (see Module 7.14), ground-level ozone is a health hazard. Exposure to ozone, which irritates the respiratory system, can cause coughing and breathing difficulties. It is especially dangerous for people with respiratory problems such as asthma. In many regions, ozone alerts are common during hot, dry summer weather. Nitrogen oxides also combine with water in the atmosphere to become nitric acid. The Clean Air Act Amendments of 1990 diminished acid precipitation from sulfur emissions (see Module 2.15), but environmental damage from nitric acid precipitation is causing new concern.

Modern agricultural practices are another major source of nitrogen. Animal wastes from intensive livestock production release ammonia into the atmosphere. Farmers use enormous amounts of nitrogen fertilizer to supplement natural nitrogen fixation by bacteria. Worldwide, the application of synthetic nitrogen fertilizer has increased 100-fold since the late 1950s. However, less than half the fertilizer is taken up by the crop plants. Some nitrogen escapes to the atmosphere, where it forms NO_2 or nitrous oxide (N_2O), an inert gas that lingers in the atmosphere and contributes to global warming (see Module 38.4). As you'll learn in the next module, nitrogen fertilizers also pollute aquatic systems.

? **What are the abiotic reservoirs of nitrogen? In what form does nitrogen occur in each reservoir?**

Atmosphere: N_2; soil: NH_4^+ and NO_3^-

▶ **Figure 37.21**
The nitrogen cycle



CONNECTION

37.22 A rapid inflow of nutrients degrades aquatic ecosystems

Low levels of nutrients, especially phosphorus and nitrogen, often limit the growth of algae and cyanobacteria—and thus primary production—in aquatic ecosystems. Standing-water ecosystems (lakes and ponds) gradually accumulate nutrients from the decomposition of organic matter and fresh influx from the land. As a result, primary production increases naturally over time in a process known as eutrophication. Human activities that add nutrients to aquatic ecosystems accelerate this process and also cause eutrophication in rivers, estuaries, coastal waters, and coral reefs.

You might think that an increase in primary production would be beneficial to a biological community. After all, Figure 37.15 shows that coral reefs and tropical rain forests, ecosystems renowned for spectacular species diversity, have the greatest net primary production. But rapid eutrophication actually lowers species diversity. In some ecosystems, cyanobacteria replace green algae as primary producers. These prokaryotes, which are often encased in a slimy coating, form extensive mats on the surface of the water that prevent light from penetrating the water **(Figure 37.22A)**. Some species of cyanobacteria can fix nitrogen, which gives them an additional advantage when phosphate is the pollutant and nitrogen is scarce. Other ecosystems are overrun by blooms of unicellular diatoms, toxin-producing dinoflagellates (see Figure 16.15B), or multicellular algae. These heavy growths, or "blooms," of cyanobacteria or algae greatly reduce oxygen levels at night, when the photosynthesizers respire. As the cyanobacteria and algae die, microbes consume a great deal of oxygen as they decompose the extra biomass. Thus, rapid nutrient enrichment results in oxygen depletion of the water. Fishes that have a high oxygen requirement cannot survive in such an environment.

In many areas, phosphate pollution comes from agricultural fertilizers. Phosphates are also a common ingredient in pesticides. Other major sources of phosphates include outflow from sewage treatment facilities and runoff of animal waste from livestock feedlots (where hundreds of animals are penned together). Sewage treatment facilities may discharge large amounts of dissolved inorganic nitrogen compounds into rivers or streams when extreme conditions (such as unusually high rainfall) overwhelm their capacity. Agricultural sources of nitrogen include feedlots and the large amounts of inorganic nitrogen fertilizers that are routinely applied to crops, lawns, and golf courses. Plants take up some of the nitrogen compounds in fertilizer, and denitrifiers convert some to atmospheric N_2 or N_2O, but nitrate is not bound tightly by soil particles and is easily washed out of the soil by rain or irrigation. As a result, chemical fertilizers often exceed the soil's natural recycling capacity.

In an example of how far-reaching this problem can be, nitrogen runoff from midwestern farm fields has been linked to a "dead zone" observed each summer in the Gulf of Mexico. Vast algal blooms, indicated in red and orange in **Figure 37.22B**, extend outward from where the Mississippi River deposits its nutrient-laden waters. As the algae die, decomposition of the huge quantities of biomass diminishes the supply of dissolved oxygen over an area that ranges from 13,000 to 22,000 km^2, or roughly 5,000 to 8,500 square miles. Oxygen depletion disrupts benthic communities, displacing fishes and invertebrates that can move and killing organisms that are attached to the substrate. More than 400 recurring and permanent coastal dead zones totaling approximately 245,000 km^2 have been documented in seas worldwide.

? How would excessive addition of mineral nutrients to a lake eventually lead to the loss of many fish species?

The nutrients initially cause population explosions of algae and cyanobacteria. Their respiration and that of the decomposers of all the detritus as the algae and cyanobacteria die consume most of the lake's oxygen, which the fish require.

▲ **Figure 37.22A** Algal growth on a pond resulting from nutrient pollution

Winter Summer

▲ **Figure 37.22B** Concentrations of phytoplankton in winter and summer. Red and orange indicate highest concentrations of phytoplankton.

CONNECTION

37.23 Ecosystem services are essential to human well-being

In the chapter introduction, we mentioned that people rely on numerous services that natural ecosystems provide. In addition to supplying fresh water and some foods, healthy ecosystems recycle nutrients, decompose wastes, and regulate climate and air quality. Wetlands buffer coastal populations against tidal waves and hurricanes, reduce the impact of flooding rivers, and filter pollutants. Natural vegetation helps retain fertile soil and prevent landslides and mudslides.

Ecosystems that we create are also essential to our well-being. For example, agricultural ecosystems supply most of our food and fibers. Although we manage these ecosystems, they are modifications of natural ecosystems and make use of ecosystem services, such as control of agricultural pests by natural predators and pollination of crops. Soil fertility, the foundation for crop growth, depends on nutrient cycling, another ecosystem service. But agricultural methods introduced over the past several decades have pushed croplands beyond their natural capacity to produce food. Large inputs of chemical fertilizers are needed to supplement soil nutrients. Synthetic pesticides are used to control the population growth of crop-eating insects and pathogens that take advantage of vast monocultures of crop species. Herbicides are applied to kill weeds that would compete with crop plants for water and nutrients. In many areas, crops require additional water supplied by irrigation.

These agricultural practices have resulted in enormous increases in food production, but at the expense of natural ecosystems and the services they provide. The detrimental effects of nutrient runoff, discussed in the previous module, are affecting both freshwater and marine ecosystems as fertilizer use increases. Pesticides may kill beneficial organisms as well as pests, and as you learned previously, chemicals that persist in the environment can be carried far from their point of origin (see Modules 34.2, 34.18, and 35.16). Perhaps most worrisome is the deterioration of fertile soil. Clearing and cultivation expose land to wind and water that erode the rich topsoil. Erosion and soil degradation are especially severe in grassland, savanna, and some forest ecosystems where low amounts of precipitation and high rates of evaporation result in low levels of soil moisture. In recent years, dust storms sweeping across overcultivated areas have removed millions of tons of topsoil from these stressed ecosystems. In China, for example, overgrazing and other poor agricultural practices are turning 900 square miles of land—an area the size of Rhode Island—into desert each year **(Figure 37.23A)**. Irrigation of arid land enables farmers to grow crops but leaves a salty residue that eventually prevents plant growth. In addition, population growth in these regions places increasing demands on the already scarce water supply.

Human activities also threaten many forest ecosystems and the services they provide. Every year, more and more land is cleared for agriculture. Some of this land is needed to feed the growing human population, but replacing worn-out cropland accounts for much of the deforestation occurring today. Forests are also cut down to provide timber and fuel wood; many people in nonindustrialized countries use wood for heating and cooking **(Figure 37.23B)**. The most immediate impact of deforestation is soil erosion. In Haiti, for example, where less than 2% of the original tree cover remains, heavy rains inevitably bring flooding and mudslides that damage crops. During recent hurricanes, floodwaters surging down stripped hillsides caused thousands of deaths. With much of the soil destabilized by the devastating earthquake in 2010, massive landslides are likely to cause further ecological and economic destruction during storms.

▲ **Figure 37.23A** A dust storm in Changling, China

The growing demand of the human population for food, fibers, and water has largely been satisfied at the expense of other ecosystem services, but these practices cannot continue indefinitely. **Sustainability** is the goal of developing, managing, and conserving Earth's resources in ways that meet the needs of people today without compromising the ability of future generations to meet theirs. In the next chapter, you'll learn how scientists are applying their knowledge of population, community, and ecosystem ecology to conserve natural ecosystems and even to repair some of the ecological damage that we have done.

? **How can clear-cutting a forest (removing all trees) damage the water quality of nearby aquatic ecosystems?**

Without the growing trees to assimilate minerals from the soil, more of the minerals run off and end up polluting water resources.

▶ **Figure 37.23B** A woman in Haiti gathering wood to process into charcoal

CHAPTER 37 REVIEW

For Practice Quizzes, BioFlix, MP3 Tutors, and Activities, go to www.masteringbiology.com.

Reviewing the Concepts

Community Structure and Dynamics (37.1–37.13)

37.1 A community includes all the organisms inhabiting a particular area. Community ecology is concerned with factors that influence the species composition and distribution of communities and with factors that affect community stability.

37.2 Interspecific interactions are fundamental to community structure. Interspecific interactions can be categorized according to their effect on the interacting populations.

37.3 Competition may occur when a shared resource is limited.

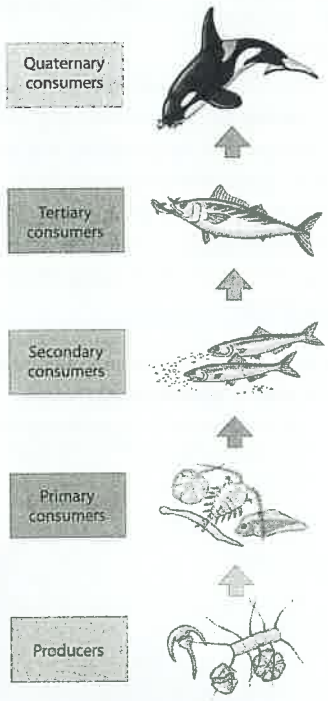
37.4 Mutualism benefits both partners.

37.5 Predation leads to diverse adaptations in prey species.

37.6 Herbivory leads to diverse adaptations in plants. Some herbivore-plant interactions illustrate coevolution or reciprocal evolutionary adaptations.

37.7 Parasites and pathogens can affect community composition.

37.8 Trophic structure is a key factor in community dynamics. Trophic structure can be represented by a food chain.



37.9 Food chains interconnect, forming food webs.

37.10 Species diversity includes relative abundance and species richness. Thus, diversity takes into account both the number of species in a community and the proportion of the community that each species represents.

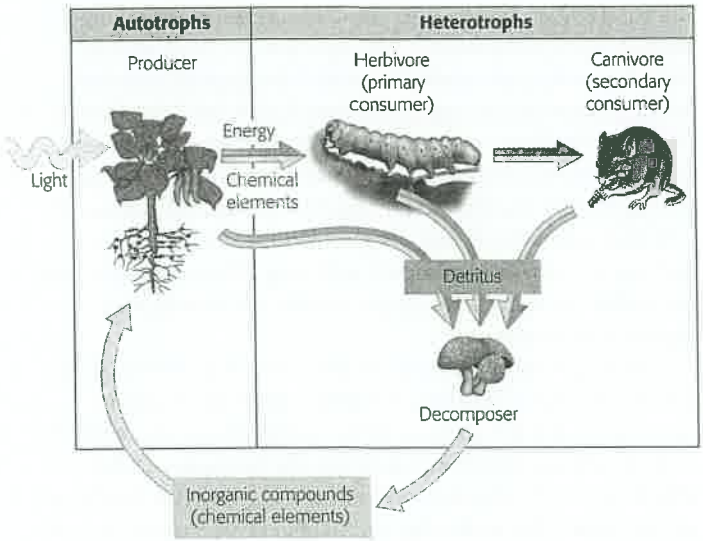
37.11 Keystone species have a disproportionate impact on diversity. Although a keystone species has low biomass or relative abundance, its removal from a community results in lower species diversity.

37.12 Disturbance is a prominent feature of most communities. Ecological succession is a transition in species composition of a community. Primary succession is the gradual colonization of barren rocks. Secondary succession occurs after a disturbance has destroyed a community but left the soil intact.

37.13 Invasive species can devastate communities. Organisms that have been introduced to non-native habitats by human actions and have established themselves at the expense of native communities are considered invasive. The absence of natural enemies often allows rapid population growth of invasive species.

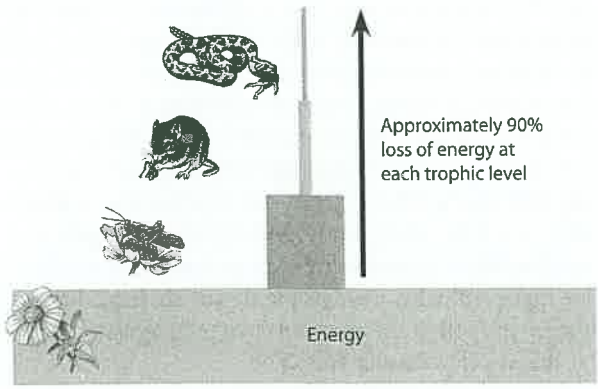
Ecosystem Structure and Dynamics (37.14–37.23)

37.14 Ecosystem ecology emphasizes energy flow and chemical cycling. An ecosystem includes a community and the abiotic factors with which it interacts.



37.15 Primary production sets the energy budget for ecosystems.

37.16 Energy supply limits the length of food chains. A pyramid of production shows the flow of energy from producers to primary consumers and to higher trophic levels. Only about 10% of the energy stored at each trophic level is available to the next level.



37.17 A pyramid of production explains the ecological cost of meat. A field of corn can support many more human vegetarians than meat-eaters.

37.18 Chemicals are cycled between organic matter and abiotic reservoirs.