CHAPTER 5

Ecosystems: Concepts and Fundamentals

Ecotourists see the first stages in ecological succession at Doñana National Park, Spain—plants that can germinate and grow in sandy soil recently deposited by the winds. Doñana National Park is one of the major stopovers for birds migrating from Europe to Africa, and is one of Europe's most important wildlife parks.

LEARNING OBJECTIVES

Life on Earth is sustained by ecosystems, which vary greatly but have certain attributes in common. After reading this chapter, you should understand . . .

- Why the ecosystem is the basic system that supports life and allows it to persist;
- What food chains, food webs, and trophic levels are;
- What ecosystem chemical cycling is;
- What the ecological community is;
- How to determine the boundaries of an ecosystem;
- How species affect one another indirectly through their ecological community;
- How ecosystems recover from disturbances through ecological succession;
- Whether ecosystems are generally in a steady state.

CASE STUDY

Sea Otters, Sea Urchins, and Kelp: Indirect Effects of Species on One Another

Sea otters, the lovable animals often shown lying faceup among kelp as they eat shellfish, play an important role in their ecosystems. Although they feed on a variety of shellfish, sea otters especially like sea urchins. Sea urchins, in turn, feed on kelp, large brown algae that form undersea "forests" and provide important habitat for many species that require kelp beds for reproduction, places to feed, or havens from predators. Sea urchins graze along the bottoms of the beds, feeding on the base of kelp, called *holdfasts*, which attach the kelp to the bottom. When holdfasts are eaten through, the kelp floats free and dies. Sea urchins thus can clear kelp beds—clear-cutting, so to speak.

While sea otters affect the abundance of kelp, their influence is indirect (Figure 5.1)—they neither feed on kelp nor protect individual kelp plants from attack by sea urchins. But sea otters reduce the number of sea urchins. With fewer sea urchins, less kelp is destroyed. With more kelp, there is more habitat for many other species; so sea otters indirectly increase the diversity of species.[1,2] This is called a **community effect**, and the otters are referred to as **keystone species** in their ecological community and ecosystem.

Sea otters originally occurred throughout a large area of the Pacific coasts, from northern Japan northeastward along the Russian and Alaskan coasts, and southward along the coast of North America to Morro Hermoso in Baja California and to Mexico.[4] But sea otters also like to eat abalone, and this brings them into direct conflict with people, since abalone is a prized seafood for us, too. They also have one of the finest furs in the world and were brought almost to extinction by commercial hunting for their fur during the 18th and 19th centuries. By the end of the 19th century, there were too few otters left to sustain commercial fur hunters.

Several small populations survived and have increased since then, so that today sea otters number in the hundreds of thousands—3,000 in California, 14,000 in southeastern Alaska, and the rest elsewhere in Alaska. According to the Marine Mammal Center, approximately 2,800 sea otters live along the coast of California,[5] a few hundred in Washington State and British Columbia, and about 100,000 worldwide, including Alaska and the coast of Siberia.[6]

Legal protection of the sea otter by the U.S. government began in 1911 and continues under the U.S. Marine Mammal Protection Act of 1972 and the Endangered Species Act of 1973. Today, however, the sea otter continues


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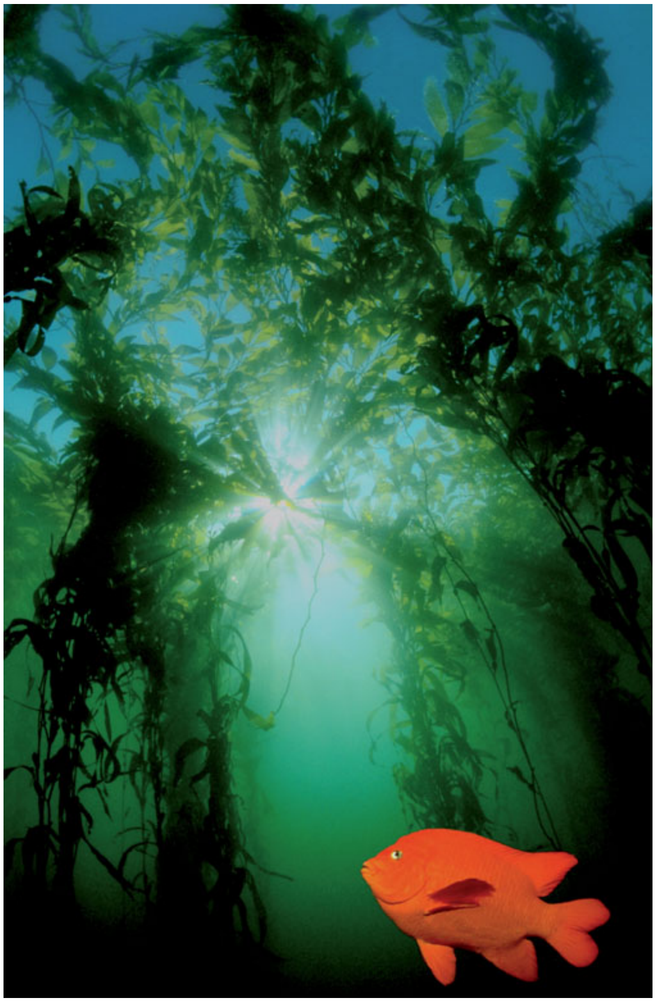
(b)

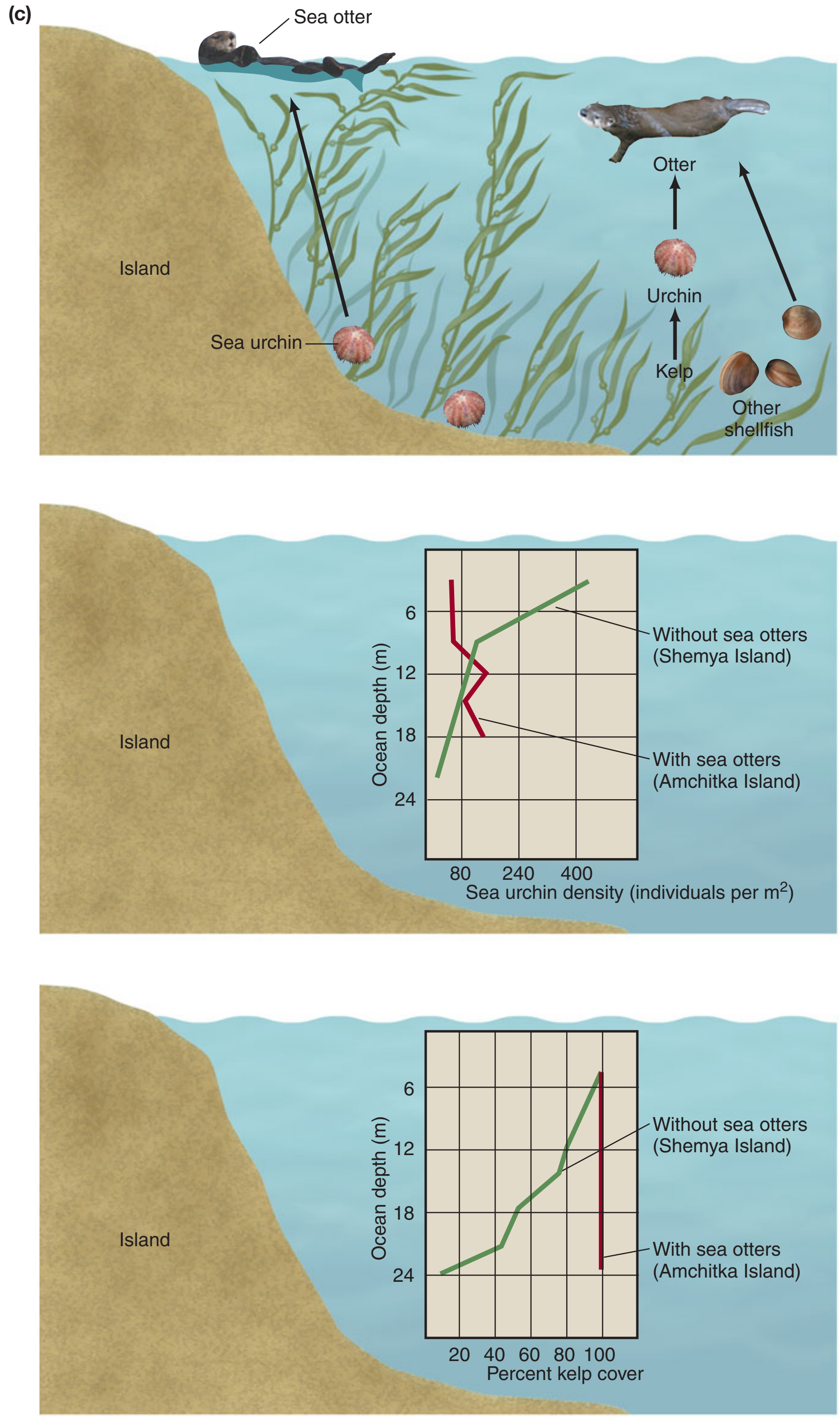

FIGURE 5.1 The effect of sea otters on kelp. (a) Sea otter eating a crab. Sea otters feed on shellfish, including sea urchins. Sea urchins feed on kelp. Where sea otters are abundant, as on Amchitka Island in the Aleutian Islands, there are few sea urchins and kelp beds are abundant (**b** and **c**). At nearby Shemya Island, which lacks sea otters, sea urchins are abundant and there is little kelp.[3] Experimental removal of sea urchins has led to an increase in kelp.[2]

to be a focus of controversy. On the one hand, fishermen argue that the sea otter population has recovered—so much so that they now interfere with commercial fishing because they take large numbers of abalone.[7] On the other hand, conservationists argue that community and ecosystem effects of sea otters make them necessary for the persistence of many oceanic species, and that there are still not enough sea otters to maintain this role at a satisfactory level. Thus, sea otters' indirect effects on many other species have practical consequences. They also demonstrate certain properties of ecosystems and ecological communities that are important to us in understanding how life persists, and how we may be able to help solve certain environmental problems.

5.1 The Ecosystem: Sustaining Life on Earth

We tend to associate life with individual organisms, for the obvious reason that it is individuals that are alive. But sustaining life on Earth requires more than individuals or even single populations or species. Life is sustained by the interactions of many organisms functioning together, interacting through their physical and chemical environments. We call this an **ecosystem**. Sustained life on Earth, then, is a characteristic of ecosystems, not of individual organisms or populations.[8] As the opening case study about sea otters illustrates, to understand important environmental issues—such as conserving endangered species, sustaining renewable resources, and minimizing the effects of toxic substances—we must understand the basic characteristics of ecosystems.

Basic Characteristics of Ecosystems

Ecosystems have several fundamental characteristics, which we can group as *structure* and *processes.*

Ecosystem Structure

An ecosystem has two major parts: nonliving and living. The nonliving part is the physical-chemical environment, including the local atmosphere, water, and mineral soil (on land) or other substrate (in water). The living part, called the **ecological community**, is the set of species interacting within the ecosystem.

Ecosystem Processes

Two basic kinds of processes must occur in an ecosystem: a cycling of chemical elements and a flow of energy. These processes are necessary for all life, but no single species can carry out all necessary chemical cycling and energy flow alone. That is why we said that sustained life on Earth is a characteristic of ecosystems, not of individuals or populations. At its most basic, an ecosystem consists of several species and a fluid medium—air, water, or both (Figure 5.2). Ecosystem energy flow places a fundamental limit on the abundance of life. Energy flow is a difficult subject, which we will discuss in Section 5.4.

Ecosystem chemical cycling is complex as well, and for that reason we have devoted a separate chapter (Chapter 6) to chemical cycling within ecosystems and throughout the entire Earth's biosphere. Briefly, 21 chemical elements are required by at least some form of life, and each chemical element required for growth and reproduction must be available to each organism at the right time, in the right amount, and in the right ratio relative to other elements. These chemical elements must also be recycled—converted to a reusable form: Wastes are converted into food, which is converted into wastes, which must be converted once again into food, with the cycling going on indefinitely if the ecosystem is to remain viable.

For complete recycling of chemical elements to take place, several species must interact. In the presence of light, green plants, algae, and photosynthetic bacteria produce sugar from carbon dioxide and water. From sugar and inorganic compounds, they make many organic compounds, including proteins and woody tissue. But no green plant, algae, or photosynthetic bacteria can decompose woody tissue back to its original inorganic compounds. Other forms of life—primarily bacteria and fungi—can decompose organic matter. But they cannot produce their own food; instead, they obtain energy and chemical nutrition from the dead tissues on which they feed. In an ecosystem, chemical elements recycle, but energy flows one way, into and out of the system, with a small fraction of it stored, as we will discuss later in this chapter.

To repeat, theoretically, at its simplest, an ecosystem consists of at least one species that produces its own food from inorganic compounds in its environment and another species that decomposes the wastes of the first species, plus a fluid medium—air, water, or both (Figure 5.2). But the reality is never as simple as that.

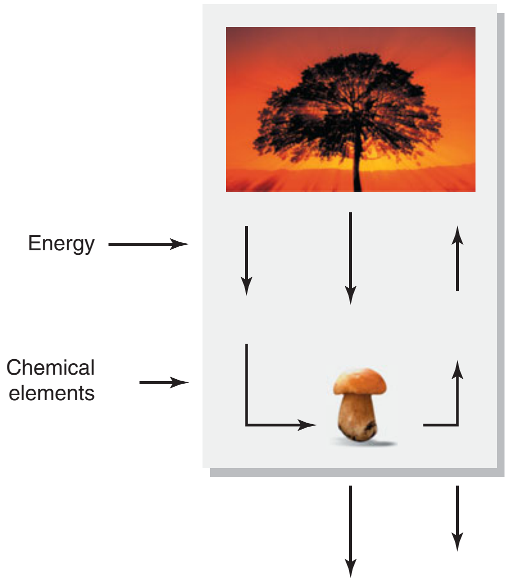

FIGURE 5.2 An idealized minimum ecosystem. Energy flows through an ecosystem one way. A small amount is stored within the system. As chemical elements cycle, there is some small loss, depending on the characteristics of the ecosystem. The size of the arrows in the figure approximates the amount of flow.

5.2 Ecological Communities and Food Chains

In practice, ecologists define the term *ecological community* in two ways. One method defines the community as a set of *interacting* species found in the same place and functioning together, thus enabling life to persist. That is essentially the definition we used earlier. A problem with this definition is that it is often difficult in practice to know the entire set of interacting species. Ecologists therefore may use a practical or an operational definition, in which the community consists of all the species found in an area, whether or not they are known to interact. Animals in different cages in a zoo could be called a community according to this definition.

One way that individuals in a community interact is by feeding on one another. Energy, chemical elements, and some compounds are transferred from creature to creature along **food chains**, the linkage of who feeds on whom. The more complex linkages are called **food webs**. Ecologists group the organisms in a food web into trophic levels. A **trophic level** (from the Greek word *trephein*, meaning to nourish, thus the "nourishing level") consists of all organisms in a food web that are the same number of feeding levels away from the original energy source. The original source of energy in most ecosystems is the sun. In other cases, it is the energy in certain inorganic compounds.

Green plants, algae, and certain bacteria produce sugars through the process of **photosynthesis**, using only energy from the sun and carbon dioxide (CO_2) from the air. They are called **autotrophs**, from the words *auto* (self) and *trephein* (to nourish), thus "self-nourishing," and are grouped into the first trophic level. All other organisms are called **heterotrophs**. Of these, **herbivores**—organisms that feed on plants, algae, or photosynthetic bacteria—are members of the second trophic level. **Carnivores**, or meat-eaters, that feed directly on herbivores make up the third trophic level. Carnivores that feed on third-level carnivores are in the fourth trophic level, and so on. **Decomposers**, those that feed on dead organic material, are classified in the highest trophic level in an ecosystem.

Food chains and food webs are often quite complicated and thus not easy to analyze. For starters, the number of trophic levels differs among ecosystems.

A Simple Ecosystem

One of the simplest natural ecosystems is a hot spring, such as those found in geyser basins in Yellowstone National Park, Wyoming.[9] They are simple because few organisms can live in these severe environments. In and near the center of a spring, water is close to the boiling point, while at the edges, next to soil and winter snow, water is much cooler. In addition, some springs are very acidic and others are very alkaline; either extreme makes a harsh environment.

Photosynthetic bacteria and algae make up the spring's first trophic level. In a typical alkaline hot spring, the hottest waters, between 70° and 80°C (158–176°F), are colored bright yellow-green by photosynthetic blue-green bacteria. One of the few kinds of photosynthetic organisms that can survive at those temperatures, these give the springs the striking appearance for which they are famous (Figure 5.3). In slightly cooler waters, 50° to 60°C (122–140°F), thick mats of other kinds of bacteria and algae accumulate, some becoming 5 cm thick (Figures 5.3 and 5.4).

Ephydrid flies make up the second (herbivore) trophic level. Note that they are the only genus on that entire trophic level, so stressful is the environment, and they live only in the cooler areas of the springs. One of these species, *Ephydra bruesi*, lays bright orange-pink egg masses on stones and twigs that project above the mat. These larvae feed on the bacteria and algae.

The third (carnivore) trophic level is made up of a dolichopodid fly, which feeds on the eggs and larvae of the herbivorous flies, and dragonflies, wasps, spiders,

FIGURE 5.3 One of the many hot springs in Yellowstone National Park. The bright yellowish-green color comes from photosynthetic bacteria, one of the few kinds of organisms that can survive in the hot temperatures and chemical conditions of the springs.

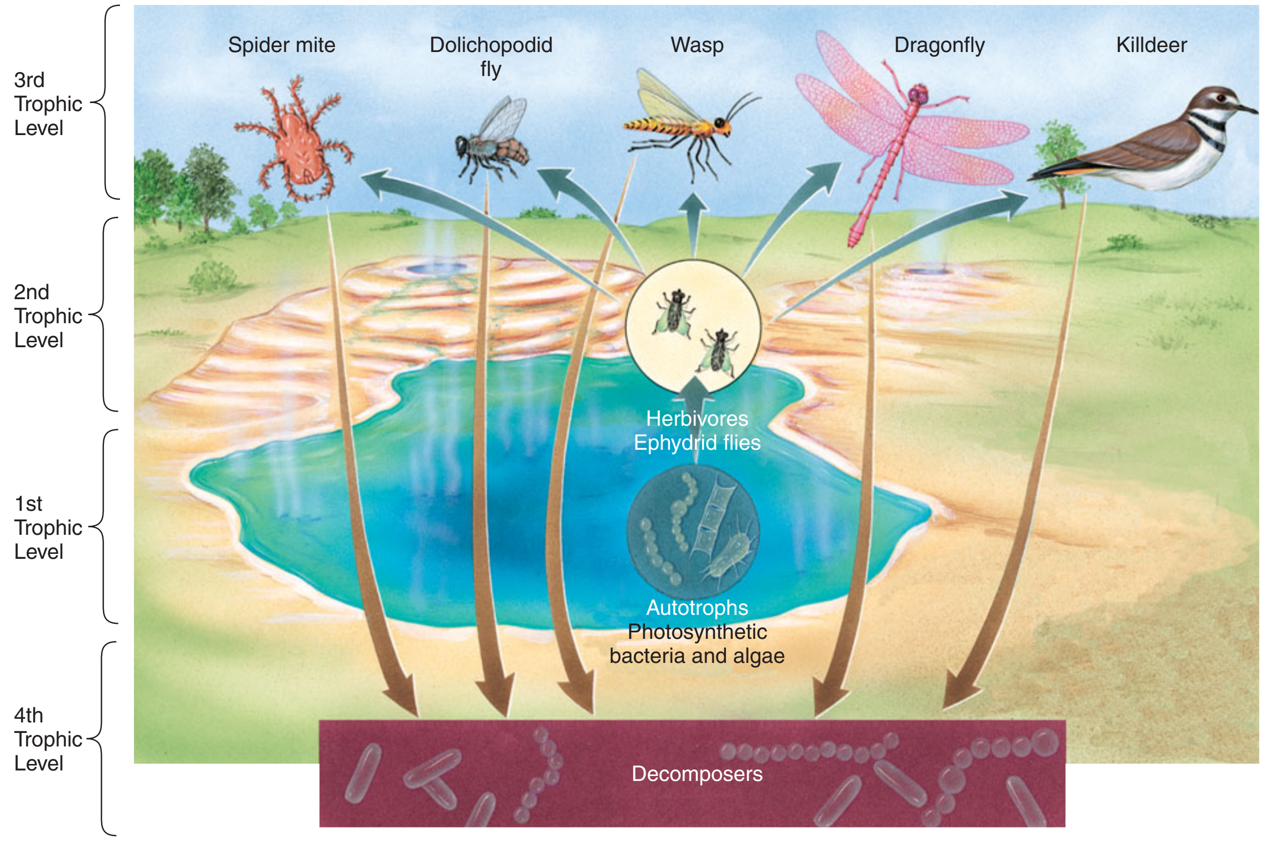

FIGURE 5.4 **Food web of a Yellowstone National Park hot spring.** Even though this is one of the simplest ecological communities in terms of the numbers of species, a fair number are found. About 20 species in all are important in this ecosystem.

tiger beetles, and one species of bird, the killdeer, that feeds on the ephydrid flies. (Note that the killdeer is a carnivore of the hot springs but also feeds widely in other ecosystems. An interesting question, little addressed in the ecological scientific literature, is how we should list this partial member of the food web: Should there be a separate category of "casual" members? What do you think?)

In addition to their other predators, the herbivorous ephydrid flies have parasites. One is a red mite that feeds on the flies' eggs and travels by attaching itself to the adult flies. Another is a small wasp that lays its eggs within the fly larvae. These are also on the third trophic level.

Wastes and dead organisms of all trophic levels are fed on by decomposers, which in the hot springs are primarily bacteria. These form the fourth trophic level.

The entire hot-springs community of organisms—photosynthetic bacteria and algae, herbivorous flies, carnivores, and decomposers—is maintained by two factors: (1) sunlight, which provides usable energy for the organisms; and (2) a constant flow of hot water, which provides a continual new supply of chemical elements required for life and a habitat in which the bacteria and algae can persist.

An Oceanic Food Chain

In oceans, food webs involve more species and tend to have more trophic levels than they do in a terrestrial ecosystem. In a typical **pelagic** (open-ocean) **ecosystem** (Figure 5.6), microscopic single-cell planktonic algae and planktonic photosynthetic bacteria are in the first trophic level. Small invertebrates called *zooplankton* and some fish feed on the algae and photosynthetic bacteria, forming the second trophic level. Other fish and invertebrates feed on these herbivores and form the third trophic level. The great baleen whales filter seawater for food, feeding primarily on small herbivorous zooplankton (mostly crustaceans), and thus the baleen whales are also in the third level. Some fish and marine mammals, such as killer whales, feed on the predatory fish and form higher trophic levels.

Food Webs Can Be Complex: The Food Web of the Harp Seal

In the abstract or in extreme environments like a hot spring, a diagram of a food web and its trophic levels may seem simple and neat. In reality, however, most food webs are complex. One reason for the complexity

A CLOSER LOOK 5.1

Land and Marine Food Webs

A Terrestrial Food Web

An example of terrestrial food webs and trophic levels is shown in Figure 5.5 for an eastern temperate woodland of North America. The first trophic level, autotrophs, includes grasses, herbs, and trees. The second trophic level, herbivores, includes mice, an insect called the pine borer, and other animals (such as deer) not shown here. The third trophic level, carnivores, includes foxes and wolves, hawks and other predatory birds, spiders, and predatory insects. People, too, are involved as **omnivores** (eaters of both plants and animals), feeding on several trophic levels. In Figure 5.5, people would be included in the fourth trophic level, the highest level in which they would take part. Decomposers, such as bacteria and fungi, feed on wastes and dead organisms of all trophic levels. Decomposers are also shown here on the fourth level. (Here's another interesting question: Should we include people *within* this ecosystem's food web? That would place us within nature. Or should we place people outside of the ecosystem, thus separate from nature?)

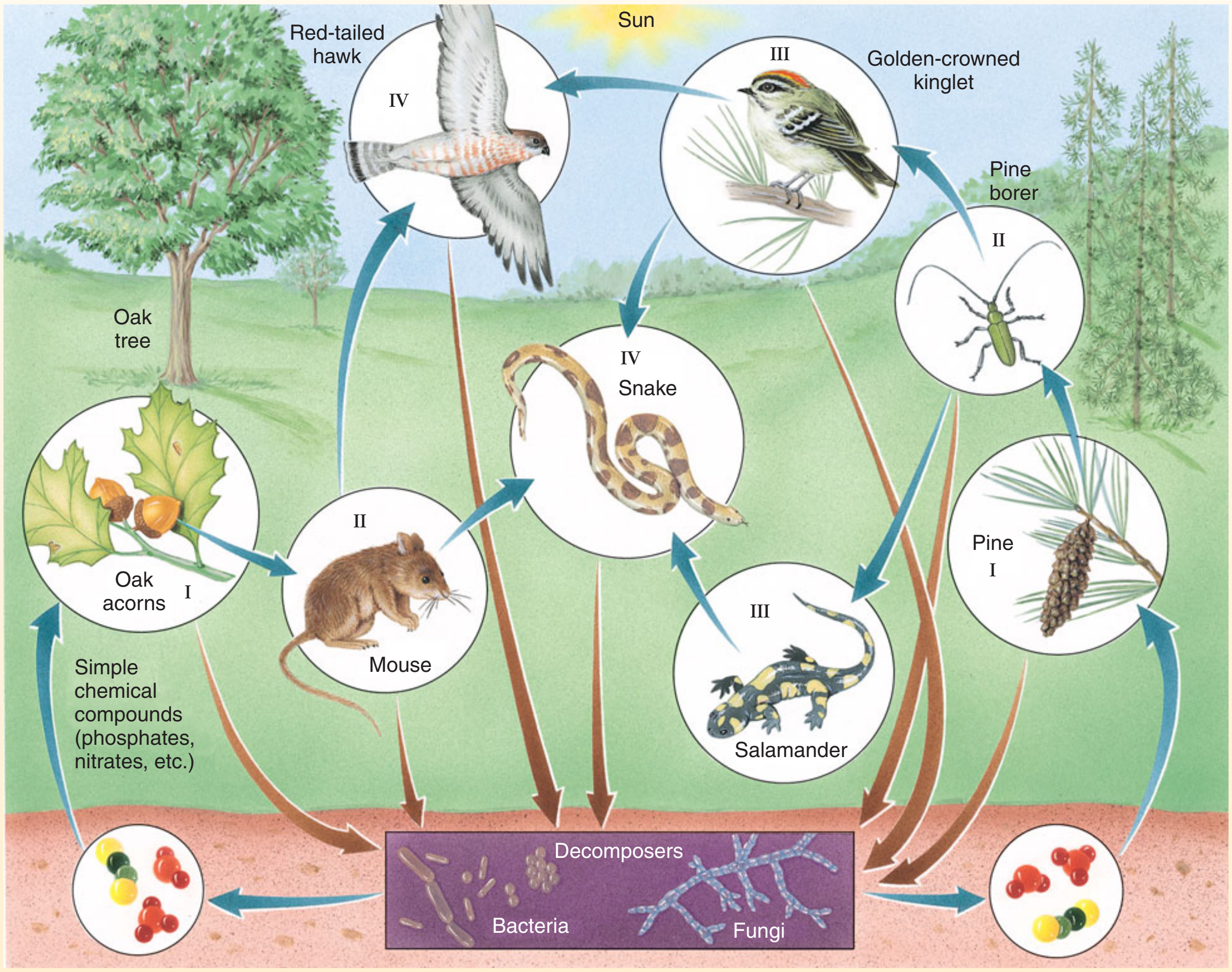

FIGURE 5.5 **A typical temperate forest food web.**

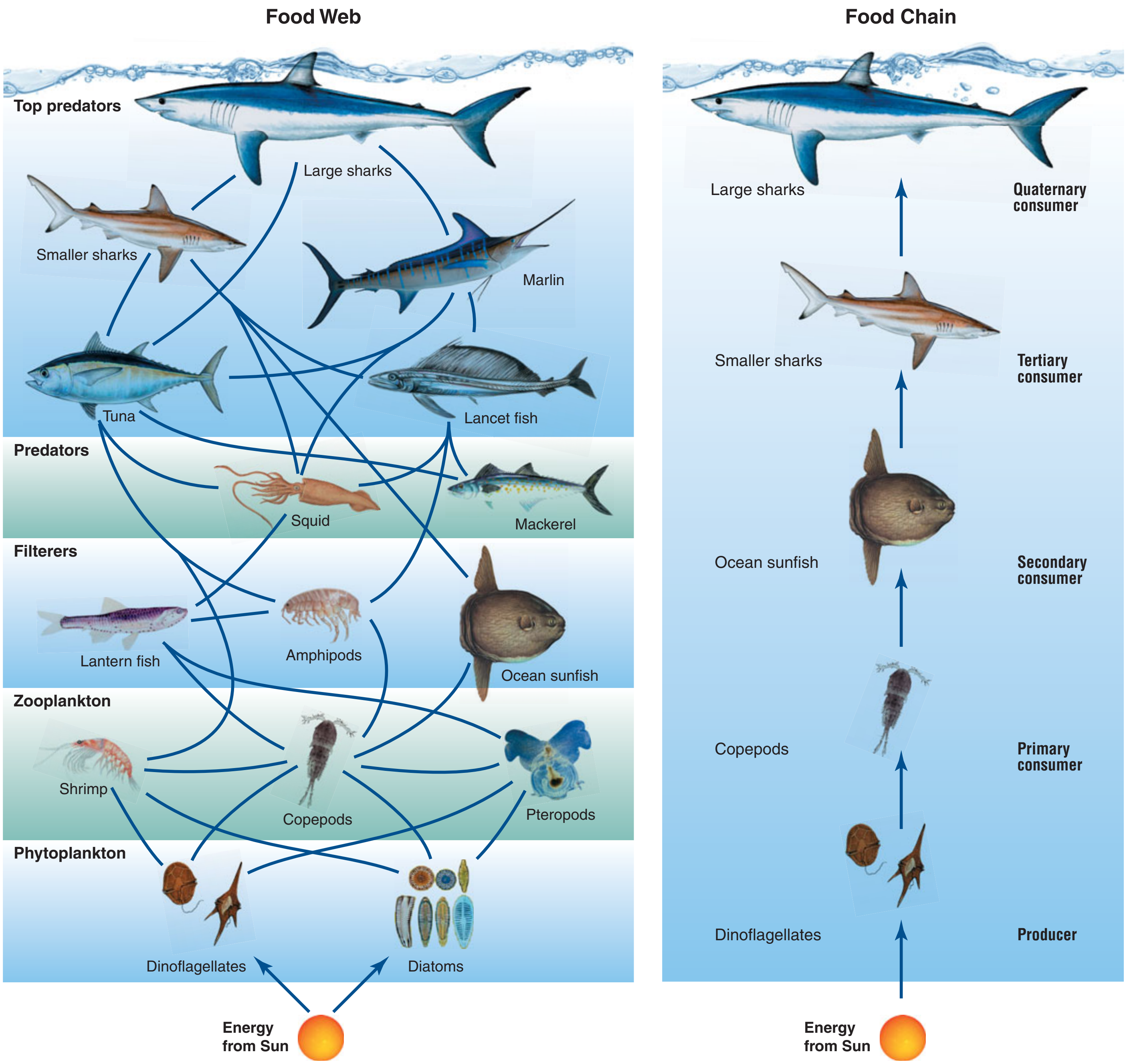

FIGURE 5.6 **An oceanic food web.** (*Source*: NOAA)

is that many creatures feed on several trophic levels. For example, consider the food web of the harp seal (Figure 5.7). This is a species of special interest because large numbers of the pups are harvested each year in Canada for their fur, giving rise to widespread controversy over the humane treatment of animals even though the species is not endangered (there are more than 5 million harp seals.)[10] This controversy is one reason that the harp seal has been well studied, so we can show its complex food web.

The harp seal is shown at the fifth level.[11] It feeds on flatfish (fourth level), which feed on sand launces (third level), which feed on euphausiids (second level), which feed on phytoplankton (first level). But the harp seal actually feeds at several trophic levels, from the second through the fourth. Thus, it feeds on predators of some of its prey and therefore competes with some of its own prey.[12] A species that feeds on several trophic levels is typically classified as belonging to the trophic level above the highest level from which it feeds. Thus, we place the harp seal on the fifth trophic level.

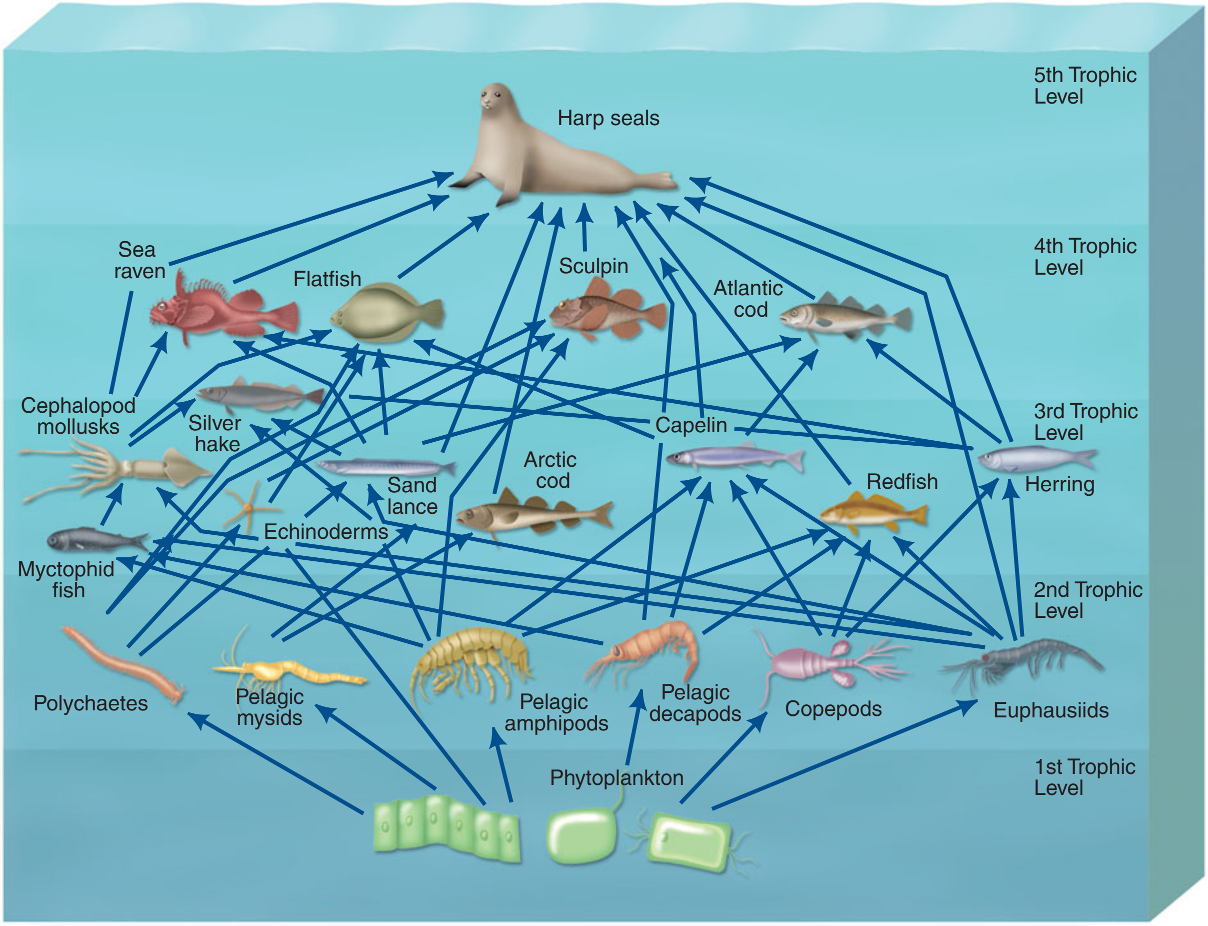

FIGURE 5.7 **Food web of the harp seal showing how complex a real food web can be.**

5.3 Ecosystems as Systems

Ecosystems are open systems: Energy and matter flow into and out of them (see Chapter 3). As we have said, an ecosystem is the minimal entity that has the properties required to sustain life. This implies that an ecosystem is real and important and therefore that we should be able to find one easily. However, ecosystems vary greatly in structural complexity and in the clarity of their boundaries. Sometimes their borders are well defined, such as between a lake and the surrounding countryside (Figure 5.8a). But sometimes the transition from one ecosystem to another is gradual—for example, the transition from deciduous to boreal forest on the slopes of Mt. Washington, N.H. (Figure 5.8b), and in the subtle gradations from grasslands to savannas in East Africa and from boreal forest to tundra in the Far North, where the trees thin out gradually and setting a boundary is difficult, and usually arbitrary.

A commonly used practical delineation of the boundary of an ecosystem on land is the **watershed**. Within a watershed, all rain that reaches the ground from any source flows out in one stream. Topography (the lay of the land) determines the watershed. When a watershed is used to define the boundaries of an ecosystem, the ecosystem is unified in terms of chemical cycling. Some classic experimental studies of ecosystems have been conducted on forested watersheds in U.S. Forest Service experimental areas, including the Hubbard Brook experimental forest in New Hampshire (Figure 5.9) and the Andrews experimental forest in Oregon. In other cases, the choice of an ecosystem's boundary may be arbitrary. For the purposes of scientific analysis, this is okay as long as this boundary is used consistently for any calculation of the exchange of chemicals and energy and the migration of organisms. Let us repeat the primary point: What all ecosystems have in common is not a particular physical size or shape but the processes we have mentioned—the flow of energy and the cycling of chemical elements, which give ecosystems the ability to sustain life.

FIGURE 5.8 **Ecosystem boundaries. (a)** Sometimes the transition from one ecosystem to another is sharp and distinct, as in the transition from lake to forest at Lake Moraine in Banff National Park, Alberta, Canada. **(b)** Sometimes the transition is indistinct and arbitrary, as in the transition from wetlands to uplands in a northern forest as seen from Mount Washington, New Hampshire. Within the distant scene are uplands and wetlands.

FIGURE 5.9 The V-shaped logged area in this picture is the site of the famous Hubbard Brook Ecosystem Study. Here, a watershed defines the ecosystem, and the V shape is an entire watershed cut as part of the experiment.

5.4 Biological Production and Ecosystem Energy Flow

All life requires energy. Energy is the ability to do work, to move matter. As anyone who has dieted knows, our weight is a delicate balance between the energy we take in through our food and the energy we use. What we do not use and do not pass on, we store. Our use of energy, and whether we gain or lose weight, follows the laws of physics. This is true not only for people but also for all populations of living things, for all ecological communities and ecosystems, and for the entire biosphere.

Ecosystem energy flow is the movement of energy through an ecosystem from the external environment through a series of organisms and back to the external environment. It is one of the fundamental processes common to all ecosystems. Energy enters an ecosystem by two pathways: energy fixed by organisms and moving through food webs within an ecosystem; and heat energy that is transferred by air or water currents or by convection through soils and sediments and warms living things. For instance, when a warm air mass passes over a forest, heat energy is transferred from the air to the land and to the organisms.

Energy is a difficult and an abstract concept. When we buy electricity, what are we buying? We cannot see it or feel it, even if we have to pay for it. At first glance, and as we think about it with our own diets, energy flow seems simple enough: We take energy in and use it, just like machines do—our automobiles, cell phones, and so on. But if we dig a little deeper into this subject, we discover a philosophical importance: We learn what distinguishes Earth's life and life-containing systems from the rest of the universe.

Although most of the time energy is invisible to us, with infrared film we can see the differences between warm and cold objects, and we can see some things about energy flow that affect life. With infrared film, warm objects appear red, and cool objects blue. Figure

5.10 shows birch trees in a New Hampshire forest, both as we see them, using standard film, and with infrared film. The infrared film shows tree leaves bright red, indicating that they have been warmed by the sun and are absorbing and reflecting energy, whereas the white birch bark remains cooler. The ability of tree leaves to absorb energy is essential; it is this source of energy that ultimately supports all life in a forest. Energy flows through life, and energy flow is a key concept.

The Laws of Thermodynamics and the Ultimate Limit on the Abundance of Life

When we discuss ecosystems, we are talking about some of the fundamental properties of life and of the ecological systems that keep life going. A question that frequently arises both in basic science and when we want to produce a lot of some kind of life—a crop,

(a) (b) (c) (d)

FIGURE 5.10 Making energy visible. Top: A birch forest in New Hampshire as we see it, using normal photographic film **(a)** and the same forest photographed with infrared film **(b)**. Red color means warmer temperatures; the leaves are warmer than the surroundings because they are heated by sunlight. Bottom: A nearby rocky outcrop as we see it, using normal photographic film **(c)** and the same rocky outcrop photographed with infrared film **(d)**. Blue means that a surface is cool. The rocks appear deep blue, indicating that they are much cooler than the surrounding trees.

WORKING IT OUT 5.1 Some Chemistry of Energy Flow

For Those Who Make Their Own Food (autotrophs)

Photosynthesis—the process by which autotrophs make sugar from sunlight, carbon dioxide, and water—is:

$$6CO_2 + 6H_2O + \text{energy} = C_6H_{12}O_6 + 6O_2$$

Chemosynthesis takes place in certain environments. In chemosynthesis, the energy in hydrogen sulfide (H_2S) is used by certain bacteria to make simple organic compounds. The reactions differ among species and depend on characteristics of the environment (Figure 5.11).

Net production for autotrophs is given as

$$NPP = GPP - R_a$$

where NPP is net primary production, GPP is gross primary production, and R_a is the respiration of autotrophs.

For Those Who Do Not Make Their Own Food (heterotrophs)

Secondary production of a population is given as

$$NSP = B_2 - B_1$$

where NSP is net secondary production, B_2 is the biomass (quantity of organic matter) at time 2, and B_1 is the biomass at time 1. (See discussion of biomass in Section 5.5.) The change in biomass is the result of the addition of weight of living individuals, the addition of newborns and immigrants, and loss through death and emigration. The biological use of energy occurs through respiration, most simply expressed as

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + \text{Energy}$$

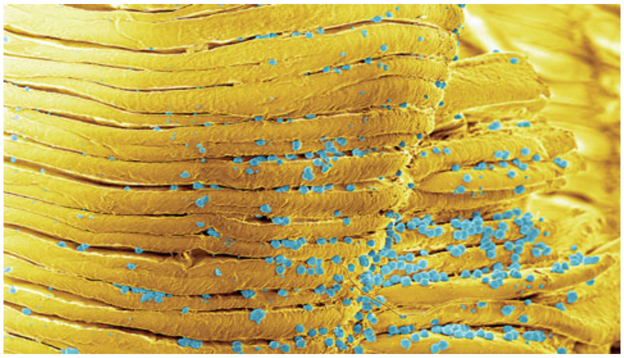

FIGURE 5.11 Deep-sea vent chemosynthetic bacteria.

biofuels, pets—is: *What ultimately limits the amount of organic matter in living things that can be produced anywhere, at any time, forever on the Earth or anywhere in the universe?*

We ask this question when we are trying to improve the production of some form of life. We want to know: How closely do ecosystems, species, populations, and individuals approach this limit? Are any of these near to being as productive as possible?

The answers to these questions, which are at the same time practical, scientifically fundamental, and philosophical, lie in the laws of thermodynamics. The **first law of thermodynamics**, known as the *law of conservation of energy* states that in any physical or chemical change, energy is neither created nor destroyed but merely changed from one form to another. (See A Closer Look 5.1.) This seems to lead us to a confusing, contradictory answer—it seems to say that we don't need to take in any energy at all! If the total amount of energy is always conserved—if it remains constant—then why can't we just recycle energy inside our bodies? The famous 20th-century physicist Erwin Schrödinger asked this question in a wonderful book entitled *What Is Life?* He wrote:

> In some very advanced country (I don't remember whether it was Germany or the U.S.A. or both) you could find menu cards in restaurants indicating, in addition to the price, the energy content of every dish. Needless to say, taken literally, this is . . . absurd. For an adult organism the energy content is as stationary as the material content. Since, surely, any calorie is worth as much as any other calorie, one cannot see how a mere exchange could help.[13]

Schrödinger was saying that, according to the first law of thermodynamics, we should be able to recycle energy in our bodies and never have to eat anything. Similarly, we can ask: Why can't energy be recycled in ecosystems and in the biosphere?

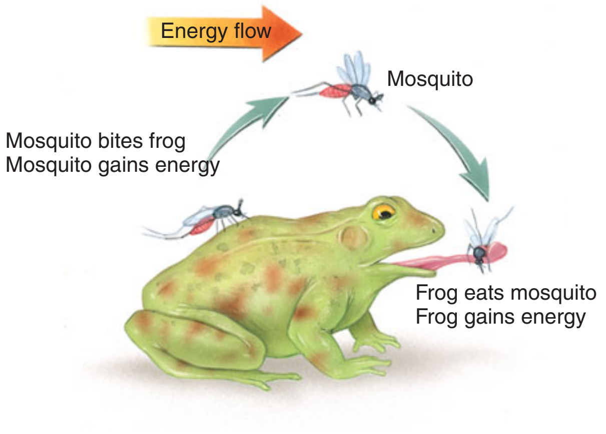

FIGURE 5.12 An impossible ecosystem. Energy always changes from a more useful, more highly organized form to a less useful, disorganized form. That is, energy cannot be completely recycled to its original state of organized, high-quality usefulness. For this reason, the mosquito–frog system will eventually stop when not enough useful energy is left. (There is also a more mundane reason: Only female mosquitoes require blood, and then only in order to reproduce. Mosquitoes are otherwise herbivorous.)

Let us imagine how that might work, say, with frogs and mosquitoes. Frogs eat insects, including mosquitoes. Mosquitoes suck blood from vertebrates, including frogs. Consider an imaginary closed ecosystem consisting of water, air, a rock for frogs to sit on, frogs, and mosquitoes. In this system, the frogs get their energy from eating the mosquitoes, and the mosquitoes get their energy from biting the frogs (Figure 5.12). Such a closed system would be a biological perpetual-motion machine. It could continue indefinitely without an input of any new material or energy. This sounds nice, but unfortunately it is impossible. Why? The general answer is found in the *second* law of thermodynamics, which addresses how energy changes in form.

To understand why we cannot recycle energy, imagine a closed system (a system that receives no input after the initial input) containing a pile of coal, a tank of water, air, a steam engine, and an engineer (Figure 5.13). Suppose the engine runs a lathe that makes furniture. The engineer lights a fire to boil the water, creating steam to run the engine. As the engine runs, the heat from the fire gradually warms the entire system.

When all the coal is completely burned, the engineer will not be able to boil any more water, and the engine will stop. The average temperature of the system is now higher than the starting temperature. The energy that was in the coal is dispersed throughout the entire system, much of it as heat in the air. Why can't the engineer recover all that energy, recompact it, put it under the boiler, and run the engine? The answer is in the **second law of thermodynamics**. Physicists have discovered that *no use of energy in the real (not theoretical) world can ever be 100% efficient.* Whenever useful work is done, some energy is inevitably converted to heat. Collecting all the energy dispersed in this closed system would require more energy than could be recovered.

Our imaginary system begins in a highly organized state, with energy compacted in the coal. It ends in a less organized state, with the energy dispersed throughout the system as heat. The energy has been degraded, and the system is said to have undergone a decrease in order. The

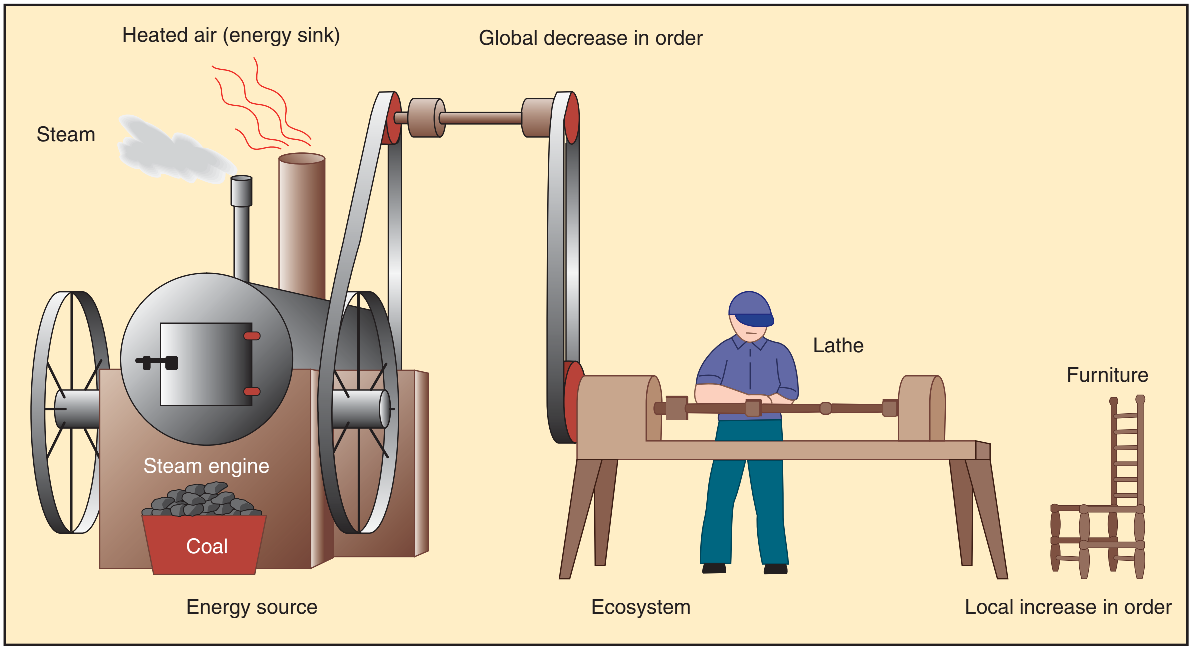

FIGURE 5.13 A system closed to the flow of energy.

measure of the decrease in order (the disorganization of energy) is called **entropy**. The engineer did produce some furniture, converting a pile of lumber into nicely ordered tables and chairs. The system had a local increase of order (the furniture) at the cost of a general increase in disorder (the state of the entire system). All energy of all systems tends to flow toward states of increasing entropy.

The second law of thermodynamics gives us a new understanding of a basic quality of life. *It is the ability to create order on a local scale that distinguishes life from its nonliving environment.* This ability requires obtaining energy in a usable form, and that is why we eat. This principle is true for every ecological level: individual, population, community, ecosystem, and biosphere. Energy must continually be added to an ecological system in a usable form. Energy is inevitably degraded into heat, and this heat must be released from the system. If it is not released, the temperature of the system will increase indefinitely. The net flow of energy through an ecosystem, then, is a one-way flow.

Based on what we have said about the energy flow through an ecosystem, we can see that an ecosystem must lie between a source of usable energy and a sink for degraded (heat) energy. The ecosystem is said to be an *intermediate system* between the energy source and the energy sink. The energy source, ecosystem, and energy sink together form a thermodynamic system. The ecosystem can undergo an increase in order, called a *local increase*, as long as the entire system undergoes a decrease in order, called a global decrease. (Note that *order* has a specific meaning in thermodynamics: Randomness is disorder; an ordered system is as far from random as possible.) To put all this simply, creating local order involves the production of organic matter. Producing organic matter requires energy; organic matter stores energy.

With these fundamentals in mind, we can turn to practical and empirical scientific problems, but this requires that we agree how to measure biological production. To complicate matters, there are several measurement units involved, depending on what people are interested in.

5.5 Biological Production and Biomass

The total amount of organic matter in any ecosystem is called its **biomass**. Biomass is increased through biological production (growth). Change in biomass over a given period is called *production*. **Biological production** is the capture of usable energy from the environment to produce organic matter (or organic compounds). This capture is often referred to as energy "fixation," and it is often said that the organism has "fixed" energy. There are two kinds of production, gross and net. **Gross production** is the increase in stored energy before any is used; **net production** is the amount of newly acquired energy stored after some energy has been used. When we use energy, we "burn" a fuel through repiration. The difference between gross and net production is like the difference between a person's gross and net income. Your gross income is the amount you are paid. Your net income is what you have left after taxes and other fixed costs. Respiration is like the expenses that are required in order for you to do your work.

Measuring Biomass and Production

Three measures are used for biomass and biological production: the quantity of organic material (biomass), energy stored, and carbon stored. We can think of these measures as the currencies of production. Biomass is usually measured as the amount per unit surface area—for example, as grams per square meter (g/m^2) or metric tons per hectare (MT/ha). Production, a rate, is the change per unit area in a unit of time—for example, grams per square meter per year. (Common units of measure of production are given in the Appendix.)

The production carried out by autotrophs is called **primary production**; that of heterotrophs is called **secondary production**. As we have said, most autotrophs make sugar from sunlight, carbon dioxide, and water in a process called photosynthesis, which releases free oxygen (see Working It Out 5.1 and 5.2). Some autotrophic bacteria can derive energy from inorganic sulfur compounds; these bacteria are referred to as **chemoautotrophs**. Such bacteria live in deep-ocean vents, where they provide the basis for a strange ecological community. Chemoautotrophs are also found in muds of marshes, where there is no free oxygen.

Once an organism has obtained new organic matter, it can use the energy in that organic matter to do things: to move, to make new compounds, to grow, to reproduce, or to store it for future uses. The use of energy from organic matter by most heterotrophic and autotrophic organisms is accomplished through respiration. In respiration, an organic compound combines with oxygen to release energy and produce carbon dioxide and water (see Working It Out 5.2). The process is similar to the burning of organic compounds but takes place within cells at much lower temperatures through enzyme-mediated reactions. *Respiration is the use of biomass to release energy that can be used to do work.* Respiration returns to the environment the carbon dioxide that had been removed by photosynthesis.

WORKING IT OUT 5.2 Gross and Net Production

The production of biomass and its use as a source of energy by autotrophs include three steps:

1. An organism produces organic matter within its body.
2. It uses some of this new organic matter as a fuel in respiration.
3. It stores some of the newly produced organic matter for future use.

The first step, production of organic matter before use, is called *gross production.* The amount left after utilization is called *net production.*

Net production = Gross production − Respiration

The gross production of a tree—or any other plant—is the total amount of sugar it produces by photosynthesis before any is used. Within living cells in a green plant, some of the sugar is oxidized in respiration. Energy is used to convert sugars to other carbohydrates; those carbohydrates to amino acids; amino acids to proteins and to other tissues, such as cell walls and new leaf tissue. Energy is also used to transport material within the plant to roots, stems, flowers, and fruits. Some energy is lost as heat in the transfer. Some is stored in these other parts of the plant for later use. For woody plants like trees, some of this storage includes new wood laid down in the trunk, new buds that will develop into leaves and flowers the next year, and new roots.

Equations for Production, Biomass, and Energy Flow

We can write a general relation between biomass (B) and net production (NP):

$$B_2 = B_1 + NP$$

where B_2 is the biomass at the end of the time period, B_1 is the amount of biomass at the beginning of the time period, and NP is the change in biomass during the time period. Thus,

$$NP = B_2 - B_1$$

General production equations are given as

$$\mathrm{GP} = \mathrm{NP} + \mathrm{R}$$

$$\mathrm{NP} = \mathrm{GP} - \mathrm{R}$$

where GP is gross production, NP is net production, and R is respiration.

Several units of measures are used in the discussion of biological production and energy flow: calories when people talk about food content; watt-hours when people talk about biofuels; and kilojoules in standard international scientific notation. To make matters even more complicated, there are two kinds of calories: the standard calorie, which is the heat required to heat one gram of water from 15.5°C to 16.5°C, and the kilocalorie, which is 1,000 of the little calories. Even more confusing, when people discuss the energy content of food and diets, they use *calorie* to mean the kilocalorie. Just remember: The calorie you see on the food package is the big calorie, the kilocalorie, equal to 1,000 little calories. Almost nobody uses the "little" calorie, regardless of what they call it. To compare, an average apple contains about 100 Kcal or 116 watt-hours. This means that an apple contains enough energy to run a 100-watt bulb for 1 hour and 9 minutes. For those of you interested in your diet and weight, a Big Mac contains 576 Kcal, which is 669 watt-hours, enough to keep that 100-watt bulb burning for 6 hours and 41 minutes.

The average energy stored in vegetation is approximately 5 Kcal/gram (21 kilojoules per gram [kJ/g]). The energy content of organic matter varies. Ignoring bone and shells, woody tissue contains the least energy per gram, about 4 Kcal/g (17 kJ/g); fat contains the most, about 9 Kcal/g (38 kJ/g); and muscle contains approximately 5–6 Kcal/g (21–25 kJ/g). Leaves and shoots of green plants have about 5 Kcal/g (21–23 kJ/g); roots have about 4.6 Kcal/g (19 kJ/g).[2]

5.6 Energy Efficiency and Transfer Efficiency

How efficiently do living things use energy? This is an important question for the management and conservation of all biological resources. We would like biological resources to use energy efficiently—to produce a lot of biomass from a given amount of energy. This is also important for attempts to sequester carbon by growing trees and other perennial vegetation to remove carbon dioxide from the atmosphere and store it in living and dead organic matter (see Chapter 20).

As you learned from the second law of thermodynamics, no system can be 100% efficient. As energy flows through a food web, it is degraded, and less and less is usable. Generally, the more energy an organism gets, the more it has for its own use. However, organisms differ in how efficiently they use the energy they obtain. A more efficient organism has an advantage over a less efficient one.

Efficiency can be defined for both artificial and natural systems: machines, individual organisms, populations, trophic levels, ecosystems, and the biosphere. **Energy efficiency** is defined as the ratio of output to input, and it is usually further defined as the amount of useful work obtained from some amount of available energy. *Efficiency* has different meanings to different users. From the point of view of a farmer, an efficient corn crop is one that converts a great deal of solar energy to sugar and uses little of that sugar to produce stems, roots, and leaves. In other words, the most efficient crop is the one that has the most harvestable energy left at the end of the season. A truck driver views an efficient truck as just the opposite: For him, an efficient truck uses as much energy as possible from its fuel and stores as little energy as possible (in its exhaust). When we view organisms as food, we define *efficiency* as the farmer does, in terms of energy storage (net production from available energy). When we are energy users, we define *efficiency* as the truck driver does, in terms of how much useful work we accomplish with the available energy.

Consider the use of energy by a wolf and by one of its principal prey, moose. The wolf needs energy to travel long distances and hunt, and therefore it will do best if it uses as much of the energy in its food as it can. For itself, a highly energy-efficient wolf stores almost nothing. But from its point of view, the best moose would be one that used little of the energy it took in, storing most of it as muscle and fat, which the wolf can eat. Thus what is efficient depends on your perspective.

A common ecological measure of energy efficiency is called *food-chain efficiency*, or *trophic-level efficiency*, which is the ratio of production of one trophic level to the production of the next-lower trophic level. This efficiency is never very high. Green plants convert only 1–3% of the energy they receive from the sun during the year to new plant tissue. The efficiency with which herbivores convert the potentially available plant energy into herbivorous energy is usually less than 1%, as is the efficiency with which carnivores convert herbivores into carnivorous energy. In natural ecosystems, the organisms in one trophic level tend to take in much less energy than the potential maximum available to them, and they use more energy than they store for the next trophic level. At Isle Royale National Park, an island in Lake Superior, wolves feed on moose in a natural wilderness. A pack of 18 wolves kills an average of one moose approximately every 2.5 days,[14] which gives wolves a trophic-level efficiency of about 0.01%.

The rule of thumb for ecological trophic energy efficiency is that more than 90% (usually much more) of all energy transferred between trophic levels is lost as heat. Less than 10% (approximately 1% in natural ecosystems) is fixed as new tissue. In highly managed ecosystems, such as ranches, the efficiency may be greater. But even in such systems, it takes an average of 3.2 kg (7 lb) of vegetable matter to produce 0.45 kg (1 lb) of edible meat. Cattle are among the least efficient producers, requiring around 7.2 kg (16 lb) of vegetable matter to produce 0.45 kg (1 lb) of edible meat. Chickens are much more efficient, using approximately 1.4 kg (3 lb) of vegetable matter to produce 0.45 kg (1 lb) of eggs or meat. Much attention has been paid to the idea that humans should eat at a lower trophic level in order to use resources more efficiently. (See Critical Thinking Issue, Should People Eat Lower on the Food Chain?)

5.7 Ecological Stability and Succession

Ecosystems are dynamic: They change over time both from external (environmental) forces and from their internal processes. It is worth repeating the point we made in Chapter 3 about dynamic systems: The classic interpretation of populations, species, ecosystems, and Earth's entire biosphere has been to assume that each is a stable, static system. But the more we study these ecological systems, the clearer it becomes that these are dynamic systems, always changing *and always requiring change.* Curiously, they persist while undergoing change. We say "curiously" because in our modern technological society we are surrounded by mechanical and electronic systems that stay the same in most characteristics and are designed to do so. We don't expect our car or television or cell phone to shrink or get larger and then smaller again; we don't expect that one component will get bigger or smaller over time. If anything like this were to happen, those systems would break.

Ecosystems, however, not only change but also then recover and overcome these changes, and life continues on. It takes some adjustment in our thinking to accept and understand such systems.

When disturbed, ecosystems can recover through **ecological succession** if the damage is not too great. We can classify ecological succession as either primary or secondary. **Primary succession** is the establishment and development of an ecosystem where one did not exist previously. Coral reefs that form on lava emitted from a volcano and cooled in shallow ocean waters are examples of primary succession. So are forests that develop on new lava flows, like those released by the volcano on the big island of Hawaii (Figure 5.14a), and forests that develop at the edges of retreating glaciers (Figure 5.14b).

Secondary succession is reestablishment of an ecosystem after disturbances. In secondary succession, there are remnants of a previous biological community, including such things as organic matter and seeds. A coral reef that has been killed by poor fishing practices, pollution, climate change, or predation, and then

(a) (b)

FIGURE 5.14 Primary succession. (a) Forests developing on new lava flows in Hawaii and **(b)** at the edge of a retreating glacier.

recovers, is an example of secondary succession.[15] Forests that develop on abandoned pastures or after hurricanes, floods, or fires are also examples of secondary succession.

Succession is one of the most important ecological processes, and the patterns of succession have many management implications (discussed in detail in Chapter 10). We see examples of succession all around us. When a house lot is abandoned in a city, weeds begin to grow. After a few years, shrubs and trees can be found; secondary succession is taking place. A farmer weeding a crop and a homeowner weeding a lawn are both fighting against the natural processes of secondary succession.

Patterns in Succession

Succession follows certain general patterns. When ecologists first began to study succession, they focused on three cases involving forests: (1) on dry sand dunes along the shores of the Great Lakes in North America; (2) in a northern freshwater bog; and (3) in an abandoned farm field. These were particularly interesting because each demonstrated a repeatable pattern of recovery, and each tended to produce a late stage that was similar to the late stages of the others.

Dune Succession

Sand dunes are continually being formed along sandy shores and then breached and destroyed by storms. In any of the Great Lakes states, soon after a dune is formed on the shores of one of the Great Lakes, dune grass invades. This grass has special adaptations to the unstable dune. Just under the surface, it puts out runners with sharp ends (if you step on one, it will hurt). The dune grass rapidly forms a complex network of underground runners, crisscrossing almost like a coarsely woven mat. Above the ground, the green stems carry out photosynthesis, and the grasses grow. Once the dune grass is established, its runners stabilize the sand, and seeds of other plants have a better chance of germinating. The seeds germinate, the new plants grow, and an ecological community of many species begins to develop. The plants of this early stage tend to be small, grow well in bright light, and withstand the harsh environment—high temperatures in summer, low temperatures in winter, and intense storms.

Slowly, larger plants, such as eastern red cedar and eastern white pine, are able to grow on the dunes. Eventually, a forest develops, which may include species such as beech and maple. A forest of this type can persist for many years, but at some point a severe storm breaches even these heavily vegetated dunes, and the process begins again (Figure 5.15).

FIGURE 5.15 Dune succession on the shores of Lake Michigan. Dune-grass shoots appear scattered on the slope, where they emerge from underground runners.

Bog Succession

A **bog** is an open body of water with surface inlets—usually small streams—but no surface outlet. As a result, the waters of a bog are quiet, flowing slowly if at all. Many bogs that exist today originated as lakes that filled depressions in the land, which in turn were created by glaciers during the Pleistocene ice age. Succession in a northern bog, such as the Livingston Bog in Michigan (Figure 5.16), begins when a sedge (a grasslike herb) puts out floating runners (Figure 5.17a, b). These runners form a complex, matlike network similar to that formed by dune grass. The stems of the sedge grow on the runners and carry out photosynthesis. Wind blows particles onto the mat, and soil, of a kind, develops. Seeds of other plants, instead of falling into the water, land on the mat and can germinate. The floating mat becomes thicker as small shrubs and trees, adapted to wet environments, grow. In the North, these include species of the blueberry family.

FIGURE 5.16 **Livingston Bog,** a famous bog in the northern part of Michigan's lower peninsula.

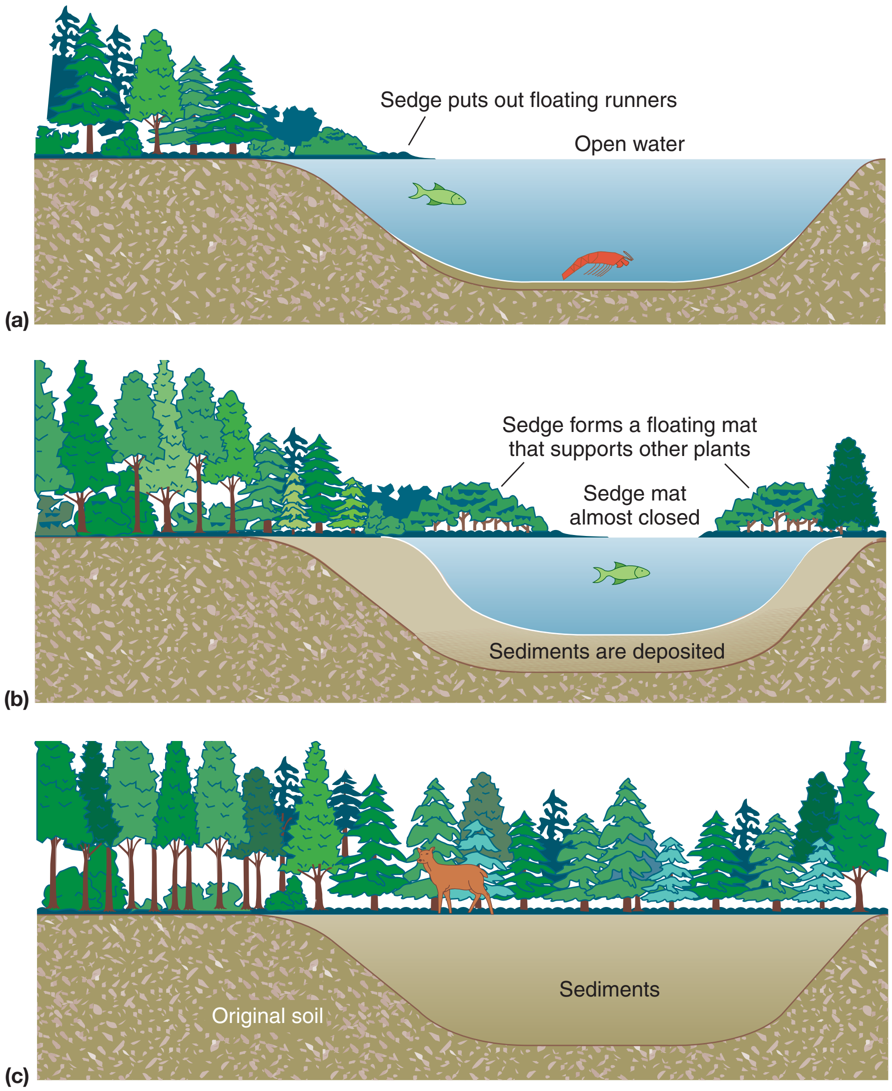

FIGURE 5.17 **Diagram of bog succession.** Open water **(a)** is transformed through formation of a floating mat of sedge and deposition of sediments **(b)** into wetland forest **(c).**

The bog also fills in from the bottom as streams carry fine particles of clay into it (Figure 5.17b, c). At the shore, the floating mat and the bottom sediments meet, forming a solid surface. But farther out, a "quaking bog" occurs. You can walk on this mat; and if you jump up and down, all the plants around you bounce and shake, because the mat is really floating. Eventually, as the bog fills in from the top and the bottom, trees grow that can withstand wetter conditions—such as northern cedar, black spruce, and balsam fir. The formerly open-water bog becomes a wetland forest. If the bog is farther south, it may eventually be dominated by beech and maple, the same species that dominate the late stages of the dunes.

Old-Field Succession

In the northeastern United States, a great deal of land was cleared and farmed in the 18th and 19th centuries. Today, much of this land has been abandoned for farming and allowed to grow back to forest (Figure 5.18). The first plants to enter the abandoned farmlands are small plants adapted to the harsh and highly variable conditions of a clearing—a wide range of temperatures and precipitation. As these plants become established, other, larger plants enter. Eventually, large trees grow, such as sugar maple, beech, yellow birch, and white pine, forming a dense forest.

Since these three different habitats—one dry (the dunes), one wet (the bog), and one in between (the old field)—tend to develop into similar forests, early ecologists believed that this late stage was in fact a steady-state condition. They referred to it as the "climatic climax," meaning that it was the final, ultimate, and permanent stage to which all land habitats would proceed if undisturbed by people. Thus, the examples of succession were among the major arguments in the early 20th century that nature did in fact achieve a constant condition, a steady state, and there actually was a balance of nature. We know today that this is not true, a point we will return to later.

Coral Reef Succession

Coral reefs (Figure 5.19) are formed in shallow warm waters by corals, small marine animals that live in colonies and are members of the phylum Coelenterata, which also includes sea anemones and jellyfishes. Corals have a whorl of tentacles surrounding the mouth, and feed by catching prey, including planktonic algae, as it passes by. The corals settle on a solid surface and produce a hard polyp of calcium carbonate (in other words, limestone). As old individuals die, this hard material becomes the surface on which new individuals establish themselves. In addition to the coelenterates, other limestone-shell-forming organisms—algae, corals, snails, urchins—live and die on the reef and are glued together primarily by a kind of algae.[16] Eventually a large and complex structure results involving many other species, including autotrophs and heterotrophs, creating one of the most species-diverse of all kinds of ecosystems. Highly valued for this diversity, for production of many edible fish, for the coral itself (used in various handicrafts and arts), and for recreation, coral reefs attract lots of attention.

Succession, in Sum

Even though the environments are very different, these four examples of ecological succession—dune, bog, old field, and coral reef—have common elements found in most ecosystems:

1. An initial kind of autotroph (green plants in three of the examples discussed here; algae and photosynthetic bacteria in marine systems; algae and photosynthetic bacteria, along with some green plants in some freshwater and near-shore marine systems). These are typically small in stature and specially adapted to the unstable conditions of their environment.

FIGURE 5.18 Old-growth eastern deciduous forest.

FIGURE 5.19 Hawaiian coral reef.

2. A second stage with autotrophs still of small stature, rapidly growing, with seeds or other kinds of reproductive structures that spread rapidly.
3. A third stage in which larger autotrophs—like trees in forest succession—enter and begin to dominate the site.
4. A fourth stage in which a mature ecosystem develops.

Although we list four stages, it is common practice to combine the first two and speak of early-, middle-, and late-successional stages. The stages of succession are described here in terms of autotrophs, but similarly adapted animals and other life-forms are associated with each stage. We discuss other general properties of succession later in this chapter.

Species characteristic of the early stages of succession are called pioneers, or **early-successional species**. They have evolved and are adapted to the environmental conditions in early stages of succession. In terrestrial ecosystems, vegetation that dominates late stages of succession, called **late-successional species**, tends to be slower-growing and longer-lived, and can persist under intense competition with other species. For example, in terrestrial ecosystems, late-successional vegetation tends to grow well in shade and have seeds that, though not as widely dispersing, can persist a rather long time. Typical **middle-successional species** have characteristics in between the other two types.

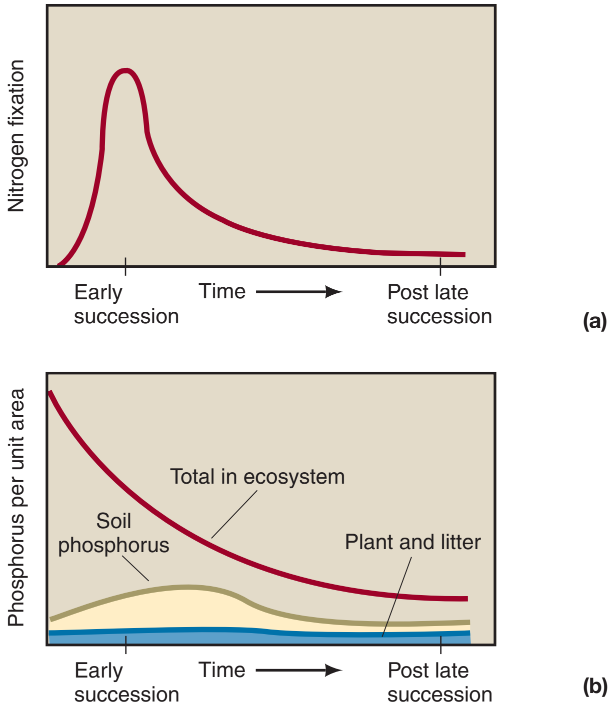

FIGURE 5.20 **(a)** Hypothesized changes in soil nitrogen during the course of soil development. **(b)** Change in total soil phosphorus over time with soil development. (P.M. Vitousek and P.S. White, Process studies in forest succession, in D.C. West, H.H. Shugart, and D.B. Botkin, eds., [New York: Springer-Verlag, 1981], Figure 17.1, p. 269.)

5.8 Chemical Cycling and Succession

One of the important effects of succession is a change in the storage of chemical elements necessary for life. On land, the storage of chemical elements essential for plant growth and function (including nitrogen, phosphorus, potassium, and calcium) generally increases during the progression from the earliest stages of succession to middle succession (Figure 5.20). There are three reasons for this:

Increased storage. Organic matter, living or dead, stores chemical elements. As long as there is an increase in organic matter within the ecosystem, there will be an increase in the storage of chemical elements.

Increased rate of uptake. For example, in terrestrial ecosystems. many plants have root nodules containing bacteria that can assimilate atmospheric nitrogen, which is then used by the plant in a process known as *nitrogen fixation.*

Decreased rate of loss. The presence of live and dead organic matter helps retard erosion. Both organic and inorganic soil can be lost to erosion by wind and water. Vegetation and, in certain marine and freshwater ecosystems, large forms of algae tend to prevent such losses and therefore increase total stored material.

Ideally, chemical elements could be cycled indefinitely in ecosystems, but in the real world there is always some loss as materials are moved out of the system by wind and water. As a result, ecosystems that have persisted continuously for the longest time are less fertile than those in earlier stages. For example, where glaciers melted back thousands of years ago in New Zealand, forests developed, but the oldest areas have lost much of their fertility and have become shrublands with less diversity and biomass. The same thing happened to ancient sand dune vegetation in Australia.[17]

5.9 How Species Change Succession

Early-successional species can affect what happens later in succession in three ways: through (1) facilitation, (2) interference, or (3) life history differences (Figure 5.21).[18,19]

Facilitation

In facilitation, an earlier-successional species changes the local environment in ways that make it suitable for another species that is characteristic of a later successional stage. Dune and bog succession illustrate facilitation. The first plant species—dune grass and floating sedge—prepare the way for other species to grow. Facilitation is common in tropical rain forests,[20] where early-successional species

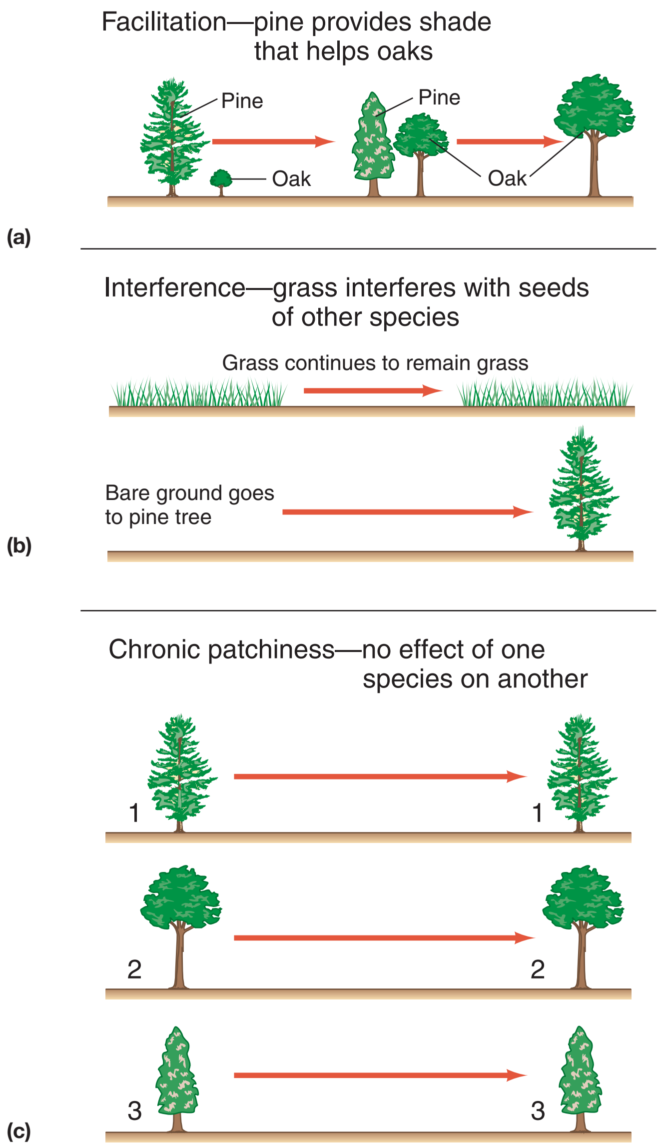

FIGURE 5.21 Interaction among species during ecological succession. (a) Facilitation. As Henry David Thoreau observed in Massachusetts more than 100 years ago, pines provide shade and act as "nurse trees" for oaks. Pines do well in openings. If there were no pines, few or no oaks would survive. Thus the pines facilitate the entrance of oaks. **(b) Interference.** Some grasses that grow in open areas form dense mats that prevent seeds of trees from reaching the soil and germinating. **(c) Chronic patchiness.** Earlier-entering species neither help nor interfere with other species; instead, as in a desert, the physical environment dominates.

speed the reappearance of the microclimatic conditions that occur in a mature forest. Because of the rapid growth of early-successional plants, after only 14 years the temperature, relative humidity, and light intensity at the soil surface in tropical forests can approximate those of a mature rain forest.[21] Once these conditions are established, species adapted to deep forest shade can germinate and persist.

Facilitation also occurs in coral reefs, mangrove swamps along ocean shores, kelp beds along cold ocean shores such as the Pacific coast of the United States and Canada's Pacific Northwest, and in shallow marine benthic areas where the water is relatively calm and large algae can become established.

Knowing the role of facilitation can be useful in the restoration of damaged areas. Plants that facilitate the presence of others should be planted first. On sandy areas, for example, dune grasses can help hold the soil before we attempt to plant shrubs or trees.

Interference

In contrast to facilitation, interference refers to situations where an earlier-successional species changes the local environment so it is *unsuitable* to another species characteristic of a later-successional stage. Interference is common, for example, in American tall-grass prairies, where prairie grasses like little bluestem form a mat of living and dead stems so dense that seeds of other plants cannot reach the ground and therefore do not germinate. Interference does not last forever, however. Eventually, some breaks occur in the grass mat—perhaps from surface-water erosion, the death of a patch of grass from disease, or removal by fire. Breaks in the grass mat allow seeds of trees to germinate. For example, in the tall-grass prairie, seeds of red cedar can then reach the ground. Once started, red cedar soon grows taller than the grasses, shading them so much that they cannot grow. More ground is open, and the grasses are eventually replaced.

The same pattern occurs in some Asian tropical rain forests. The grass, *Imperata*, forms stands so dense that seeds of later-successional species cannot reach the ground. *Imperata* either replaces itself or is replaced by bamboo, which then replaces itself. Once established, *Imperata* and bamboo appear able to persist for a long time. Once again, when and if breaks occur in the cover of these grasses, other species can germinate and grow, and a forest eventually develops.

Life History Differences

In this case, changes in the time it takes different species to establish themselves give the appearance of a succession caused by species interactions, but it is not. In cases where no species interact through succession, the result is termed **chronic patchiness**. Chronic patchiness is characteristic of highly disturbed environments and highly stressful ones in terms of temperature, precipitation, or chemical availability, such as deserts. For example, in the warm deserts of California, Arizona, and Mexico, the major shrub species grow in patches, often consisting of mature individuals with few seedlings. These patches tend to persist for long periods until there is a disturbance.[22] Similarly, in highly polluted environments, a sequence of species replacement may not occur. Chronic patchiness also describes planktonic ecological communities and their ecosystems, which occur in the constantly moving waters of the upper ocean and the upper waters of ponds, lakes, rivers, and streams.

CRITICAL THINKING ISSUE

Should People Eat Lower on the Food Chain?

The energy content of a food chain is often represented by an energy pyramid, such as the one shown here in Figure 5.22a for a hypothetical, idealized food chain. In an energy pyramid, each level of the food chain is represented by a rectangle whose area is more or less proportional to the energy content of that level. For the sake of simplicity, the food chain shown here assumes that each link in the chain has only one source of food.

Assume that if a 75 kg (165 lb) person ate frogs (and some people do!), he would need 10 a day, or 3,000 a year (approximately 300 kg, or 660 lb). If each frog ate 10 grasshoppers a day, the 3,000 frogs would require 9 million grasshoppers a year to supply their energy needs, or approximately 9,000 kg (19,800 lb) of grasshoppers. A horde of grasshoppers of that size would require 333,000 kg (732,600 lb) of wheat to sustain them for a year.

As the pyramid illustrates, the energy content decreases at each higher level of the food chain. The result is that the amount of energy at the top of a pyramid is related to the number of layers the pyramid has. For example, if people fed on grasshoppers rather than frogs, each person could probably get by on 100 grasshoppers a day. The 9 million grasshoppers could support 300 people for a year, rather than only one. If, instead of grasshoppers, people ate wheat, then 333,000 kg of wheat could support 666 people for a year.

This argument is often extended to suggest that people should become herbivores (vegetarians) and eat directly from the lowest level of all food chains, the autotrophs. Consider, however, that humans can eat only parts of some plants. Herbivores can eat some parts of plants that humans cannot eat, and some plants that humans cannot eat at all. When people eat these herbivores, more of the energy stored in plants becomes available for human consumption.

The most dramatic example of this is in aquatic food chains. Because people cannot digest most kinds of algae, which are the base of most aquatic food chains, they depend on eating fish that eat algae and fish that eat other fish. So if people were to become entirely herbivorous, they would be excluded from many food chains. In addition, there are major areas of Earth where crop production damages the land but grazing by herbivores does not. In those cases, conservation of soil and biological diversity lead to arguments that support the use of grazing animals for human food. This creates an environmental issue: How low on the food chain should people eat?

Critical Thinking Questions

1. Why does the energy content decrease at each higher level of a food chain? What happens to the energy lost at each level?
2. The pyramid diagram uses mass as an indirect measure of the energy value for each level of the pyramid. Why is it appropriate to use mass to represent energy content?
3. Using the average of 21 kilojoules (kJ) of energy to equal 1 g of completely dried vegetation (see Working It Out 5.2) and assuming that wheat is 80% water, what is the energy content of the 333,000 kg of wheat shown in the pyramid?
4. Make a list of the environmental arguments for and against an entirely vegetarian diet for people. What might be the consequences for U.S. agriculture if everyone in the country began to eat lower on the food chain?
5. How low do you eat on the food chain? Would you be willing to eat lower? Explain.

FIGURE 5.22 **(a)** Energy pyramid. **(b)** Grasshoppers. **(c)** Frogs that eat grasshoppers.

SUMMARY

- An ecosystem is the simplest entity that can sustain life. At its most basic, an ecosystem consists of several species and a fluid medium (air, water, or both). The ecosystem must sustain two processes—the cycling of chemical elements and the flow of energy.
- The living part of an ecosystem is the ecological community, a set of species connected by food webs and trophic levels. A food web or food chain describes who feeds on whom. A trophic level consists of all the organisms that are the same number of feeding steps from the initial source of energy.
- Community-level effects result from indirect interactions among species, such as those that occur when sea otters influence the abundance of sea urchins.
- Ecosystems are real and important, but it is often difficult to define the limits of a system or to pinpoint all the interactions that take place. Ecosystem management is considered key to the successful conservation of life on Earth.
- Energy flows one way through an ecosystem; the second law of thermodynamics places a limit on the abundance of productivity of life and requires the one-way flow.
- Chemical elements cycle, and in theory could cycle forever, but in the real world there is always some loss.
- Ecosystems recover from changes through ecological succession, which has repeatable patterns.
- Ecosystems are non-steady-state systems, undergoing changes all the time and requiring change.

REEXAMINING THEMES AND ISSUES

Human Population

The human population depends on many ecosystems that are widely dispersed around the globe. Modern technology may appear to make us independent of these natural systems. In fact, though, the more connections we establish through modern transportation and communication, the more kinds of ecosystems we depend on. Therefore, the ecosystem concept is one of the most important we will learn about in this book.

Sustainability

The ecosystem concept is at the heart of managing for sustainability. When we try to conserve species or manage living resources so that they are sustainable, we must focus on their ecosystem and make sure that it continues to function.

Global Perspective

Our planet has sustained life for approximately 3.5 billion years. To understand how Earth as a whole has sustained life for such a long time, we must understand the ecosystem concept because the environment at a global level must meet the same basic requirements as those of any local ecosystem.

Urban World

Cities are embedded in larger ecosystems. But like any life-supporting system, a city must meet basic ecosystem needs. This is accomplished through connections between cities and surrounding environments. Together, these function as ecosystems or sets of ecosystems. To understand how we can create pleasant and sustainable cities, we must understand the ecosystem concept.

People and Nature

The feelings we get when we hike through a park or near a beautiful lake are as much a response to an ecosystem as to individual species. This illustrates the deep connection between people and ecosystems. Also, many effects we have on nature are at the level of an ecosystem, not just on an individual species.

Science and Values

The introductory case study about sea otters, sea urchins, and kelp illustrates the interactions between values and scientific knowledge about ecosystems. Science can tell us how organisms interact. This knowledge confronts us with choices. Do we want abalone to eat, sea otters to watch, kelp forests for biodiversity? The choices we make depend on our values.

KEY TERMS

autotrophs **84**
biological production **93**
biomass **93**
bog **97**
carnivores **84**
chemoautotrophs **93**
chronic patchiness **100**
community effect **81**
decomposers **84**
early-successional species **99**
ecological community **83**
ecological succession **95**
ecosystem **83**
ecosystem energy flow **89**
energy efficiency **95**
entropy **93**
first law of thermodynamics **91**
food chains **84**
food webs **84**
gross production **93**
herbivores **84**
heterotrophs **84**
keystone species **81**
late-successional species **99**
middle-successional species **99**
net production **93**
omnivores **86**
pelagic ecosystem **85**
photosynthesis **84**
primary production **93**
primary succession **95**
secondary production **93**
secondary succession **95**
second law of thermodynamics **92**
succession **96**
trophic level **84**
watershed **88**

STUDY QUESTIONS

1. Farming has been described as managing land to keep it in an early stage of succession. What does this mean, and how is it achieved?

2. Redwood trees reproduce successfully only after disturbances (including fire and floods), yet individual redwood trees may live more than 1,000 years. Is redwood an early- or late-successional species?

3. What is the difference between an ecosystem and an ecological community?

4. What is the difference between the way energy puts limits on life and the way phosphorus does so?

5. Based on the discussion in this chapter, would you expect a highly polluted ecosystem to have many species or few species? Is our species a keystone species? Explain.

6. Keep track of the food you eat during one day and make a food chain linking yourself with the sources of those foods. Determine the biomass (grams) and energy (kilocalories) you have eaten. Using an average of 5 kcal/g, then using the information on food packaging or assuming that your net production is 10% efficient in terms of the energy intake, how much additional energy might you have stored during the day? What is your weight gain from the food you have eaten?

7. Which of the following are ecosystems? Which are ecological communities? Which are neither?
(a) Chicago
(b) A 1,000-ha farm in Illinois
(c) A sewage-treatment plant
(d) The Illinois River
(e) Lake Michigan

FURTHER READING

Modern Studies

Botkin, D.B., *No Man's Garden: Thoreau and a New Vision for Civilization and Nature* (Washington, DC: Island Press, 2001).

Chapin, F. Stuart III, Harold A. Mooney, Melissa C. Chapin, and Pamela Matson, *Principles of Terrestrial Ecosystem Ecology* (New York: Springer, 2004, paperback). Kaiser et al., *Marine Ecology: Processes, Systems, and Impacts* (New York: Oxford University Press, 2005).

Some Classic Studies and Books

Blum, H.F., *Time's Arrow and Evolution* (New York: Harper & Row, 1962). A very readable book discussing how life is connected to the laws of thermodynamics and why this matters.

Bormann, F.H., and G.E. Likens, *Pattern and Process in a Forested Ecosystem*, 2nd ed. (New York: Springer-Verlag, 1994). A synthetic view of the northern hardwood ecosystem, including its structure, function, development, and relationship to disturbance.

Gates, D.M., *Biophysical Ecology* (New York: Springer-Verlag, 1980). A discussion about how energy in the environment affects life.

Morowitz, H.J., *Energy Flow in Biology* (Woodbridge, CT: Oxbow, 1979). The most thorough and complete discussion available about the connection between energy and life, at all levels, from cells to ecosystems to the biosphere.

Odum, Eugene, and G.W. Barrett, *Fundamentals of Ecology* (Duxbury, MA: Brooks/Cole, 2004). Odum's original textbook was a classic, especially in providing one of the first serious introductions to ecosystem ecology. This is the latest update of the late author's work, done with his protégé.

Schrödinger, E. (ed. Roger Penrose), *What Is Life?: With Mind and Matter and Autobiographical Sketches (Canto)* (Cambridge: Cambridge University Press, 1992). The original statement about how the use of energy differentiates life from other phenomena in the universe. Easy to read and a classic.