28

Dynamics of Ecosystems

Concept Outline

FIGURE 28.1
Mushrooms serve a greater function than haute cuisine. Mushrooms and other organisms are crucial recyclers in ecosystems, breaking down dead and decaying material and releasing critical elements such as carbon and nitrogen back into nutrient cycles.

The earth is a closed system with respect to chemicals, but an open system in terms of energy. Collectively, the organisms in ecosystems regulate the capture and expenditure of energy and the cycling of chemicals (figure 28.1). As we will see in this chapter, all organisms, including humans, depend on the ability of other organisms—plants, algae, and some bacteria—to recycle the basic components of life. In chapter 29, we consider the many different types of ecosystems that constitute the biosphere. Chapters 30 and 31 then discuss the many threats to the biosphere and the species it contains.

28.1 Chemicals cycle within ecosystems.

All of the chemical elements that occur in organisms cycle through ecosystems in **biogeochemical cycles,** cyclical paths involving both biological and chemical processes. On a global scale, only a very small portion of these substances is contained within the bodies of organisms; almost all exists in nonliving reservoirs: the atmosphere, water, or rocks. Carbon (in the form of carbon dioxide), nitrogen, and oxygen enter the bodies of organisms primarily from the atmosphere, while phosphorus, potassium, sulfur, magnesium, calcium, sodium, iron, and cobalt come from rocks. All organisms require carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur in relatively large quantities; they require other elements in smaller amounts.

The cycling of materials in ecosystems begins when these chemicals are incorporated into the bodies of organisms from nonliving reservoirs such as the atmosphere or the waters of oceans or rivers. Many minerals, for example, first enter water from weathered rock, then pass into organisms when they drink the water. Materials pass from the organisms that first acquire them into the bodies of other organisms that eat them, until ultimately, through decomposition, they complete the cycle and return to the nonliving world.

The Water Cycle

The water cycle (figure 28.2) is the most familiar of all biogeochemical cycles. All life depends directly on the presence of water; the bodies of most organisms consist mainly of this substance. Water is the source of hydrogen ions, whose movements generate ATP in organisms. For that reason alone, it is indispensable to their functioning.

The Path of Free Water

The oceans cover three-fourths of the earth's surface. From the oceans, water evaporates into the atmosphere, a process powered by energy from the sun. Over land approximately 90% of the water that reaches the atmosphere is moisture that evaporates from the surface of plants through a process called transpiration (see chapter 40). Most precipitation falls directly into the oceans, but some falls on land, where it passes into surface and subsurface bodies of fresh water. Only about 2% of all the water on earth is captured in any form—frozen, held in the soil, or incorporated into the bodies of organisms. All of the rest is free water, circulating between the atmosphere and the oceans.
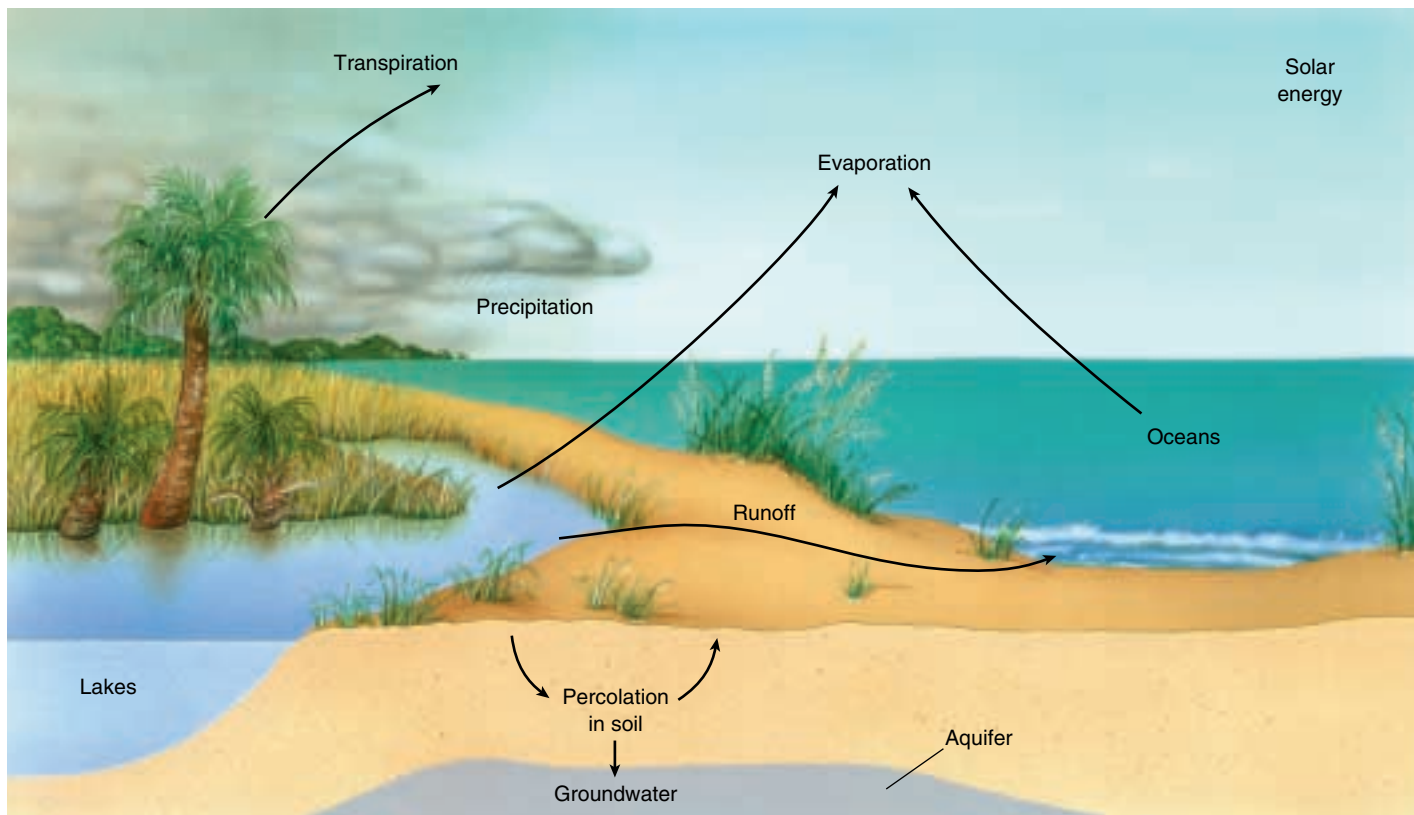

FIGURE 28.2
The water cycle. Water circulates from atmosphere to earth and back again.

The Importance of Water to Organisms

Organisms live or die on the basis of their ability to capture water and incorporate it into their bodies. Plants take up water from the earth in a continuous stream. Crop plants require about 1000 kilograms of water to produce one kilogram of food, and the ratio in natural communities is similar. Animals obtain water directly or from the plants or other animals they eat. The amount of free water available at a particular place often determines the nature and abundance of the living organisms present there.

Groundwater

Much less obvious than surface water, which we see in streams, lakes, and ponds, is groundwater, which occurs in aquifers—permeable, saturated, underground layers of rock, sand, and gravel. In many areas, groundwater is the most important reservoir of water. It amounts to more than 96% of all fresh water in the United States. The upper, unconfined portion of the groundwater constitutes the water table, which flows into streams and is partly accessible to plants; the lower confined layers are generally out of reach, although they can be "mined" by humans. The water table is recharged by water that percolates through the soil from precipitation as well as by water that seeps downward from ponds, lakes, and streams. The deep aquifers are recharged very slowly from the water table.

Groundwater flows much more slowly than surface water, anywhere from a few millimeters to a meter or so per day. In the United States, groundwater provides about 25% of the water used for all purposes and provides about 50% of the population with drinking water. Rural areas tend to depend almost exclusively on wells to access groundwater, and its use is growing at about twice the rate of surface water use. In the Great Plains of the central United States, the extensive use of the Ogallala Aquifer as a source of water for agricultural needs as well as for drinking water is depleting it faster than it can be naturally recharged. This seriously threatens the agricultural production of the area and similar problems are appearing throughout the drier portions of the globe.

Because of the greater rate of groundwater use, and because it flows so slowly, the increasing chemical pollution of groundwater is also a very serious problem. It is estimated that about 2% of the groundwater in the United States is already polluted, and the situation is worsening. Pesticides, herbicides, and fertilizers have become a serious threat to water purity. Another key source of groundwater pollution consists of the roughly 200,000 surface pits, ponds, and lagoons that are actively used for the disposal of chemical wastes in the United States alone. Because of the large volume of water, its slow rate of turnover, and its inaccessibility, removing pollutants from aquifers is virtually impossible.

FIGURE 28.3
Deforestation breaks the water cycle. As time goes by, the consequences of tropical deforestation may become even more severe, as the extensive erosion in this deforested area of Madagascar shows.

Breaking the Water Cycle

In dense forest ecosystems such as tropical rainforests, more than 90% of the moisture in the ecosystem is taken up by plants and then transpired back into the air. Because so many plants in a rainforest are doing this, the vegetation is the primary source of local rainfall. In a very real sense, these plants create their own rain: the moisture that travels up from the plants into the atmosphere falls back to earth as rain.

Where forests are cut down, the organismic water cycle is broken, and moisture is not returned to the atmosphere. Water drains away from the area to the sea instead of rising to the clouds and falling again on the forest. As early as the late 1700s, the great German explorer Alexander von Humbolt reported that stripping the trees from a tropical rainforest in Colombia prevented water from returning to the atmosphere and created a semiarid desert. It is a tragedy of our time that just such a transformation is occurring in many tropical areas, as tropical and temperate rainforests are being clear-cut or burned in the name of "development" (figure 28.3). Much of Madagascar, a California-sized island off the east coast of Africa, has been transformed in this century from lush tropical forest into semiarid desert by deforestation. Because the rain no longer falls, there is no practical way to reforest this land. The water cycle, once broken, cannot be easily reestablished.

Water cycles between oceans and atmosphere. Some 96% of the fresh water in the United States consists of groundwater, which provides 25% of all the water used in this country.

The Carbon Cycle

The **carbon cycle** is based on carbon dioxide, which makes up only about 0.03% of the atmosphere (figure 28.4). Worldwide, the synthesis of organic compounds from carbon dioxide and water through photosynthesis (see chapter 10) utilizes about 10% of the roughly 700 billion metric tons of carbon dioxide in the atmosphere each year. This enormous amount of biological activity takes place as a result of the combined activities of photosynthetic bacteria, protists, and plants. All terrestrial heterotrophic organisms obtain their carbon indirectly from photosynthetic organisms. When the bodies of dead organisms decompose, microorganisms release carbon dioxide back to the atmosphere. From there, it can be reincorporated into the bodies of other organisms.

Most of the organic compounds formed as a result of carbon dioxide fixation in the bodies of photosynthetic organisms are ultimately broken down and released back into the atmosphere or water. Certain carbon-containing compounds, such as cellulose, are more resistant to breakdown than others, but certain bacteria and fungi, as well as a few kinds of insects, are able to accomplish this feat. Some cellulose, however, accumulates as undecomposed organic matter such as peat. The carbon in this cellulose may eventually be incorporated into fossil fuels such as oil or coal.

In addition to the roughly 700 billion metric tons of carbon dioxide in the atmosphere, approximately 1 trillion metric tons are dissolved in the ocean. More than half of this quantity is in the upper layers, where photosynthesis takes place. The fossil fuels, primarily oil and coal, contain more than 5 trillion additional metric tons of carbon, and between 600 million and 1 trillion metric tons are locked up in living organisms at any one time. In global terms, photosynthesis and respiration (see chapters 9 and 10) are approximately balanced, but the balance has been shifted recently because of the consumption of fossil fuels. The combustion of coal, oil, and natural gas has released large stores of carbon into the atmosphere as carbon dioxide. The increase of carbon dioxide in the atmosphere appears to be changing global climates, and may do so even more rapidly in the future, as we will discuss in chapter 30.

About 10% of the estimated 700 billion metric tons of carbon dioxide in the atmosphere is fixed annually by the process of photosynthesis.
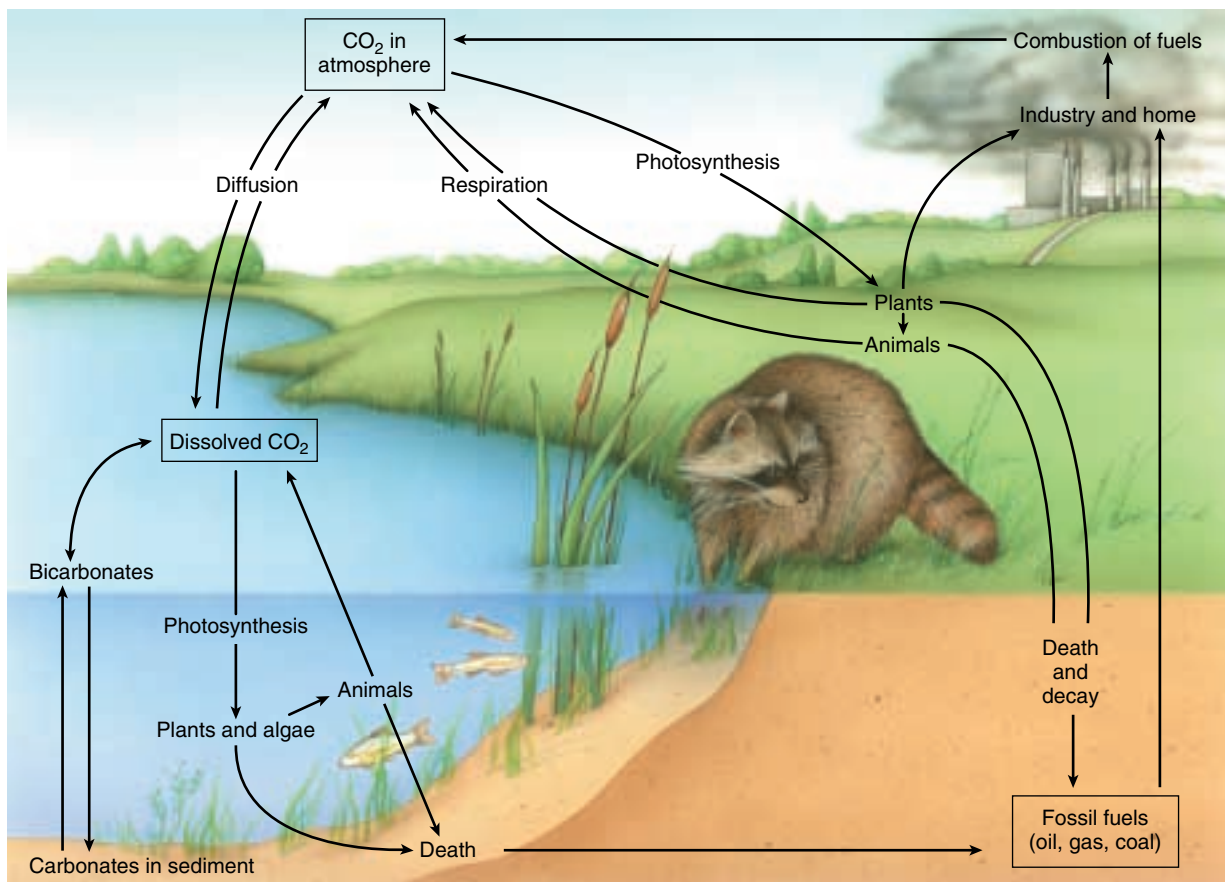

FIGURE 28.4
The carbon cycle. Photosynthesis captures carbon; respiration returns it to the atmosphere.

The Nitrogen Cycle

Relatively few kinds of organisms—all of them bacteria—can convert, or fix, atmospheric nitrogen (78% of the earth's atmosphere) into forms that can be used for biological processes via the **nitrogen cycle** (figure 28.5). The triple bond that links together the two atoms that make up diatomic atmospheric nitrogen (N_2) makes it a very stable molecule. In living systems the cleavage of atmospheric nitrogen is catalyzed by a complex of three proteins—ferredoxin, nitrogen reductase, and nitrogenase. This process uses ATP as a source of energy, electrons derived from photosynthesis or respiration, and a powerful reducing agent. The overall reaction of nitrogen fixation is written:

$$N_2 + 3H_2 \rightarrow 2NH_3$$
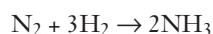
Some genera of bacteria have the ability to fix atmospheric nitrogen. Most are free-living, but some form symbiotic relationships with the roots of legumes (plants of the pea family, Fabaceae) and other plants. Only the symbiotic bacteria fix enough nitrogen to be of major significance in nitrogen production. Because of the activities of such organisms in the past, a large reservoir of ammonia and nitrates now exists in most ecosystems. This reservoir is the immediate source of much of the nitrogen used by organisms.

Nitrogen-containing compounds, such as proteins in plant and animal bodies, are decomposed rapidly by certain bacteria and fungi. These bacteria and fungi use the amino acids they obtain through decomposition to synthesize their own proteins and to release excess nitrogen in the form of ammonium ions (NH_4^+), a process known as **ammonification.** The ammonium ions can be converted to soil nitrites and nitrates by certain kinds of organisms and which then can be absorbed by plants.

A certain proportion of the fixed nitrogen in the soil is steadily lost. Under anaerobic conditions, nitrate is often converted to nitrogen gas (N_2) and nitrous oxide (N_2O), both of which return to the atmosphere. This process, which several genera of bacteria carry out, is called **denitrification.**

> **Nitrogen becomes available to organisms almost entirely through the metabolic activities of bacteria, some free-living and others which live symbiotically in the roots of legumes and other plants.**

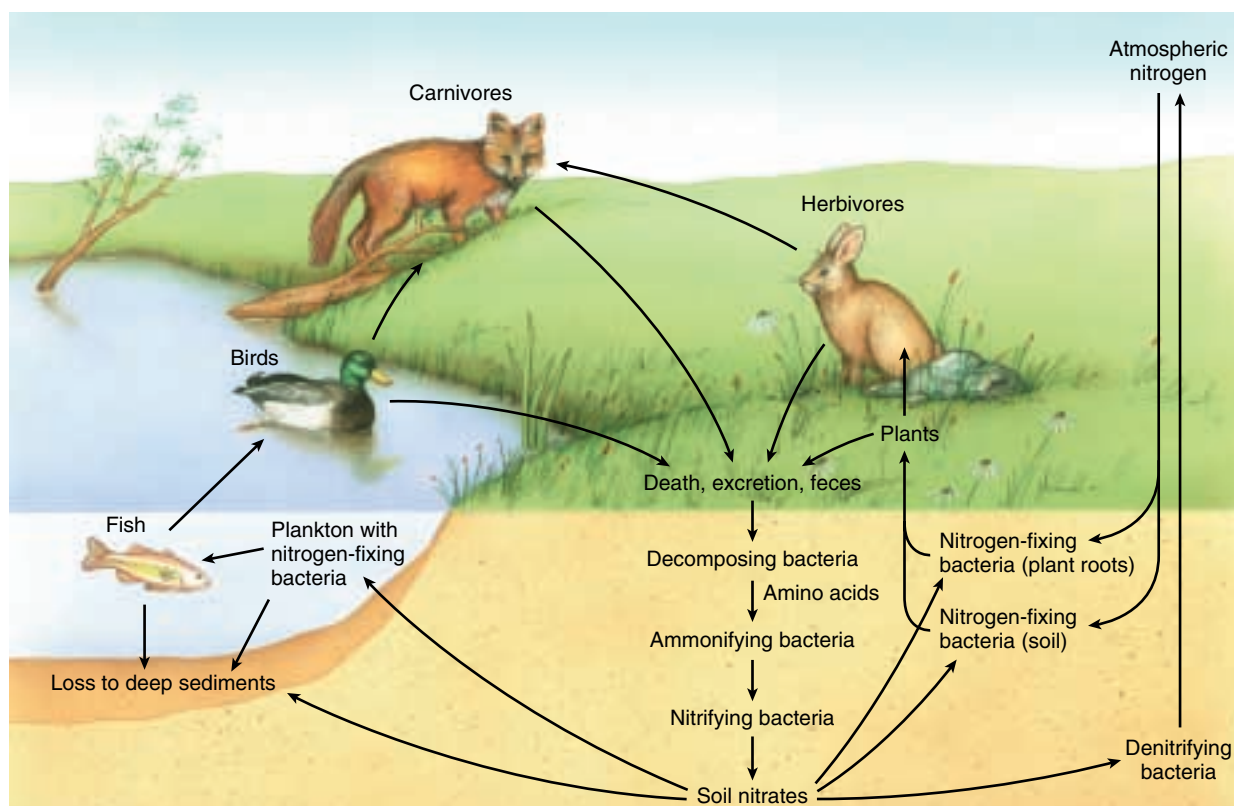**FIGURE 28.5**
The nitrogen cycle. Certain bacteria fix atmospheric nitrogen, converting it to a form living organisms can use. Other bacteria decompose nitrogen-containing compounds from plant and animal materials, returning it to the atmosphere.

The Phosphorus Cycle

In all biogeochemical cycles other than those involving water, carbon, oxygen, and nitrogen, the reservoir of the nutrient exists in mineral form, rather than in the atmosphere. The **phosphorus cycle** (figure 28.6) is presented as a representative example of all other mineral cycles. Phosphorus, a component of ATP, phospholipids, and nucleic acid, plays a critical role in plant nutrition.

Of all the required nutrients other than nitrogen, phosphorus is the most likely to be scarce enough to limit plant growth. Phosphates, in the form of phosphorus anions, exist in soil only in small amounts. This is because they are relatively insoluble and are present only in certain kinds of rocks. As phosphates weather out of soils, they are transported by rivers and streams to the oceans, where they accumulate in sediments. They are naturally brought back up again only by the uplift of lands, such as occurs along the Pacific coast of North and South America, creating upwelling currents. Phosphates brought to the surface are assimilated by algae, and then by fish, which are in turn eaten by birds. Seabirds deposit enormous amounts of guano (feces) rich in phosphorus along certain coasts. Guano deposits have traditionally been used for fertilizer. Crushed phosphate-rich rocks, found in certain regions, are also used for fertilizer. The seas are the only inexhaustible source of phosphorus, making deep-seabed mining look increasingly commercially attractive.

Every year, millions of tons of phosphate are added to agricultural lands in the belief that it becomes fixed to and enriches the soil. In general, three times more phosphate than a crop requires is added each year. This is usually in the form of **superphosphate,** which is soluble calcium dihydrogen phosphate, $Ca(H_2PO_4)_2$, derived by treating bones or apatite, the mineral form of calcium phosphate, with sulfuric acid. But the enormous quantities of phosphates that are being added annually to the world's agricultural lands are not leading to proportionate gains in crops. Plants can apparently use only so much of the phosphorus that is added to the soil.

> **Phosphates are relatively insoluble and are present in most soils only in small amounts. They often are so scarce that their absence limits plant growth.**
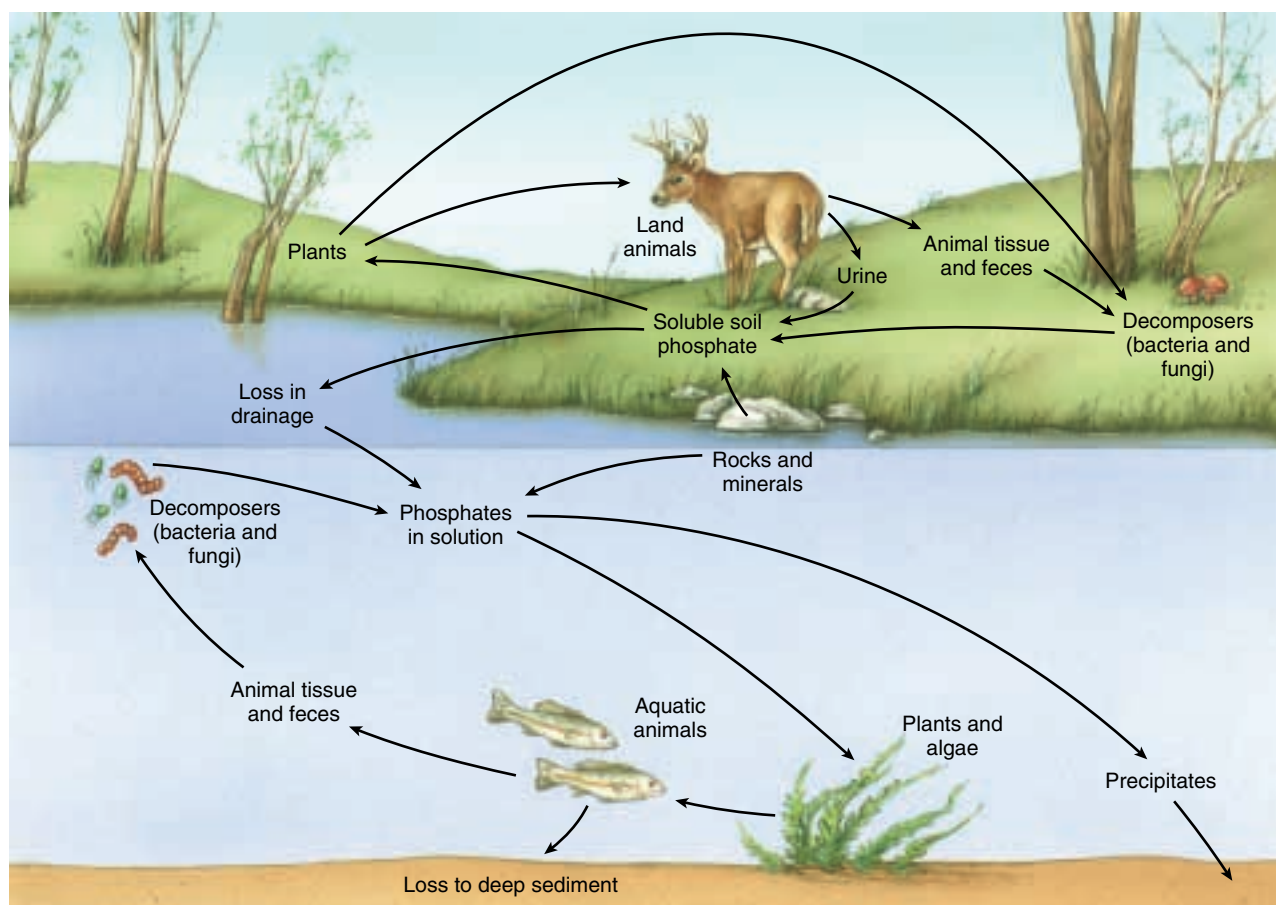

FIGURE 28.6
The phosphorus cycle. Phosphates weather from soils into water, enter plants and animals, and are redeposited in the soil when plants and animals decompose.

Biogeochemical Cycles Illustrated: Recycling in a Forest Ecosystem

An ongoing series of studies conducted at the Hubbard Brook Experimental Forest in New Hampshire has revealed in impressive detail the overall recycling pattern of nutrients in an ecosystem. The way this particular ecosystem functions, and especially the way nutrients cycle within it, has been studied since 1963 by Herbert Bormann of the Yale School of Forestry and Environmental Studies, Gene Likens of the Institute of Ecosystem Studies, and their colleagues. These studies have yielded much of the available information about the cycling of nutrients in forest ecosystems. They have also provided the basis for the development of much of the experimental methodology that is being applied successfully to the study of other ecosystems.

Hubbard Brook is the central stream of a large watershed that drains a region of temperate deciduous forest. To measure the flow of water and nutrients within the Hubbard Brook ecosystem, concrete weirs with V-shaped notches were built across six tributary streams. All of the water that flowed out of the valleys had to pass through the notches, as the weirs were anchored in bedrock. The researchers measured the precipitation that fell in the six valleys, and determined the amounts of nutrients that were present in the water flowing in the six streams. By these methods, they demonstrated that the undisturbed forests in this area were very efficient at retaining nutrients; the small amounts of nutrients that precipitated from the atmosphere with rain and snow were approximately equal to the amounts of nutrients that ran out of the valleys. These quantities were very low in relation to the total amount of nutrients in the system. There was a small net loss of calcium—about 0.3% of the total calcium in the system per year—and small net gains of nitrogen and potassium.

In 1965 and 1966, the investigators felled all the trees and shrubs in one of the six watersheds and then prevented regrowth by spraying the area with herbicides. The effects were dramatic. The amount of water running out of that valley increased by 40%. This indicated that water that previously would have been taken up by vegetation and ultimately evaporated into the atmosphere was now running off. For the four-month period from June to September 1966, the runoff was four times higher than it had been during comparable periods in the preceding years. The amounts of nutrients running out of the system also greatly increased; for example, the loss of calcium was 10 times higher than it had been previously. Phosphorus, on the other hand, did not increase in the stream water; it apparently was locked up in the soil.

The change in the status of nitrogen in the disturbed valley was especially striking (figure 28.7). The undisturbed ecosystem in this valley had been accumulating nitrogen at a rate of about 2 kilograms per hectare per year,

(a)
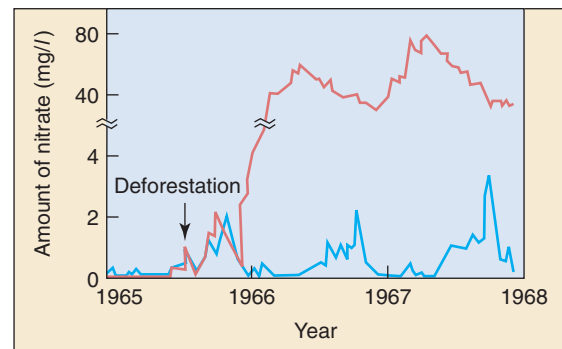
(b)

FIGURE 28.7
The Hubbard Brook experiment. (*a*) A 38-acre watershed was completely deforested, and the runoff monitored for several years. (*b*) Deforestation greatly increased the loss of minerals in runoff water from the ecosystem. The red curve represents nitrate in the runoff water from the deforested watershed; the blue curve, nitrate in runoff water from an undisturbed neighboring watershed.

but the deforested ecosystem *lost* nitrogen at a rate of about 120 kilograms per hectare per year. The nitrate level of the water rapidly increased to a level exceeding that judged safe for human consumption, and the stream that drained the area generated massive blooms of cyanobacteria and algae. In other words, the fertility of this logged-over valley decreased rapidly, while at the same time the danger of flooding greatly increased. This experiment is particularly instructive at the start of the twenty-first century, as large areas of tropical rain forest are being destroyed to make way for cropland, a topic that will be discussed further in chapter 30.

When the trees and shrubs in one of the valleys in the Hubbard Brook watershed were cut down and the area was sprayed with herbicide, water runoff and the loss of nutrients from that valley increased. Nitrogen, which had been accumulating at a rate of about 2 kilograms per hectare per year, was lost at a rate of 120 kilograms per hectare per year.

Trophic Levels

An ecosystem includes autotrophs and heterotrophs. **Autotrophs** are plants, algae, and some bacteria that are able to capture light energy and manufacture their own food. To support themselves, **heterotrophs,** which include animals, fungi, most protists and bacteria, and nongreen plants, must obtain organic molecules that have been synthesized by autotrophs. Autotrophs are also called **primary producers,** and heterotrophs are also called **consumers.**

Once energy enters an ecosystem, usually as the result of photosynthesis, it is slowly released as metabolic processes proceed. The autotrophs that first acquire this energy provide all of the energy heterotrophs use. The organisms that make up an ecosystem delay the release of the energy obtained from the sun back into space.

Green plants, the primary producers of a terrestrial ecosystem, generally capture about 1% of the energy that falls on their leaves, converting it to food energy. In especially productive systems, this percentage may be a little higher. When these plants are consumed by other organisms, only a portion of the plant's accumulated energy is actually converted into the bodies of the organisms that consume them.

Several different levels of consumers exist. The **primary consumers,** or herbivores, feed directly on the green plants. **Secondary consumers,** carnivores and the parasites of animals, feed in turn on the herbivores. **Decomposers** break down the organic matter accumulated in the bodies of other organisms. Another more general term that includes decomposers is **detritivores.** Detritivores live on the refuse of an ecosystem. They include large scavengers, such as crabs, vultures, and jackals, as well as decomposers.

All of these categories occur in any ecosystem. They represent different **trophic levels,** from the Greek word *trophos*, which means "feeder." Organisms from each trophic level, feeding on one another, make up a series called a **food chain** (figure 28.8). The length and complexity of food chains vary greatly. In real life, it is rather rare for a given kind of organism to feed only on one other type of organism. Usually, each organism feeds on two or more kinds and in turn is eaten by several other kinds of organisms. When diagrammed, the relationship appears as a series of branching lines, rather than a straight line; it is called a **food web** (figure 28.9).

A certain amount of the chemical-bond energy ingested by the organisms at a given trophic level goes toward staying alive (for example, carrying out mechanical motion). Using the chemical-bond energy converts it to heat, which organisms cannot use to do work. Another portion of the chemical-bond energy taken in is retained as chemical-bond energy within the organic molecules produced by growth. Usually 40% or less of the energy ingested is
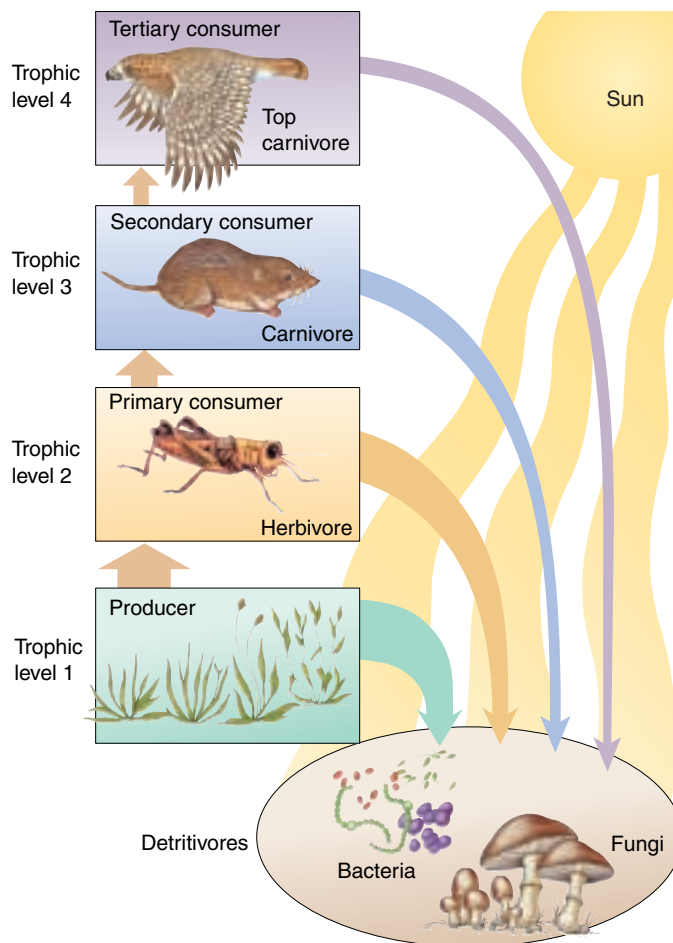

FIGURE 28.8
Trophic levels within a food chain. Plants obtain their energy directly from the sun, placing them at trophic level 1. Animals that eat plants, such as grasshoppers, are primary consumers or herbivores and are at trophic level 2. Animals that eat plant-eating animals, such as shrews, are carnivores and are at trophic level 3 (secondary consumers); animals that eat carnivorous animals, such as hawks, are tertiary consumers at trophic level 4. Detritivores use all trophic levels for food.

stored by growth. An invertebrate typically uses about a quarter of this 40% for growth; in other words, about 10% of the food an invertebrate eats is turned into its own body and thus into potential food for its predators. Although the comparable figure varies from approximately 5% in carnivores to nearly 20% for herbivores, 10% is a good average value for the amount of organic matter that reaches the next trophic level.

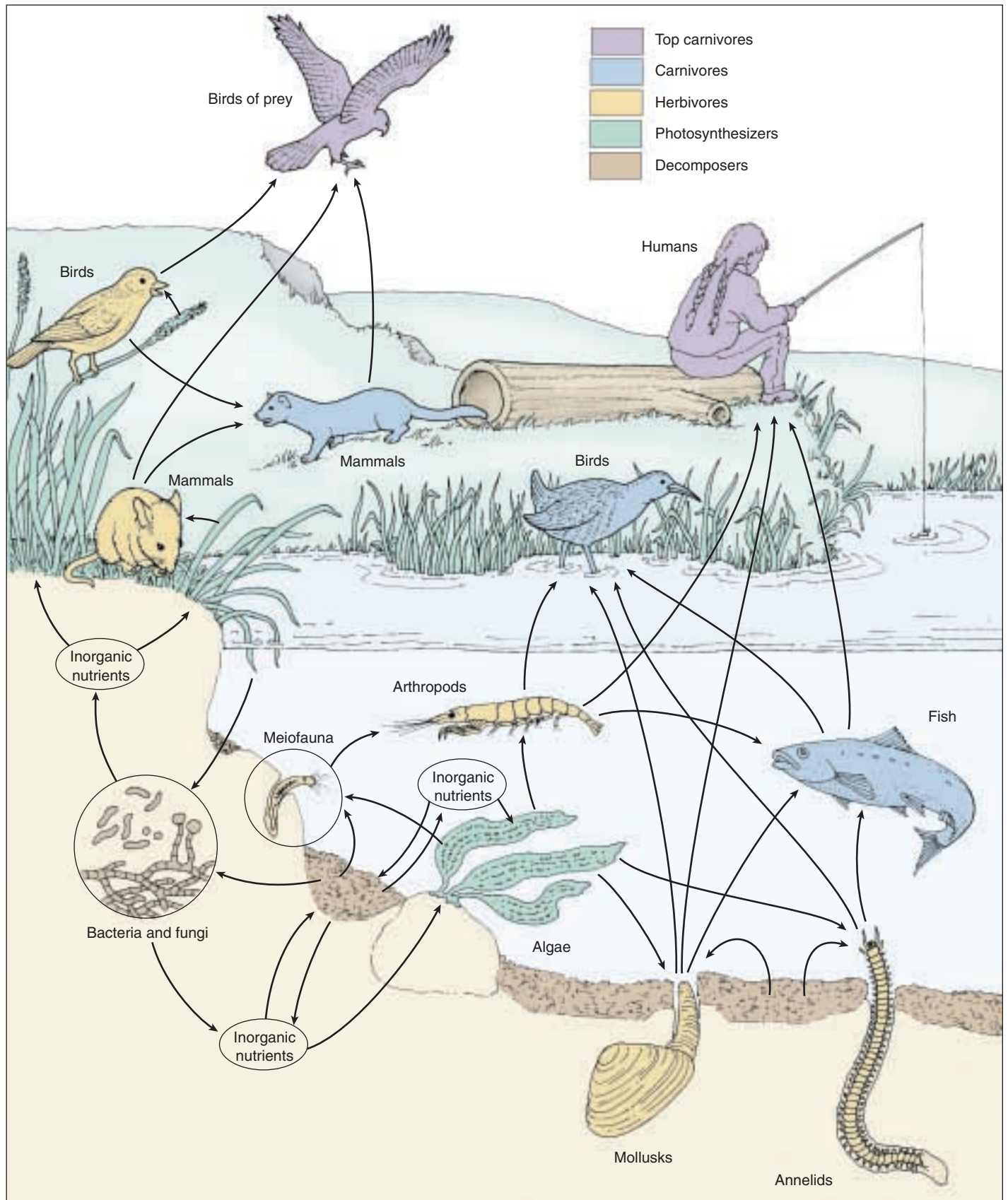**Energy passes through ecosystems, a good deal being lost at each step.**

FIGURE 28.9
The food web in a salt marsh shows the complex interrelationships among organisms. The meiofauna are very small animals that live between the grains of sand.

Primary Productivity

Approximately 1 to 5% of the solar energy that falls on a plant is converted to the chemical bonds of organic material. **Primary production** or **primary productivity** are terms used to describe the amount of organic matter produced from solar energy in a given area during a given period of time. **Gross primary productivity** is the total organic matter produced, including that used by the photosynthetic organism for respiration. **Net primary productivity (NPP),** therefore, is a measure of the amount of organic matter produced in a community in a given time that is available for heterotrophs. It equals the gross primary productivity minus the amount of energy expended by the metabolic activities of the photosynthetic organisms. The net weight of all of the organisms living in an ecosystem, its **biomass,** increases as a result of its net production.

Productive Biological Communities

Some ecosystems have a high net primary productivity. For example, tropical forests and wetlands normally produce between 1500 and 3000 grams of organic material per square meter per year. By contrast, corresponding figures for other communities include 1200 to 1300 grams for temperate forests, 900 grams for savanna, and 90 grams for deserts (table 28.1).

Table 28.1   Terrestrial Ecosystem Productivity Per Year

Ecosystem Type	Net Primary Productivity (NPP)	
	NPP per Unit Area (g/m^2)	World NPP (10^9 tons)
Extreme desert, rock, sand, and ice	3	0.07
Desert and semidesert shrub	90	1.6
Tropical rain forest	2200	37.4
Savanna	900	13.5
Cultivated land	650	9.1
Boreal forest	800	9.6
Temperate grassland	600	5.4
Woodland and shrubland	700	6.0
Tundra and alpine	140	1.1
Tropical seasonal forest	1600	12.0
Temperate deciduous forest	1200	8.4
Temperate evergreen forest	1300	6.5
Wetlands	2000	4.0

Source: After Whittaker, 1975.

Secondary Productivity

The rate of production by heterotrophs is called **secondary productivity.** Because herbivores and carnivores cannot carry out photosynthesis, they do not manufacture biomolecules directly from CO_2. Instead, they obtain them by eating plants or other heterotrophs. Secondary productivity by herbivores is approximately an order of magnitude less than the primary productivity upon which it is based. Where does all the energy in plants that is not captured by herbivores go (figure 28.10)? First, much of the biomass is not consumed by herbivores and instead supports the decomposer community (bacteria, fungi and detritivorous animals). Second, some energy is not assimilated by the herbivore's body but is passed on as feces to the decomposers. Third, not all the chemical-bond energy which herbivores assimilate is retained as chemical-bond energy in the organic molecules of their tissues. Some of it is lost as heat produced by work.

Primary productivity occurs as a result of photosynthesis, which is carried out by green plants, algae, and some bacteria. Secondary productivity is the production of new biomass by heterotrophs.

17%
Growth

33%
Cellular
respiration

50%
Feces

FIGURE 28.10
How heterotrophs utilize food energy. A heterotroph assimilates only a fraction of the energy it consumes. For example, if the "bite" of a herbivorous insect comprises 500 Joules of energy (1 Joule = 0.239 calories), about 50%, 250 J, is lost in feces, about 33%, 165 J, is used to fuel cellular respiration, and about 17%, 85 J, is converted into insect biomass. Only this 85 J is available to the next trophic level.
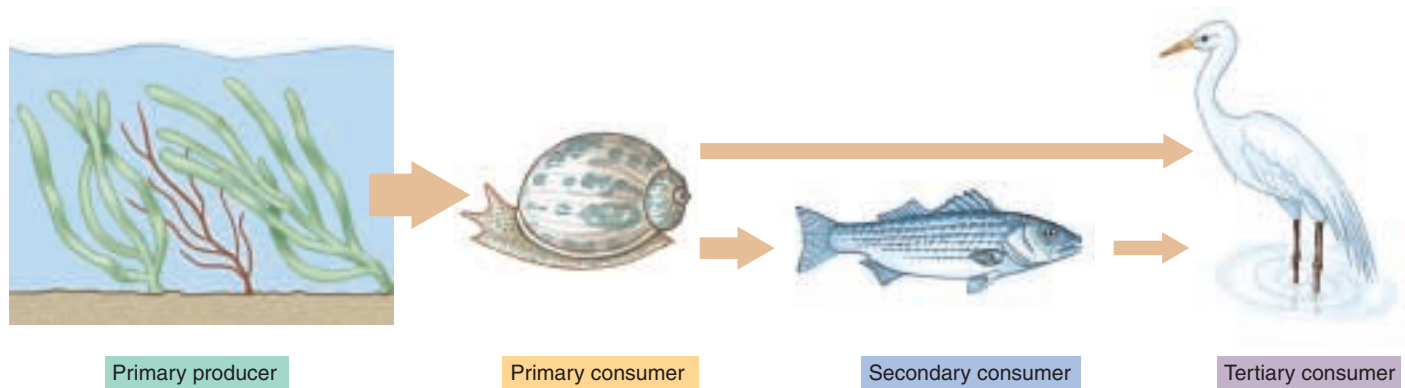
FIGURE 28.11
A food chain. Because so much energy is lost at each step, food chains usually consist of just three or four steps.

The Energy in Food Chains

Food chains generally consist of only three or four steps (figure 28.11). So much energy is lost at each step that very little usable energy remains in the system after it has been incorporated into the bodies of organisms at four successive trophic levels.

Community Energy Budgets

Lamont Cole of Cornell University studied the flow of energy in a freshwater ecosystem in Cayuga Lake in upstate New York. He calculated that about 150 of each 1000 calories of potential energy fixed by algae and cyanobacteria are transferred into the bodies of small heterotrophs (figure 28.12). Of these, about 30 calories are incorporated into the bodies of smelt, small fish that are the principal secondary consumers of the system. If humans eat the smelt, they gain about 6 of the 1000 calories that originally entered the system. If trout eat the smelt and humans eat the trout, humans gain only about 1.2 calories.

Factors Limiting Community Productivity

Communities with higher productivity can in theory support longer food chains. The limit on a community's productivity is determined ultimately by the amount of sunlight it receives, for this determines how much photosynthesis can occur. This is why in the deciduous forests of North America the net primary productivity increases as the growing season lengthens. NPP is higher in warm climates than cold ones not only because of the longer growing seasons, but also because more nitrogen tends to be available in warm climates, where nitrogen-fixing bacteria are more active.

Considerable energy is lost at each stage in food chains, which limits their length. In general, more productive food chains can support longer food chains.

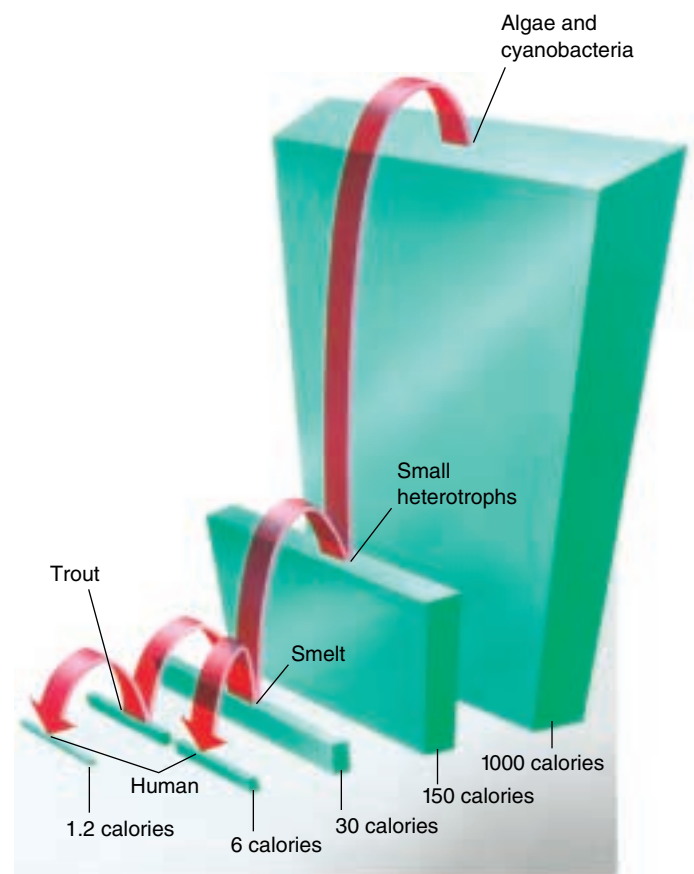**FIGURE 28.12**
The food web in Cayuga Lake. Autotrophic plankton (algae and cyanobacteria) fix the energy of the sun, heterotrophic plankton feed on them, and are both consumed by smelt. The smelt are eaten by trout, with about a fivefold loss in fixed energy; for humans, the amount of smelt biomass is at least five times greater than that available in trout, although humans prefer to eat trout.

Ecological Pyramids

A plant fixes about 1% of the sun's energy that falls on its green parts. The successive members of a food chain, in turn, process into their own bodies about 10% of the energy available in the organisms on which they feed. For this reason, there are generally far more individuals at the lower trophic levels of any ecosystem than at the higher levels. Similarly, the biomass of the primary producers present in a given ecosystem is greater than the biomass of the primary consumers, with successive trophic levels having a lower and lower biomass and correspondingly less potential energy.

These relationships, if shown diagrammatically, appear as pyramids (figure 28.13). We can speak of "pyramids of biomass," "pyramids of energy," "pyramids of number," and so forth, as characteristic of ecosystems.

Inverted Pyramids

Some aquatic ecosystems have inverted biomass pyramids. For example, in a planktonic ecosystem—dominated by small organisms floating in water—the turnover of photosynthetic phytoplankton at the lowest level is very rapid, with zooplankton consuming phytoplankton so quickly that the phytoplankton (the producers at the base of the food chain) can never develop a large population size. Because the phytoplankton reproduce very rapidly, the community can support a population of heterotrophs that is larger in biomass and more numerous than the phytoplankton (see figure 28.13b).

Top Carnivores

The loss of energy that occurs at each trophic level places a limit on how many top-level carnivores a community can support. As we have seen, only about one-thousandth of the energy captured by photosynthesis passes all the way through a three-stage food chain to a tertiary consumer such as a snake or hawk. This explains why there are no predators that subsist on lions or eagles—the biomass of these animals is simply insufficient to support another trophic level.

In the pyramid of numbers, top-level predators tend to be fairly large animals. Thus, the small residual biomass available at the top of the pyramid is concentrated in a relatively small number of individuals.

Because energy is lost at every step of a food chain, the biomass of primary producers (photosynthesizers) tends to be greater than that of the herbivores that consume them, and herbivore biomass greater than the biomass of the predators that consume them.

Pyramid of numbers

(a)

Pyramid of biomass

(b)

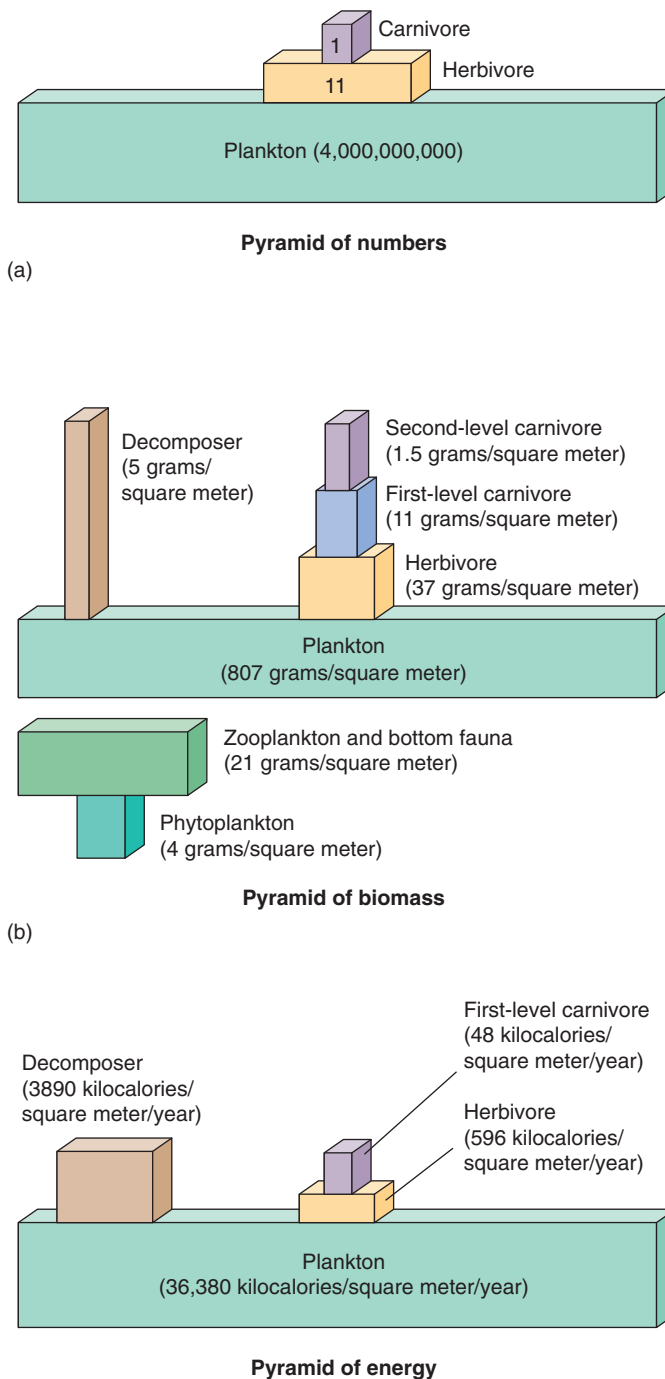**Pyramid of energy**

(c)

FIGURE 28.13
Ecological pyramids. Ecological pyramids measure different characteristics of each trophic level. (*a*) Pyramid of numbers. (*b*) Pyramids of biomass, both normal (*top*) and inverted (*bottom*). (*c*) Pyramid of energy.

Interactions among Different Trophic Levels

The existence of food webs creates the possibility of inter-actions among species at different trophic levels. Predators will not only have effects on the species upon which they prey, but also, indirectly, upon the plants eaten by these prey. Conversely, increases in primary productivity will not only provide more food for herbivores but, indirectly, lead also to more food for carnivores.

Trophic Cascades

When we look at the world around us, we see a profusion of plant life. Why is this? Why don't herbivore populations increase to the extent that all available vegetation is con-sumed? The answer, of course, is that predators keep the herbivore populations in check, thus allowing plant popula-tions to thrive. This phenomenon, in which the effect of one trophic level flows down to lower levels, is called a **trophic cascade**.

Experimental studies have confirmed the existence of trophic cascades. For example, in one study in New Zealand, sections of a stream were isolated with a mesh that prevented fish from entering. In some of the enclosures, brown trout were added, whereas other enclosures were left without large fish. After 10 days, the number of inverte-brates in the trout enclosures was one-half of that in the controls (figure 28.14). In turn, the biomass of algae, which invertebrates feed upon, was five times greater in the trout enclosures than in the controls.

The logic of trophic cascades leads to the prediction that a fourth trophic level, carnivores that preyed on other car-nivores, would also lead to cascading effects. In this case, the top predators would keep lower-level predator popula-tions in check, which should lead to a profusion of herbi-vores and a paucity of vegetation. In an experiment similar to the one just described, enclosures were created in free-flowing streams in northern California. In this case, large predatory fish were added to some enclosures and not oth-ers. In the large fish enclosures, the number of smaller predators, such as damselfly nymphs was greatly reduced, leading to an increase in their prey, including algae-eating insects, which lead, in turn, to decreases in the biomass of algae (figure 28.15).

FIGURE 28.14
Trophic cascades. Streams with trout have fewer herbivorous invertebrates and more algae than streams without trout.

FIGURE 28.15
Four-level trophic cascades. Streams with fish have fewer lower-level predators, such as damselflies, more herbivorous insects (exemplified by the number of chironomids, a type of aquatic insect), and lower levels of algae.
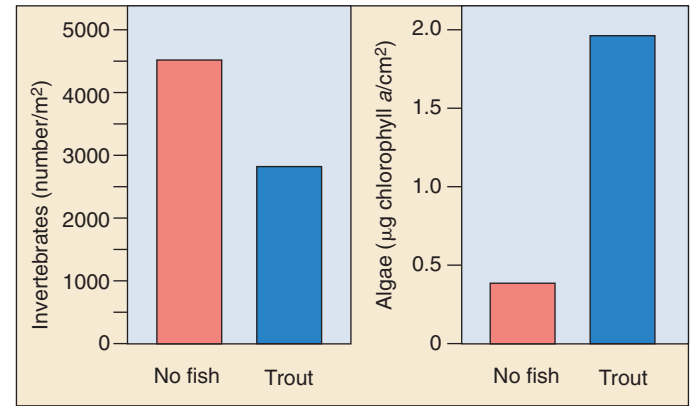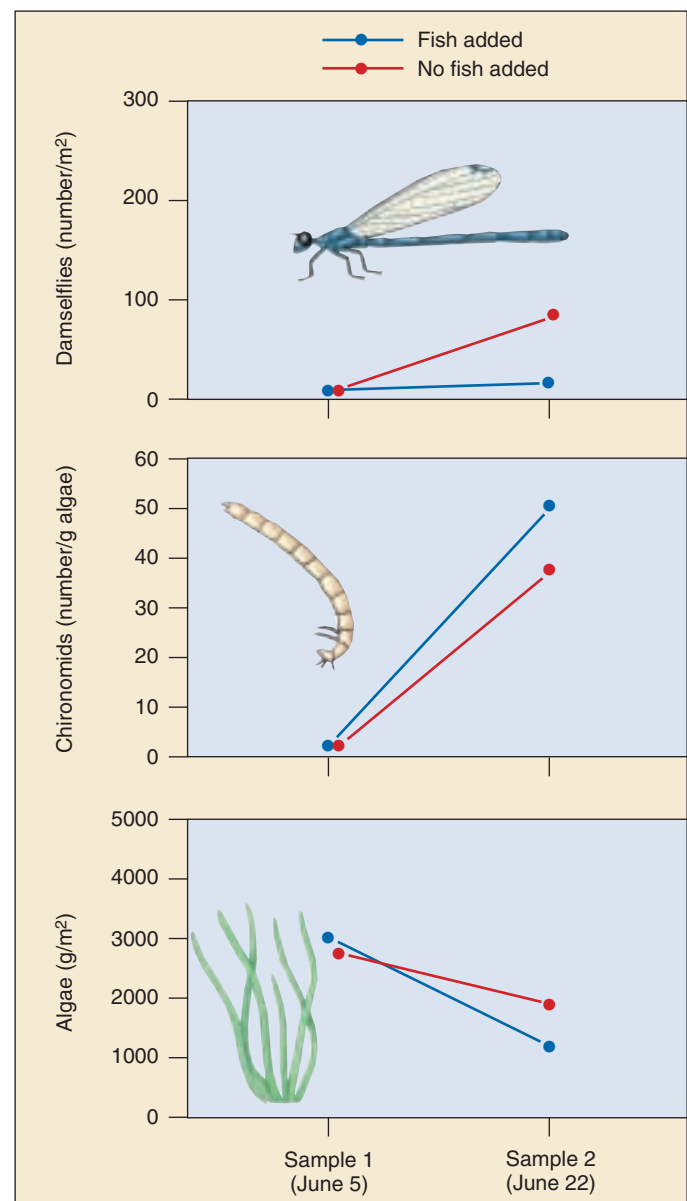
Human Effects on Trophic Cascades

Humans have inadvertently created a test of the trophic cascade hypothesis by removing top predators from ecosystems. The great naturalist Aldo Leopold captured the results long before the trophic cascade hypothesis had ever been scientifically articulated when he wrote in the *Sand County Almanac:*

"I have lived to see state after state extirpate its wolves. I have watched the face of many a new wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddle horn."

Many similar examples exist in nature in which the removal of predators has led to cascading effects on lower trophic levels. On Barro Colorado Island, a hilltop turned into an island by the construction of the Panama Canal at the beginning of the last century, large predators such as jaguars and mountain lions are absent. As a result, smaller predators whose populations are normally held in check—including monkeys, peccaries (a relative of the pig), coatimundis and armadillos—have become extraordinarily abundant. These animals will eat almost anything they find. Ground-nesting birds are particularly vulnerable, and many species have declined; at least 15 bird species have vanished from the island entirely. Similarly, in woodlots in the midwestern United States, raccoons, opossums, and foxes have become abundant due to the elimination of larger predators, and populations of ground-nesting birds have declined greatly.

Bottom-Up Effects

Conversely, factors acting at the bottom of food webs may have consequences that ramify to higher trophic levels, leading to what are termed **bottom-up effects**. The basic idea is when the productivity of an ecosystem is low, herbivore populations will be too small to support any predators. Increases in productivity will be entirely devoured by the herbivores, whose populations will increase in size. At some point, herbivore populations will become large enough that predators can be supported. Thus, further increases in productivity will not lead to increases in herbivore populations, but, rather to increases in predator populations. Again, at some level, top predators will become established that can prey on lower-level predators. With the lower-level predator populations in check, herbivore populations will again increase with increasing productivity (figure 28.16).

Experimental evidence for the role of bottom-up effects was provided in an elegant study conducted on the Eel River in northern California. Enclosures were constructed that excluded large fish. A roof was placed above each enclosure. Some roofs were clear and let light pass
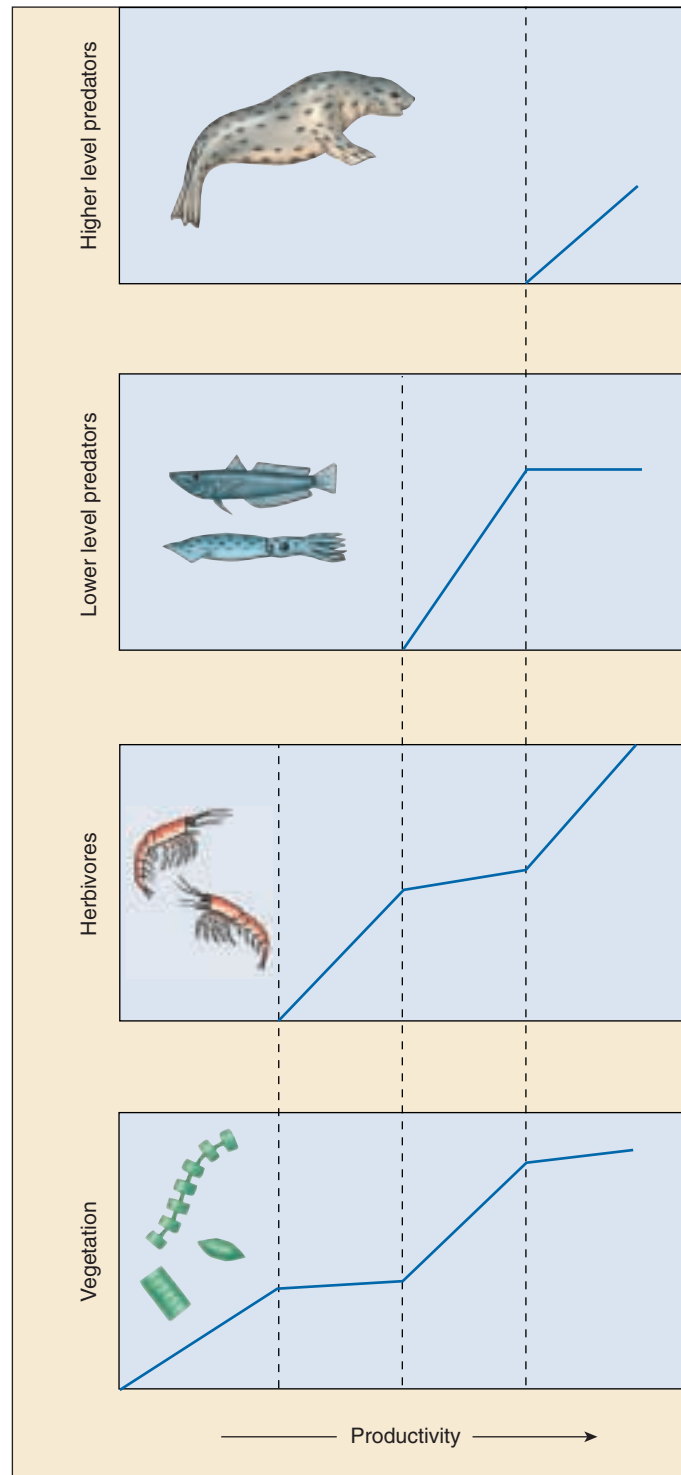
FIGURE 28.16
Bottom-up effects. At low levels of productivity, herbivore populations cannot be maintained. Above some threshold, increases in productivity lead to increases in herbivore biomass; vegetation biomass no longer increases with productivity because it is converted into herbivore biomass. Similarly, above another threshold, herbivore biomass gets converted to carnivore biomass. At this point, vegetation biomass is no longer constrained by herbivores, and so again increases with increasing productivity.

through, whereas others produced light or deep shade. The result was that the enclosures differed in the amount of sunlight reaching them. As one might expect, the primary productivity differed and was greatest in the unshaded enclosures. This increased productivity led to both more vegetation and more predators, but the trophic level sandwiched in between, the herbivores, did not increase, precisely as the bottom-up hypothesis predicted (figure 28.17).

Relative Importance of Trophic Cascades and Bottom-Up Effects

Neither trophic cascades nor bottom-up effects are inevitable. For example, if two species of herbivores exist in an ecosystem and compete strongly, and if one species is much more vulnerable to predation than the other, then top-down effects will not propagate to the next lower trophic level. Rather, increased predation will simply decrease the population of the vulnerable species while increasing the population of its competitor, with potentially no net change on the vegetation in the next lower trophic level.

Similarly, productivity increases might not move up through all trophic levels. In some cases, for example, prey populations increase so quickly that their predators cannot control them. In such cases, increases in productivity would not move up the food chain.

In other cases, trophic cascades and bottom-up effects may reinforce each other. In one experiment, large fish were removed from one lake, leaving only minnows, which ate most of the algae-eating zooplankton. By contrast, in the other lake, there were few minnows and much zooplankton. The researchers then added nutrients to both lakes. In the minnow lake, there were few zooplankton, so the resulting increase in algal productivity did not propagate up the food chain and large mats of algae formed. By comparison, in the large fish lake, increased productivity moved up the food chain and algae populations were controlled. In this case, both top-down and bottom-up processes were operating.

Nature, of course, is not always so simple. In some cases, species may simultaneously operate on multiple trophic levels, such as the jaguar which eats both smaller carnivores and herbivores, or the bear which eats both fish and berries. Nature is often much more complicated than a simple, linear food chain, as figure 28.9 indicates. Ecologists are currently working to apply theories of food chain interactions to these more complicated situations.

Because of the linked nature of food webs, species on different trophic levels will effect each other, and these effects can promulgate both up and down the food web.
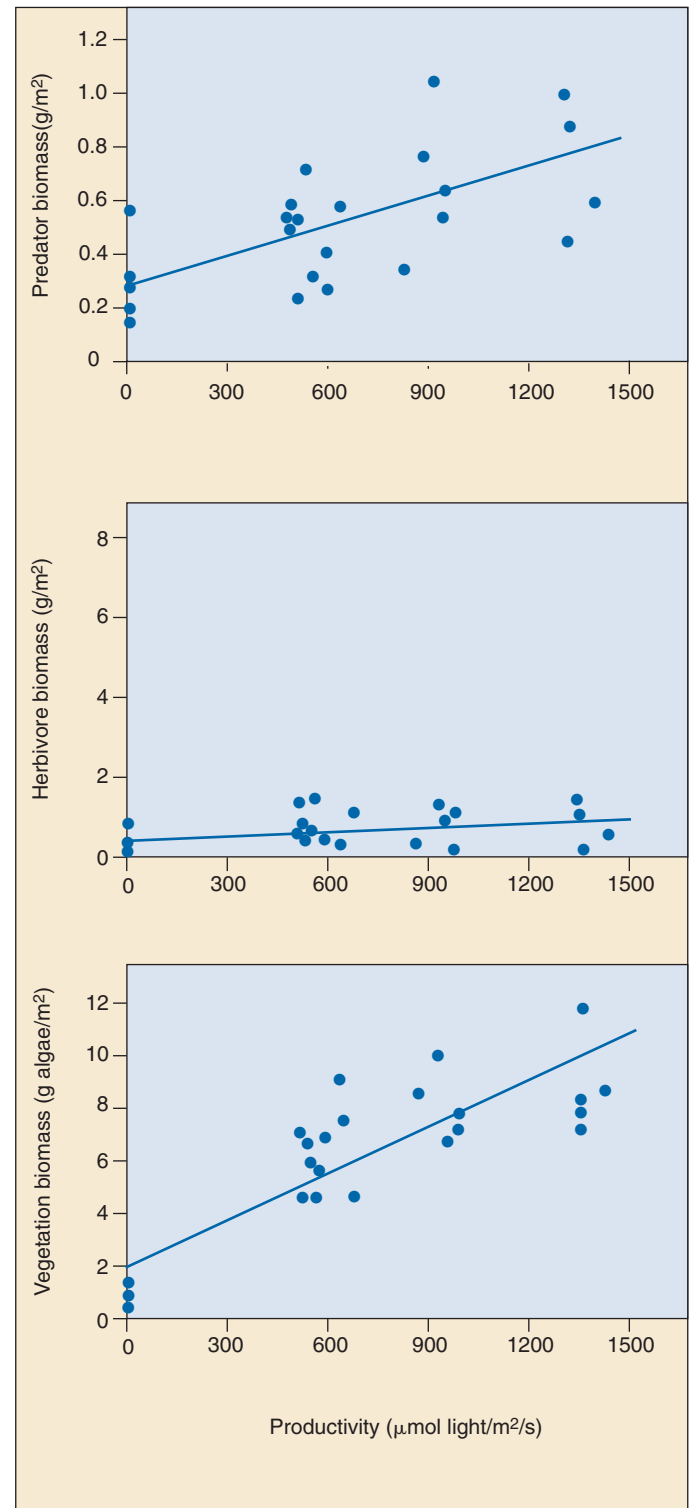

FIGURE 28.17
Bottom-up effects on a stream ecosystem. As predicted, increases in productivity—which are a function of the amount of light hitting the stream and leading to photosynthesis—lead to increases in the amount of vegetation. However, herbivore biomass does not increase with increased productivity because it is converted into predator biomass.

28.4 Biodiversity promotes ecosystem stability.

Effects of Species Richness

Ecologists have long debated what are the consequences of differences in species richness among communities. One theory is that more species-rich communities are more stable; that is, more constant in composition and better able to resist disturbance. This hypothesis has been elegantly studied by David Tilman and colleagues at the University of Minnesota's Cedar Creek Natural History Area. These workers monitored 207 small rectangular plots of land (8 to 16 m^2) for 11 years. In each plot, they counted the number of prairie plant species and measured the total amount of plant biomass (that is, the mass of all plants on the plot). Over the course of the study, plant species richness was related to community stability—plots with more species showed less year-to-year variation in biomass (figure 28.18). Moreover, in two drought years, the decline in biomass was negatively related to species richness; in other words, plots with more species were less affected. In a related experiment, when seeds of other plant species were added to different plots, the ability of these species to become established was negatively related to species richness. More diverse communities, in other words, are more resistant to invasion by new species, another measure of community stability.

Species richness may also have effects on other ecosystem processes. In a follow-up study, Tilman established another 147 plots in which they experimentally varied the number of plant species. Each of the plots was monitored to estimate how much growth was occurring and how much nitrogen the growing plants were taking up from the soil. Tilman found that the more species a plot had, the greater nitrogen uptake and total amount of biomass produced. In his study, increased biodiversity clearly leads to greater productivity (figure 28.19).

Laboratory studies on artificial ecosystems have provided similar results. In one elaborate study, ecosystems covering 1 m^2 were constructed in growth chambers that controlled temperature, light levels, air currents, and atmospheric gas concentrations. A variety of plants, insects, and other animals were introduced to construct ecosystems composed of 9, 15, or 31 species with the lower diversity treatments containing a subset of the species in the higher diversity enclosures. As with Tilman's experiments, the amount of biomass produced was related to species richness, as was the amount of carbon dioxide consumed, a measure of respiration occurring in the ecosystem.

Tilman's conclusion that healthy ecosystems depend on diversity is not accepted by all ecologists. Critics question the validity and relevance of these biodiversity studies, claiming their experimental design is critically flawed. Tilman's Cedar Creek result was a statistical arti-
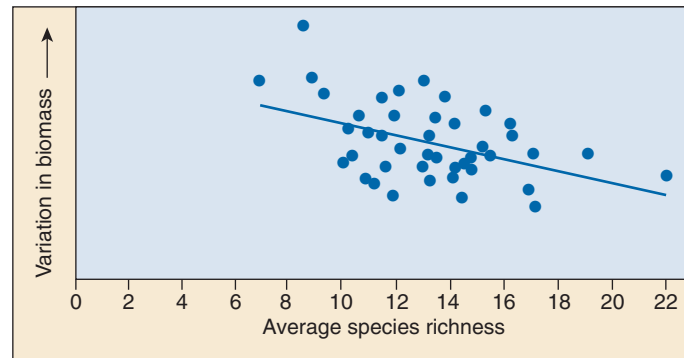

FIGURE 28.18
Effect of species richness on ecosystem stability. In the Cedar Creek experimental fields, each square is a 100-square-foot experimental plot. Experimental plots with more plant species seem to show less variation in the total amount of biomass produced, and thus more community stability.
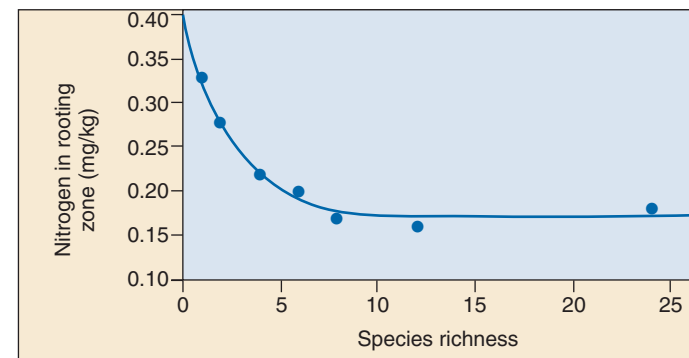

FIGURE 28.19
Effect of species richness on productivity. In Tilman's experimental studies, plots with more species took up more nitrogen from the soil, leaving less in the rooting zone. The increased amount of nitrogen absorption is an indicator of increased growth, increased biomass, and thus increased productivity.

fact, they argue—the more species you add to a mix, the greater the probability that you will add a highly productive one. Adding taller or highly productive plants of course increases productivity, they explain. To show a real benefit from diversity, experimental plots would have to exhibit "overyielding"—plot productivity would have to be greater than that of the single most productive species grown in isolation. The long-simmering debate continues.

Controversial experimental field studies support the hypothesis that species-rich communities are more stable.

Causes of Species Richness

While ecologists still argue about why some ecosystems are more stable than others—better able to avoid permanent change and return to normal after disturbances like land clearing, fire, invasion by plagues of insects, or severe storm damage—most ecologists now accept as a working hypothesis that biologically diverse ecosystems are generally more stable than simple ones. Ecosystems with many different kinds of organisms support a more complex web of interactions, and an alternative niche is thus more likely to exist to compensate for the effect of a disruption.

Factors Promoting Species Richness

How does the number of species in a community affect the functioning of the ecosystem? How does ecosystem functioning affect the number of species in a community? It is often extremely difficult to sort out the relative contributions of different factors. With regard to determinants of species richness in a community, of the many variables that may play a role, we will discuss three: ecosystem productivity, spatial heterogeneity, and climate. Two additional factors that may play an important role, the evolutionary age of the community and the degree to which the community has been disturbed, will be examined later in this chapter.

Ecosystem Productivity. Ecosystems differ in productivity, which is a measure of how much new growth they can produce. Surprisingly, the relationship between productivity and species richness is not linear. Rather, ecosystems with intermediate levels of productivity tend to have the most species (figure 28.20). Why this is so is a topic of considerable current debate. One possibility is that levels of productivity are linked to numbers of predators. At low productivity, there are few predators and superior competitors eliminate most species, whereas at high productivity, there are so many predators that only the most predation-resistant species survive. At intermediate levels, however, predators may act as keystone species, maintaining species richness.

Spatial Heterogeneity. Environments that are more spatially heterogeneous—that contain more soil types, topographies, and other habitat variations—can be expected to accommodate more species because they provide a greater variety of microhabitats, microclimates, places to hide from predators, and so on. In general, the species richness of animals tends to reflect the species richness of the plants in their community, while plant species richness reflects the spatial heterogeneity of the ecosystem. The plants provide a biologically derived spatial heterogeneity of microhabitats to the animals. Thus, the number of lizard species in the American Southwest mirrors the structural diversity of the plants (figure 28.21).
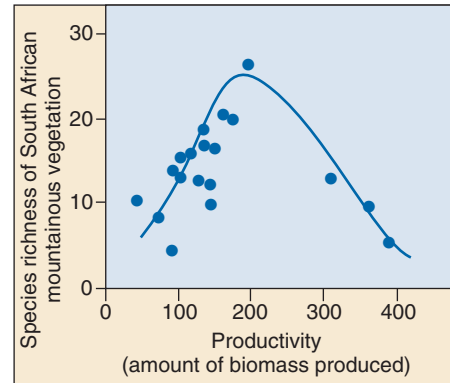

FIGURE 28.20 Productivity. In fynbos plant communities of mountainous areas of South Africa, species richness of plants peaks at intermediate levels of productivity (biomass).
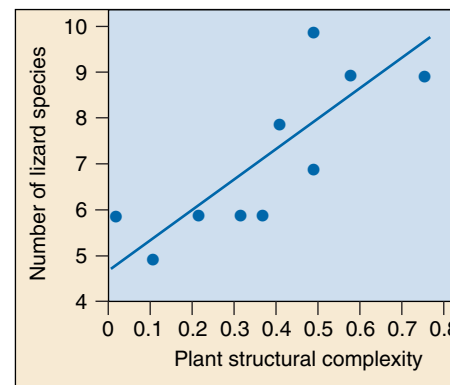

FIGURE 28.21 Spatial heterogeneity. The species richness of desert lizards is positively correlated with the structural complexity of the plant cover in desert sites in the American Southwest.
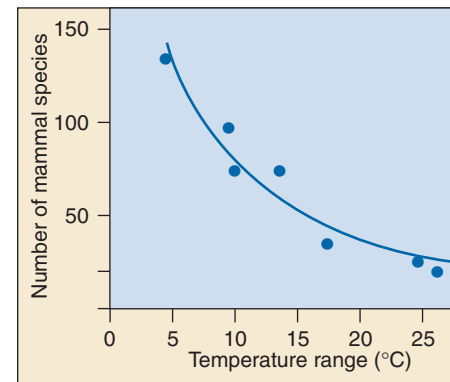

FIGURE 28.22 Climate. The species richness of mammals is inversely correlated with monthly mean temperature range along the west coast of North America.

Climate. The role of climate is more difficult to assess. On the one hand, more species might be expected to coexist in a seasonal environment than in a constant one, because a changing climate may favor different species at different times of the year. On the other hand, stable environments are able to support specialized species that would be unable to survive where conditions fluctuate. Thus, the number of mammal species along the west coast of North America increases as the temperature range decreases (figure 28.22).

Species richness promotes ecosystem productivity and is fostered by spatial heterogeneity and stable climate.

Biogeographic Patterns of Species Diversity

Since before Darwin, biologists have recognized that there are more different kinds of animals and plants in the tropics than in temperate regions. For many species, there is a steady increase in species richness from the arctic to the tropics. Called a **species diversity cline,** such a biogeographic gradient in numbers of species correlated with latitude has been reported for plants and animals, including birds (figure 28.23), mammals, reptiles.

Why Are There More Species in the Tropics?

For the better part of a century, ecologists have puzzled over the cline in species diversity from the arctic to the tropics. The difficulty has not been in forming a reasonable hypothesis of why there are more species in the tropics, but rather in sorting through the many reasonable hypotheses that suggest themselves. Here we will consider five of the most commonly discussed suggestions:

Evolutionary age. It has often been proposed that the tropics have more species than temperate regions because the tropics have existed over long and uninterrupted periods of evolutionary time, while temperate regions have been subject to repeated glaciations. The greater age of tropical communities would have allowed complex population interactions to coevolve within them, fostering a greater variety of plants and animals in the tropics.

However, recent work suggests that the long-term stability of tropical communities has been greatly exaggerated. An examination of pollen within undisturbed soil cores reveals that during glaciations the tropical forests contracted to a few small refuges surrounded by grassland. This suggests that the tropics have not had a continuous record of species richness over long periods of evolutionary time.

Higher productivity. A second often-advanced hypothesis is that the tropics contain more species because this part of the earth receives more solar radiation than temperate regions do. The argument is that more solar energy, coupled to a year-round growing season, greatly increases the overall photosynthetic activity of plants in the tropics. If we visualize the tropical forest as a pie (total resources) being cut into slices (species niches), we can see that a larger pie accommodates more slices. However, many field studies have indicated that species richness is highest at intermediate levels of productivity. Accordingly, increasing productivity would be expected to lead to lower, not higher, species richness. Perhaps the long column of vegetation down through which light passes in a tropical forest produces a wide range of frequencies and intensities, creating a greater variety of light environments and so promoting species diversity.
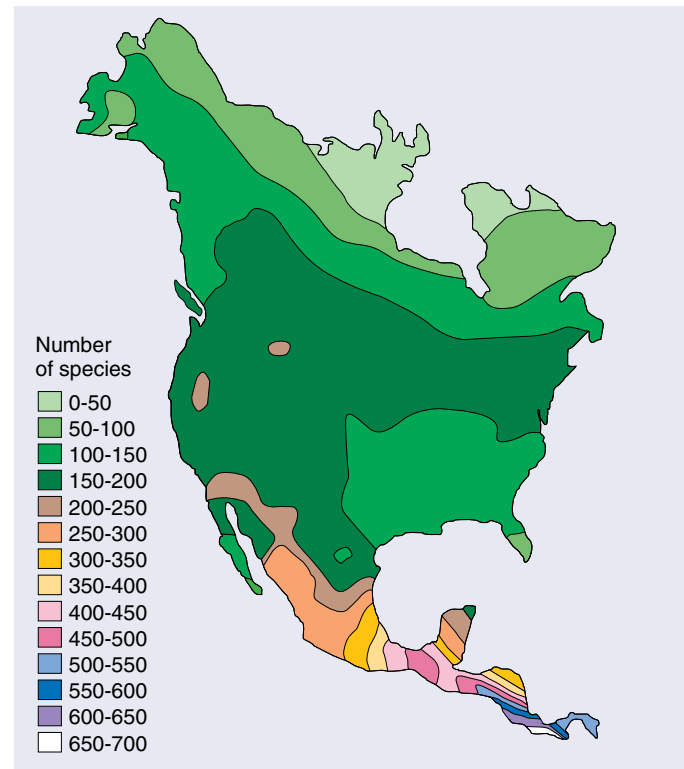

Number of species

- 0-50
- 50-100
- 100-150
- 150-200
- 200-250
- 250-300
- 300-350
- 350-400
- 400-450
- 450-500
- 500-550
- 550-600
- 600-650
- 650-700

FIGURE 28.23
A latitudinal cline in species richness. Among North and Central American birds, a marked increase in the number of species occurs as one moves toward the tropics. Fewer than 100 species are found at arctic latitudes, while more than 600 species live in southern Central America.

Predictability. There are no winters in the tropics. Tropical temperatures are stable and predictable, one day much like the next. These unchanging environments might encourage specialization, with niches subdivided to partition resources and so avoid competition. The expected result would be a larger number of more specialized species in the tropics, which is what we see. Many field tests of this hypothesis have been carried out, and almost all support it, reporting larger numbers of narrower niches in tropical communities than in temperate areas.

Predation. Many reports indicate that predation may be more intense in the tropics. In theory, more intense predation could reduce the importance of competition, permitting greater niche overlap and thus promoting greater species richness.

Spatial heterogeneity. As noted earlier, spatial heterogeneity promotes species richness. Tropical forests, by virtue of their complexity, create a variety of microhabitats and so may foster larger numbers of species.

No one really knows why there are more species in the tropics, but there are plenty of suggestions.

Island Biogeography

One of the most reliable patterns in ecology is the observation that larger islands contain more species than smaller islands. In 1967, Robert MacArthur of Princeton University and Edward O. Wilson of Harvard University proposed that this **species-area relationship** was a result of the effect of area on the likelihood of species extinction and colonization.

The Equilibrium Model

MacArthur and Wilson reasoned that species are constantly being dispersed to islands, so islands have a tendency to accumulate more and more species. At the same time that new species are added, however, other species are lost by extinction. As the number of species on an initially empty island increases, the rate of colonization must decrease as the pool of potential colonizing species not already present on the island becomes depleted. At the same time, the rate of extinction should increase—the more species on an island, the greater the likelihood that any given species will perish. As a result, at some point, the number of extinctions and colonizations should be equal and the number of species should then remain constant. Every island of a given size, then, has a characteristic equilibrium number of species that tends to persist through time (the intersection point in figure 28.24*a*), although the individual species will change as species become extinct and new species colonize.

MacArthur and Wilson's equilibrium theory proposes that island species richness is a dynamic equilibrium between colonization and extinction. Both island size and distance from the mainland would play important roles. We would expect smaller islands to have higher rates of extinction because their population sizes would, on average, be smaller. Also, we would expect fewer colonizers to reach islands that lie farther from the mainland. Thus, small islands far from the mainland have the fewest species; large islands near the mainland have the most (figure 28.24*b*).

The predictions of this simple model bear out well in field data. Asian Pacific bird species (figure 28.24*c*) exhibit a positive correlation of species richness with island size, but a negative correlation of species richness with distance from the mainland.

Testing the Equilibrium Model

Field studies in which small islands have been censused, cleared, and allowed to recolonize tend to support the equilibrium model. However, long-term experimental field studies are suggesting that the situation is more complicated than MacArthur and Wilson envisioned. Their theory predicts a high level of **species turnover** as some species perish and others arrive. However, studies on island birds and spiders indicate that very little turnover occurs from year to year. Moreover, those species that do come and go are a subset of species that never attain high populations. A substantial proportion of the species appears to maintain high populations and rarely go extinct. These studies, of course, have only been going on for 20 years or less. It is possible that over periods of centuries, rare species may become common and vice versa so that, over such spans of time, the equilibrium theory is a good description of what determines island species richness. Future research is necessary to fully understand the dynamics of species richness.

> **Species richness on islands is a dynamic equilibrium between colonization and extinction.**
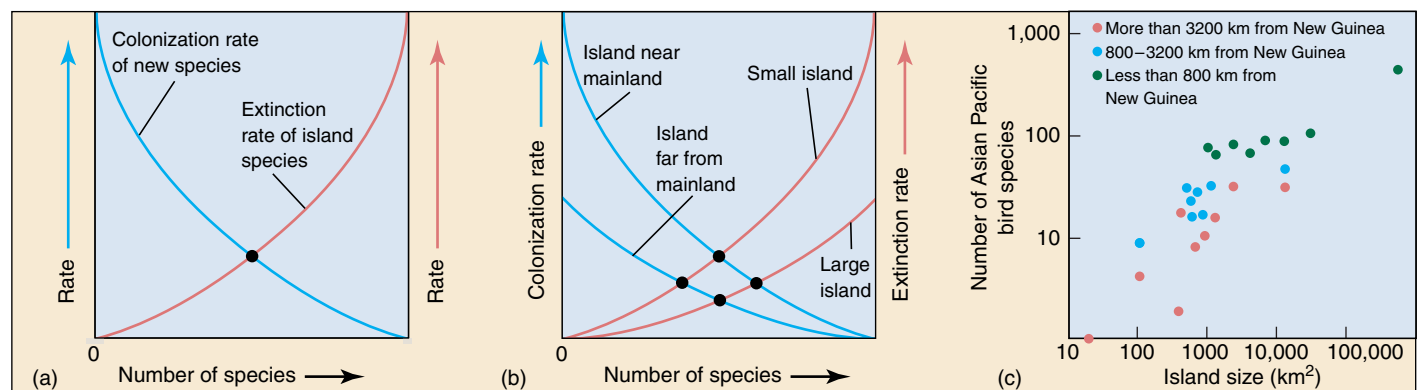

FIGURE 28.24
The equilibrium model of island biogeography. (*a*) Island species richness reaches an equilibrium (*black dot*) when the colonization rate of new species equals the extinction rate of species on the island. (*b*) The equilibrium shifts when the colonization rate is affected by distance from the mainland and when the extinction rate is affected by size of the island. Species richness is positively correlated with island size and inversely correlated with distance from the mainland. (*c*) The effect of distance from a larger island—which can be the source of colonizing species—is readily apparent. More distant islands have fewer species compared to nearer islands of the same size.

Summary	*Questions*	*Media Resources*

28.1 Chemicals cycle within ecosystems.

- Fully 98% of the water on earth cycles through the atmosphere. In the United States, 96% of the fresh water is groundwater.
- About 10% of the roughly 700 billion metric tons of free carbon dioxide in the atmosphere is fixed each year through photosynthesis. About as much carbon exists in living organisms at any one time as is present in the atmosphere.
- Carbon, nitrogen, and oxygen have gaseous or liquid reservoirs, as does water. All of the other nutrients, such as phosphorus, are contained in solid mineral reservoirs.
- Phosphorus is a key component of many biological molecules; it weathers out of soils and is transported to the world's oceans.

1. What are the primary reservoirs for the chemicals in biogeochemical cycles? Are more of the life-sustaining chemicals found in these reservoirs or in the earth's living organisms?

2. What is denitrification? Which organisms carry it out?

3. How is the phosphorus cycle different from the water, carbon, nitrogen, and oxygen cycles? What are the natural sources for phosphorus?

4. What effect does deforestation have on the water cycle and overall fertility of the land?

- Activity: Nutrient Cycle
- Activity: Carbon Cycle
- Ecosystem Introduction
- Ecosystem Concept Quiz
- Water Cycle
- Ground Water
- Water Qaulity
- Nutrient Cycles

- Carbon Cycle
- Nitrogen Cycle

28.2 Ecosystems are structured by who eats whom.

- Plants convert about 1 to 5% of the light energy that falls on their leaves to food energy. Producers, the herbivores that eat them, and the carnivores that eat the herbivores constitute three trophic levels.
- At each level, only about 10% of the energy available in the food is fixed in the body of the consumer. For this reason, food chains are always relatively short.

5. How might an increase in the number of predators affect lower levels of a food chain. How might an increase in nutrients affect upper levels?

- Activity: Energy flow
- Energy Flow

28.3 Energy flows through ecosystems.

- The primary productivity of a community is a measure of the biomass photosynthesis produces within it.
- As energy passes through the trophic levels of an ecosystem, much is lost at each step. Ecological pyramids reflect this energy loss.

6. What is the difference between primary productivity, gross primary productivity, and net primary productivity?

7. Which type of diet, carnivorous or herbivorous, provides more food value to any given living organism?

- Exponential Population Growth

- Student Research: Assessing Paleoenvironments

28.4 Biodiversity promotes ecosystem stability.

- Increasing the number of species in a community seems to promote ecosystem productivity. Controversial experiments suggest that communities with increased species richness are more stable and less vulnerable to disturbance.

8. Why might rain forests have high levels of species diversity?

9. Why do distant islands tend to have fewer species than nearer islands of the same size? Why do different-sized islands tend to differ in species number?

- On Science Article: Is Biodiversity Good?
- Bioethics Case Study: Wolves in Yellowstone
- Book review: *Island of the Colorblind* by Sacks
- *The Song of the Dodo* by Quammen