Deforestation in the mountains of Haiti has disrupted natural cycles.

Reversing the Deforestation of Haiti
Even before the devastating earthquake of 2010, life in Haiti was hard. On the streets of the capital city, Port-au-Prince, people would line up to buy charcoal to cook their meals. According to the United Nations, 76 percent of Haitians lived on less than $2.00 a day. Because other forms of cooking fuel, including oil and propane, were too expensive, people turned to the forests, cutting trees to make charcoal from firewood. Relying on charcoal for fuel has had a serious impact on the forests of Haiti. In 1923, 60 percent of this mountainous country was covered in forest. However, as the population grew and demand for charcoal increased, the amount of forest shrunk. By 2006, more than 9 million people lived in this small nation, and less than 2 percent of its land remained forested. Today, most trees in Haiti are cut before they grow to more than a few centimeters in diameter. This rate of deforestation is not sustainable for the people or for the forest.

By 2006, more than 9 million people lived in this small nation, and less than 2 percent of its land remained forested.

Deforestation allows water to run rapidly down the mountains, leading to more extreme flooding.

Deforestation disrupts the ecosystem services that living trees provide. In Chapter 1 we saw some of the consequences of subjecting land to such massive deforestation. When Haitian forests are clear-cut, the land becomes much more susceptible to erosion. When trees are cut, their roots die, and dead tree roots can no longer stabilize the soil. Without roots to anchor it, the soil is eroded away by the heavy rains of tropical storms and hurricanes. Unimpeded by vegetation, the rainwater runs
quickly down the mountainsides, dislodging the topsoil that is so important for forest growth. In addition, oversaturation of the soil causes massive mudslides that destroy entire villages.

But the news from Haiti is not all bad. For more than two decades, the U.S. Agency for International Development has funded the planting of 60 million trees there. Unfortunately, the local people can’t afford to let them grow while they are in desperate need of firewood and charcoal. A more successful effort has been the planting of mango trees (*Mangifera indica*). A mature mango tree can provide $70 to $150 worth of mangoes annually. Their value provides an economic incentive for allowing trees to reach maturity. The deforestation problem is also being addressed through efforts to develop alternative fuel sources, such as discarded paper processed into dried cakes that can be burned.

Extensive forest removal is a problem in many developing nations, not just in Haiti. In many places, widespread removal trees on mountains has led to rapid soil erosion and substantial disruptions of the natural cycles of water and soil nutrients, which in turn have led to long-term degradation of the environment. The results not only illustrate the connectedness of ecological systems, but also show how forest ecosystems, like all ecosystems, can be influenced by human decisions.


**Key Ideas**

The collections of living and nonliving components on Earth can be thought of as ecological systems, commonly called *ecosystems*. Ecosystems control the movement of the energy, water, and nutrients that organisms must have to grow and reproduce. Understanding the processes that determine these movements is the goal of ecosystem ecology.

After reading this chapter you should be able to

- list the basic components of an ecosystem.
- describe how energy flows through ecosystems.
- describe how carbon, nitrogen, and phosphorus cycle within ecosystems.
- explain how ecosystems respond to natural and anthropogenic disturbances.
- discuss the values of ecosystems and how humans depend on them.

### 3.1 Ecosystem ecology examines interactions between the living and nonliving world
An important aspect of ecosystems is how the components are interrelated. An ecosystem is a particular location on Earth distinguished by its particular mix of interacting biotic and abiotic components. For example, a forest contains many interacting biotic components, such as trees, wildflowers, birds, mammals, insects, fungi, and bacteria, that are quite distinct from those in a grassland. Collectively, all the living organisms in an ecosystem represent the ecosystem’s biodiversity. Ecosystems also have abiotic components such as sunlight, temperature, soil, water, pH, and nutrients. The abiotic components of the ecosystem determine which organisms can live there. The components of a particular ecosystem are highly dependent on climate. For example, ecosystems in the dry desert of Death Valley, California, where temperatures can reach 50°C (120°F), are very different from those on the continent of Antarctica, where temperatures may drop as low as −85°C (−120°F). Similarly, water can range from being immeasurable in deserts to being a defining part of the ecosystem in lakes and oceans. On less extreme scales, small differences in precipitation and the ability of the soil to retain water can favor different terrestrial ecosystem types. Regions with greater quantities of water in the soil can support trees, whereas regions with less water in the soil can support only grasses.

### 3.1.1 Ecosystem Boundaries

The biotic and abiotic components of an ecosystem provide the boundaries that distinguish one ecosystem from another. Some ecosystems have well-defined boundaries, whereas others do not. A cave, for example, is a well-defined ecosystem (FIGURE 3.1). It contains identifiable biotic components, such as animals and microorganisms that are specifically adapted to live in a cave environment, as well as distinctive abiotic components, including temperature, salinity, and water that flows through the cave as an underground stream. Roosting bats fly out of the cave each night and consume insects. When the bats return to the cave and defecate, their feces provide energy that passes through the relatively few animal species that live in the cave. In many caves, for example, small invertebrate animals consume the feces and are in turn consumed by cave salamanders.
Figure 3.1 A cave ecosystem. Cave ecosystems typically have distinct boundaries and are home to highly adapted species.

The cave ecosystem is relatively easy to study because its boundaries are clear. With the exception of the bats feeding outside the cave, the cave ecosystem is easily defined as everything from the point where the stream enters the cave to the point where it exits. Likewise, many aquatic ecosystems, such as lakes, ponds, and streams, are relatively easy to define because the ecosystem’s boundaries correspond to the boundaries between land and water. Knowing the boundaries of an ecosystem makes it easier to identify the system’s biotic and abiotic components and to trace the cycling of energy and matter through the system.

In most cases, however, determining where one ecosystem ends and another begins is difficult. For this reason, ecosystem boundaries are often subjective. Environmental scientists might define a terrestrial ecosystem as the range of a particular species of interest, such as the area where wolves roam, or they might define it using topographic features, such as two mountain ranges enclosing a valley. The boundaries of some managed ecosystems, such as national parks, are set according to administrative rather than scientific criteria. Yellowstone National Park, for example, was once managed as its own ecosystem, until scientists began to realize that many species of conservation interest, such as grizzly bears (*Ursus arctos horribilis*), spent time both inside and outside the 1-million-hectare (2.5-million-acre) park. To manage these species
effectively, scientists had to think much more broadly: they had to include nearly 20 million hectares (50 million acres) of public and private land outside the park. This larger region was named the Greater Yellowstone Ecosystem. As the name suggests, the actual ecosystem extends well beyond the administrative boundaries of the park (FIGURE 3.2a).

**Figure 3.2** Large and small ecosystems. (a) The Greater Yellowstone Ecosystem includes the land within Yellowstone National Park and many adjacent properties. (b) Some ecosystems are very small, such as a rain-filled tree hole that houses a diversity of microbes and aquatic insects.
As we saw in Chapter 2, not all ecosystems are as vast as the Greater Yellowstone Ecosystem. Some can be quite small, such as a water-filled hole in a fallen tree trunk or an abandoned car tire that fills with rainwater (FIGURE 3.2b). Such tiny ecosystems include all the physical and chemical components necessary to support a diverse set of species, such as microbes, mosquito larvae, and other insects. Therefore, ecosystems can occur in a wide range of sizes.

### 3.1.2 Ecosystem Processes

Although it is helpful to divide locations on Earth into distinct ecosystems, it is important to remember that each ecosystem interacts with surrounding ecosystems through the exchange of energy and matter. Organisms, such as bats flying to and from their cave, and chemical elements, such as carbon or nitrogen dissolved in water, move across ecosystem boundaries. As a result, changes in any one ecosystem can ultimately have far-reaching effects on the global environment.

**CHECKPOINT**

- What is an ecosystem and what are its components?
- How would you know when you left one ecosystem and entered another?
- How are ecosystem boundaries imposed by humans sometimes different from natural boundaries?

- **3. Energy flows through ecosystems**

To understand how ecosystems function and how to best protect and manage them, ecosystem ecologists study not only the biotic and abiotic components that define an ecosystem, but also the processes that move energy and matter within it. Plants absorb energy directly from the Sun. That energy is then spread throughout an ecosystem as herbivores (animals that eat plants) feed on plants and carnivores (animals that eat other animals) feed on herbivores. Consider the Serengeti Plain in East Africa, shown in FIGURE 3.3. There are millions of herbivores, such as zebras and wildebeests, in the Serengeti ecosystem, but far fewer carnivores, such as lions (Panthera leo) and cheetahs (Acinonyx jubatus), that feed on those herbivores. In accordance with the second law of thermodynamics, when one organism consumes another, not all of the energy in the consumed organism is transferred to the consumer. Some of that energy is lost as heat. Therefore, all the carnivores in an area contain less energy than all the herbivores in the same area.
because all the energy going to the carnivores must come from the animals they eat. To better understand these energy relationships, let’s trace this energy flow in more detail.

**Figure 3.3 Serengeti Plain of Africa.** The Serengeti ecosystem has more plants than herbivores, and more herbivores than carnivores.

### 3.2.1 Photosynthesis and Respiration

[Notes/Highlighting]
Photosynthesis and respiration.

Figure 3.4 Photosynthesis is a process by which producers use solar energy to convert carbon dioxide and water into glucose and oxygen. Respiration is a process by which organisms convert glucose and oxygen into water and carbon dioxide, releasing the energy needed to live, grow, and reproduce. All organisms, including producers, perform respiration.

Nearly all of the energy that powers ecosystems comes from the Sun as solar energy, which is a form of kinetic energy. Plants, algae, and other organisms that use the Sun’s energy to produce usable forms of energy are called producers, or autotrophs. Through the process of photosynthesis, producers use solar energy to convert carbon dioxide (CO$_2$) and water (H$_2$O) into glucose (C$_6$H$_{12}$O$_6$), a form of potential energy that can be used by a wide range of organisms. As we can see in FIGURE 3.4, the process also produces oxygen (O$_2$) as a waste product. That is why plants and other producers are beneficial to our atmosphere: they produce the oxygen we need to breathe.

Producers use the glucose they produce by photosynthesis to store energy and to build structures such as leaves, stems, and roots. Other organisms, such as the herbivores on the Serengeti Plain, eat the tissues of producers and gain energy from the chemical energy contained in those tissues. They do this through cellular respiration, a process.
that unlocks the chemical energy stored in the cells of organisms. Respiration is the opposite of photosynthesis: cells convert glucose and oxygen into energy, carbon dioxide, and water. In essence, they run photosynthesis backward to recover the solar energy stored in glucose. All organisms—including producers—carry out respiration to fuel their own metabolism and growth. Thus producers both produce and consume oxygen. When the Sun is shining and photosynthesis occurs, producers generate more oxygen via photosynthesis than they consume via respiration, and there is a net production of oxygen. At night, producers only respire, consuming oxygen without generating it. Overall, producers photosynthesize more than they respire. The net effect is an excess of oxygen that is released into the air and an excess of carbon that is stored in the tissues of producers.

3.2.2 Trophic Levels, Food Chains, and Food Webs

Unlike producers, which make their own food, consumers, or heterotrophs, are incapable of photosynthesis and must obtain their energy by consuming other organisms. In FIGURE 3.5, we can see that heterotrophs fall into several different categories. Heterotrophs that consume producers are called herbivores or primary consumers. Primary consumers include a variety of familiar plant- and algae-eating animals, such as zebras, grasshoppers, and tadpoles. Heterotrophs that obtain their energy by eating other consumers are called carnivores. Carnivores that eat primary consumers are called secondary consumers. Secondary consumers include creatures such as lions, hawks, and rattlesnakes. Rarer are tertiary consumers: carnivores that eat secondary consumers. Animals such as bald eagles (Haliaeetus leucocephalus) can be tertiary consumers: algae (producers) living in lakes convert sunlight into glucose, zooplankton (primary consumers) eat the algae, fish (secondary consumers) eat the zooplankton, and eagles (tertiary consumers) eat the fish. We call these successive levels of organisms consuming one another trophic levels (from the Greek word which means “nourishment“). The sequence of consumption from producers through tertiary consumers is known as a food chain. In a food chain, energy moves from one trophic level to the next.
A food chain helps us visualize how energy and matter move between trophic levels. However, species in natural ecosystems are rarely connected in such a simple, linear fashion. A more realistic type of model, shown in FIGURE 3.6, is known as a food web. Food webs take into account the complexity of nature, and they illustrate one of the most important concepts of ecology: that all species in an ecosystem are connected to one another.
Figure 3.6  A simplified food web. Food webs are more realistic representations of trophic relationships than simple food chains. They include scavengers, detritivores, and decomposers, and they recognize that some species feed at multiple trophic levels. Arrows indicate the direction of energy movement. Actual food webs are even more complex than this one. For instance, in an actual ecosystem, many more organisms are present. In addition, for simplicity, not all possible arrows are shown.

Not all organisms fit neatly into a single trophic level. Some organisms, called omnivores, operate at several trophic levels. Omnivores include grizzly bears, which eat berries and fish, and the Venus flytrap (Dionaea muscipula), which can photosynthesize and also digests insects that become trapped in its leaves. In
addition, each trophic level eventually produces dead individuals and waste products that feed other organisms. Scavengers are carnivores, such as vultures, that consume dead animals. Detritivores are organisms, such as dung beetles, that specialize in breaking down dead tissues and waste products (referred to as detritus) into smaller particles. These particles can then be further processed by decomposers: the fungi and bacteria that complete the breakdown process by recycling the nutrients from dead tissues and wastes back into the ecosystem. Without scavengers, detritivores, and decomposers, there would be no way of recycling organic matter and energy, and the world would rapidly fill up with dead plants and animals.

3.2.3 Ecosystem Productivity

The amount of energy available in an ecosystem determines how much life the ecosystem can support. For example, the amount of sunlight that reaches a lake surface determines how much algae can live in the lake. In turn, the amount of algae determines the number of zooplankton the lake can support, and the size of the zooplankton population determines the number of fish the lake can support. If we wish to understand how ecosystems function, or how to manage and protect them, it is important to understand where the energy in an ecosystem comes from and how it is transferred through food webs. To do this, environmental scientists look at the total amount of solar energy that the producers in an ecosystem capture via photosynthesis over a given amount of time. This measure is known as the gross primary productivity (GPP) of the ecosystem.

Note that the term gross, as used here, indicates the total amount of energy captured by producers. In other words, GPP does not subtract the energy lost when the producers respire. The energy captured minus the energy respired by producers is the ecosystem’s net primary productivity (NPP):

\[ \text{NPP} = \text{GPP} - \text{respiration by producers} \]

You can think of GPP and NPP in terms of a paycheck. GPP is like the total amount your employer pays you. NPP is the actual amount you take home after taxes are deducted. GPP is essentially a measure of how much photosynthesis is occurring over some amount of time. Determining GPP is a challenge for scientists because a plant rarely photosynthizes without simultaneously respiring. However, if we can determine the rate of photosynthesis and the rate of respiration, we can use this information to calculate GPP.

We can determine the rate of photosynthesis by measuring the compounds that participate in the reaction. So, for example, we can measure the rate at which \( \text{CO}_2 \) is
taken up during photosynthesis and the rate at which CO₂ is produced during respiration. A common approach to measuring GPP is to first measure the production of CO₂ in the dark. Because no photosynthesis occurs in the dark, this measure eliminates CO₂ uptake by photosynthesis. Next, we measure the uptake of CO₂ in sunlight. This measure gives us the net movement of CO₂ when respiration and photosynthesis are both occurring. By adding the amount of CO₂ produced in the dark to the amount of CO₂ taken up in the sunlight, we can determine the gross amount of CO₂ that is taken up during photosynthesis:

\[
\text{CO}_2 \text{ taken up during photosynthesis} = \text{CO}_2 \text{ taken up in sunlight} + \text{CO}_2 \text{ produced in the dark}
\]

In this way, we can derive the GPP of an ecosystem per day within a given area. We can give our answer in units of kilograms of carbon taken up per square meter per day (kg C/m²/day).

**Figure 3.7** Gross and net primary productivity. Producers typically capture only about 1 percent of available solar energy via photosynthesis. The energy they capture (gross primary productivity, or GPP) can be divided into energy used for the producers’ respiration and energy available for the producers’ growth and reproduction (net primary productivity, or NPP).

Converting sunlight into chemical energy is not an efficient process. As **FIGURE 3.7** shows, of the total amount of solar energy that reaches the producers in an ecosystem—the sunlight on a pond surface, for example—only about 1 percent, on average, is converted into chemical energy via photosynthesis. Most of that solar energy is lost from the ecosystem as heat that returns to the atmosphere. Some of the lost energy consists of wavelengths of light that producers cannot absorb. Those
wavelengths are either reflected from the surfaces of producers or pass through their tissues.

The NPP of ecosystems ranges from 25 to 50 percent of GPP, or as little as 0.25 percent of the solar energy striking the plant. Clearly, it takes a lot of energy to conduct photosynthesis. Let’s look at the math. On average, of the 1 percent of the Sun’s energy that is captured by a producer (its individual GPP), about 60 percent is used to fuel the producer’s respiration. The remaining energy (its individual NPP) is about 40 percent of the original 1 percent (see Figure 3.7). This 40 percent can be used to support the producer’s growth and reproduction. A forest in North America, for example, might have a GPP of 2.5 kg C/m²/year and lose 1.5 kg C/m²/year to respiration by the plants in the forest. Because NPP = GPP – respiration, the NPP of the forest is 1 kg C/m²/year (1.8 pounds C/yd²/year). This means that the plants living in 1 m² of forest will add 1 kg of carbon to their tissues every year by means of growth and reproduction. So, in this example, NPP is 40 percent of GPP.

Measurement of NPP allows us to compare the productivity of different ecosystems, as shown in Figure 3.8. It is perhaps not surprising that producers grow best in ecosystems where they have plenty of sunlight, lots of available water and nutrients, and warm temperatures, such as tropical rainforests and salt marshes, which are the most productive ecosystems on Earth. Conversely, producers grow poorly in the cold regions of the Arctic, dry deserts, and the dark regions of the deep sea. In general, the greater the productivity of an ecosystem, the more primary consumers can be supported.
Figure 3.8  Net primary productivity varies among ecosystems. Productivity is highest where temperatures are warm and water and solar energy are abundant. As a result, NPP varies tremendously among different areas of the world. [After R. H. Whittaker and G. E. Likens, Primary production: The biosphere and man, Human Ecology 1 (1973): 357–369.]

Measuring NPP is also a useful way to measure change in an ecosystem. For example, after a drastic change alters an ecosystem, the amount of stored energy (NPP) tells us whether the new system is more or less productive than the previous system.

3.2.4 Energy Transfer Efficiency and Trophic Pyramids

The energy in an ecosystem can be measured in terms of biomass, which is the total mass of all living matter in a specific area. The net primary productivity of an ecosystem—its NPP—establishes the rate at which biomass is produced over a given amount of time. To analyze the productivity of an ecosystem, scientists calculate the biomass of all individuals accumulated over a given amount of time.
The amount of biomass present in an ecosystem at a particular time is its **standing crop**. It is important to differentiate standing crop, which measures the *amount* of energy in a system at a given time, from productivity, which measures the *rate* of energy production over a span of time. For example, slow-growing forests have low productivity; the trees add only a small amount of biomass through growth and reproduction each year. However, the standing crop of long-lived trees—the biomass of trees that has accumulated over hundreds of years—is quite high. In contrast, the high growth rates of algae living in the ocean make them extremely productive. But because primary consumers eat these algae so rapidly, the standing crop of algae at any particular time is relatively low.

Not all of the energy contained in a particular trophic level is in a usable form. Some parts of plants are not digestible and are excreted by primary consumers. Secondary consumers such as owls consume the muscles and organs of their prey, but they cannot digest bones and hair. Of the food that is digestible, some fraction of the energy it contains is used to power the consumer’s day-to-day activities, including moving, eating, and (for birds and mammals) maintaining a constant body temperature. That energy is ultimately lost as heat. Any energy left over may be converted into consumer biomass by growth and reproduction and thus becomes available for consumption by organisms at the next higher trophic level. The proportion of consumed energy that can be passed from one trophic level to another is referred to as **ecological efficiency**.

![Trophic pyramid for the Serengeti ecosystem.](image)

**Figure 3.9** **Trophic pyramid for the Serengeti ecosystem.** This trophic pyramid represents the amount of energy that is present at each trophic level, measured in joules (J). While this pyramid assumes 10 percent ecological efficiency, actual ecological efficiencies range from 5 to 20 percent across different ecosystems. For most ecosystems, graphing the numbers of individuals or biomass within each trophic level would produce a similar pyramid.

Ecological efficiencies are fairly low: they range from 5 to 20 percent and average about 10 percent across all ecosystems. In other words, of the total biomass available at a given trophic level, only about 10 percent can be converted into energy at the next
higher trophic level. We can represent the distribution of biomass among trophic levels using a **trophic pyramid**, like the one for the Serengeti ecosystem shown in **FIGURE 3.9**. Trophic pyramids tend to look similar across ecosystems. Most energy (and biomass) is found at the producer level, and energy (and biomass) decrease as we move up the pyramid.

The Serengeti ecosystem offers a good example of a trophic pyramid. The biomass of producers (grasses and shrubs) is much greater than the biomass of primary consumers (such as gazelles, wildebeests, and zebras) for which the producers serve as food. Likewise, the biomass of primary consumers is much greater than the biomass of secondary consumers (such as lions and cheetahs). The flow of energy between trophic levels helps to determine the population sizes of the various species within each trophic level. As we saw earlier in this chapter, the number of primary consumers in an area is generally higher than that of the carnivores they sustain.

The principle of ecological efficiency also has implications for the human diet. For example, if all humans were to act only as primary consumers—that is, become vegetarians—we would harvest much more energy from any given area. How would this work?

Suppose an acre of cropland could produce 1,000 kg of soybeans. This food could feed humans directly. Or, if we assume 10 percent ecological efficiency, it could be fed to cattle to produce approximately 100 kg of meat. In terms of biomass, there would be 10 times more food available for humans acting as primary consumers by eating soybeans than for humans acting as secondary consumers by eating beef. However, 1 kg of soybeans actually contains about 2.5 times as many calories as 1 kg of beef. Therefore, 1 acre of land would produce 25 times more calories when used for soybeans than when used for beef. In general, when we act as secondary consumers, the animals we eat require land to support the producers they consume. When we act as primary consumers, we require only the land necessary to support the producers we eat.

**CHECKPOINT**

- Why is photosynthesis an important process?
- What determines the productivity of an ecosystem?
- How efficiently is energy transferred between trophic levels in an ecosystem?

3.3 Matter cycles through the biosphere

The combination of all ecosystems on Earth forms the **biosphere**. The **biosphere** is the region of our planet where life resides. It forms a 20 km (12-mile) thick shell around
Energy flows through the biosphere: it enters as energy from the Sun, moves among the living and nonliving components of ecosystems, and is ultimately emitted into space by Earth and its atmosphere. As a result, energy must be constantly replenished by the Sun. Matter, in contrast, does not enter or leave the biosphere, but cycles within the biosphere in a variety of forms. As we saw in Chapter 2, Earth is an open system with respect to energy, but a closed system with respect to matter. The movements of matter within and between ecosystems involve biological, geological, and chemical processes. For this reason, these cycles are known as biogeochemical cycles. To keep track of the movement of matter in biogeochemical cycles, we refer to the components that contain the matter, including air, water, and organisms, as pools. Processes that move matter between pools are known as flows.

All of Earth’s living organisms are composed of chemical elements—mostly carbon, hydrogen, nitrogen, oxygen, and phosphorus. Organisms survive by constantly acquiring these various elements, either directly from their environment or by consuming other organisms, breaking down the digestible material, and rearranging the elements into usable compounds. The elements eventually leave the biotic components of the ecosystem when they are excreted as wastes or released by decomposition. Understanding the sources of these elements and how they flow between the biotic and abiotic components of ecosystems helps us to understand how ecosystems function and the ways in which human activities can alter these processes. The specific chemical forms elements take determine how they cycle within the biosphere. In this section we will look at the elements that are the most important to the productivity of photosynthetic organisms. We will begin with the hydrologic cycle—the movement of water. Then we will explore the cycles of carbon, nitrogen, and phosphorus. Finally, we will take a brief look at the cycles of calcium, magnesium, potassium, and sulfur.

### 3.3.1 The Hydrologic Cycle

Water is essential to life. It makes up over one-half of a typical mammal’s body weight, and no organism can survive without it. Water allows essential molecules to move within and between cells, draws nutrients into the leaves of trees, dissolves and removes toxic materials, and performs many other critical biological functions. On a larger scale, water is the primary agent responsible for dissolving and transporting the
chemical elements necessary for living organisms. The movement of water through the biosphere is known as the **hydrologic cycle**. **FIGURE 3.10** shows how the hydrologic cycle works. Heat from the Sun causes water to evaporate from oceans, lakes, and soils. Solar energy also provides the energy for photosynthesis, during which plants release water from their leaves into the atmosphere—a process known as **transpiration**. The water vapor that enters the atmosphere eventually cools and forms clouds, which, in turn, produce precipitation in the form of rain, snow, and hail. Some precipitation falls back into the ocean and some falls on land.

**Figure 3.10**  *The hydrologic cycle.* Water moves from the atmosphere to Earth’s surface and back to the atmosphere.

When water falls on land, it may take one of three distinct routes. First, it may return to the atmosphere by evaporation or, after being taken up by plant roots, by
transpiration. The combined amount of evaporation and transpiration, called **evapotranspiration**, is often used by scientists as a measure of the water moving through an ecosystem. Alternatively, water can be absorbed by the soil and percolate down into the groundwater. Finally, water can move as **runoff** across the land surface and into streams and rivers, eventually reaching the ocean—the ultimate pool of water on Earth. As water in the ocean evaporates, the cycle begins again.

The hydrologic cycle is instrumental in the cycling of elements. Many elements are carried to the ocean or taken up by organisms in dissolved form. As you read about biogeochemical cycles, notice the role that water plays in these processes.

**HUMAN ACTIVITIES AND THE HYDROLOGIC CYCLE** Because Earth is a closed system with respect to matter, water never leaves it. Nevertheless, human activities can alter the hydrologic cycle in a number of ways. For example, harvesting trees from a forest can reduce evapotranspiration by reducing plant biomass. If evapotranspiration decreases, then runoff or percolation will increase. On a moderate or steep slope, most water will leave the land surface as runoff. That is why, as we saw at the opening of this chapter, clear-cutting a mountain slope can lead to erosion and flooding. Similarly, paving over land surfaces to build roads, businesses, and homes reduces the amount of percolation that can take place in a given area, increasing runoff and evaporation. Humans can also alter the hydrologic cycle by diverting water from one area to another to provide water for drinking, irrigation, and industrial uses.

### 3.3.2 The Carbon Cycle

The elements carbon (C), nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), and sulfur (S) cycle through trophic levels in similar ways. Producers obtain these elements from the atmosphere or as ions dissolved in water. Consumers then obtain these elements by eating producers. Finally, decomposers absorb these elements from dead producers and consumers and their waste products. Through the process of decomposition, they convert the elements into forms that are once again available to producers.

Carbon is the most important element in living organisms; it makes up about 20 percent of their total body weight. Carbon is the basis of the long chains of organic molecules that form the membranes and walls of cells, constitute the backbones of proteins, and store energy for later use. Other than water, there are few molecules in the bodies of organisms that do not contain carbon.
FIGURE 3.11 illustrates the six processes that drive the carbon cycle: photosynthesis, respiration, exchange, sedimentation and burial, extraction, and combustion. These processes can be categorized as either fast or slow. The fast part of the cycle involves processes that are associated with living organisms. The slow part of the cycle involves carbon that is held in rocks, in soils, or as petroleum hydrocarbons (the materials we use as fossil fuels). Carbon may be stored in these forms for millions of years.
Producers take up carbon from the atmosphere and water via photosynthesis and pass it on to consumers and decomposers. Some inorganic carbon sediments out of the water to form sedimentary rock while some organic carbon may be buried and become fossil fuels. Respiration by organisms returns carbon back to the atmosphere and water. Combustion of fossil fuels and other organic matter returns carbon back to the atmosphere.
Let’s take a closer look at the carbon cycle, beginning with photosynthesis. When producers photosynthesize, they take in CO$_2$ and incorporate the carbon into their tissues. Some of this carbon is returned to the atmosphere when organisms respire. It is also returned to the atmosphere after organisms die. In the latter case, the carbon that was part of the live biomass pool becomes part of the dead biomass pool. Decomposers break down the dead material, returning CO$_2$ to the atmosphere via respiration and continuing the cycle.

A large amount of carbon is exchanged between the atmosphere and the ocean. The amount of CO$_2$ released from the ocean into the atmosphere roughly equals the amount of atmospheric CO$_2$ that diffuses into ocean water. Some of the CO$_2$ dissolved in the ocean enters the food web via photosynthesis by algae. Some combines with calcium ions in the water to form calcium carbonate (CaCO$_3$), a compound that can precipitate out of the water and form limestone and dolomite rock via sedimentation and burial. Although sedimentation is a very slow process, the small amounts of calcium carbonate sediment formed each year have accumulated over millions of years to produce the largest carbon pool in the slow part of the carbon cycle.

A small fraction of the organic carbon in the dead biomass pool is buried and incorporated into ocean sediments before it can decompose into its constituent elements. This organic matter becomes fossilized and, over millions of years, some of it may be transformed into fossil fuels. The amount of carbon removed from the food web by this slow process is roughly equivalent to the amount of carbon returned to the atmosphere by weathering of carbon-containing rocks (such as limestone) and by volcanic eruptions, so the slow part of the carbon cycle is in steady state.

The fifth process in the carbon cycle is the extraction of fossil fuels by humans. This process is a relatively recent phenomenon that began when human society started to rely on coal, oil, and natural gas as energy sources. Extraction by itself does not alter the carbon cycle, however. It is the subsequent step of combustion that makes the difference. Combustion, whether of fossil fuels or of timber in a forest fire, releases carbon into the atmosphere as CO$_2$ or into the soil as ash.

Respiration, decomposition, and combustion operate in very similar ways: all three processes cause organic molecules to be broken down to produce CO$_2$, water, and energy. The difference is that respiration and decomposition are biotic processes, whereas in combustion, the breakdown process occurs abiotically.

In the absence of human disturbance, the exchange of carbon between Earth’s surface and atmosphere is in steady state. Carbon taken up by photosynthesis eventually ends up in the soil. Decomposers in the soil gradually release that carbon at roughly the same rate it is added. Similarly, the gradual movement of carbon into the buried or fossil fuel pools is offset by the slow processes that release it. Before the Industrial
Revolution, atmospheric carbon concentrations had changed very little for 10,000 years (see FIGURE 1.8). So, until recently, carbon entering any of these pools was balanced by carbon leaving these pools.

Since the Industrial Revolution, however, human activities have had a major influence on carbon cycling. The best-known and most significant human alteration of the carbon cycle is the combustion of fossil fuels. This process releases fossilized carbon into the atmosphere, which increases atmospheric carbon concentrations and upsets the balance between Earth’s carbon pools and the atmosphere. The excess CO$_2$ in the atmosphere acts to increase the retention of heat energy in the biosphere. The result, global warming, is a major concern among environmental scientists and policy makers.

Tree harvesting is another human activity that can affect the carbon cycle. Trees store a large amount of carbon in their wood, both above and below ground. The destruction of forests by cutting and burning increases the amount of CO$_2$ in the atmosphere. Unless enough new trees are planted to recapture the carbon, the destruction of forests will upset the balance of CO$_2$. To date, large areas of forest, including tropical forests as well as North American and European temperate forests, have been converted into pastures, grasslands, and croplands. In addition to destroying a great deal of biodiversity, this destruction of forests has added large amounts of carbon to the atmosphere. The increases in atmospheric carbon due to human activities have been partly offset by an increase in carbon absorption by the ocean. Still, the harvesting of trees remains a concern.

### 3.3.3 The Nitrogen Cycle

We have seen that water and carbon, both essential to life, cycle through the biosphere in complex ways. Now we turn to some of the other elements that play an important part in the life of ecosystems. There are six key elements, known as **macronutrients**, that organisms need in relatively large amounts: nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur.

Organisms need nitrogen—the most abundant element in the atmosphere—in relatively high amounts. Because so much of it is required, nitrogen is often a **limiting nutrient** for producers. In other words, a lack of nitrogen constrains the growth of the organism. Adding other nutrients, such as water or phosphorus, will not improve plant growth in nitrogen-poor soil.

Nitrogen is used to form **amino acids**, the building blocks of proteins, and **nucleic acids**, the building blocks of DNA and RNA. In humans, nitrogen makes up about 3
percent of total body weight. The movement of nitrogen from the atmosphere through many transformations within the soil, then into plants, and then back into the atmosphere makes the nitrogen cycle one of the more interesting and complex biogeochemical cycles. **FIGURE 3.12** shows the complex processes of the nitrogen cycle. Although Earth’s atmosphere is 78 percent nitrogen by volume, the vast majority of that nitrogen is in a form that most producers cannot use. Nitrogen gas (N$_2$) molecules consist of two N atoms tightly bound together. Only a few organisms can convert N$_2$ gas directly into ammonia (NH$_3$) by a process known as **nitrogen fixation**. This process is the first step in the nitrogen cycle. Nitrogen-fixing organisms include cyanobacteria (also known as blue-green algae) and certain bacteria that live within the roots of legumes (plants such as peas, beans, and a few species of trees). These nitrogen-fixing bacteria possess specialized enzymes that can break the strong N$_2$ bond and add hydrogen ions to form NH$_3$, which is readily converted into its ionic form, ammonium (NH$_4^+$), in the soil.
Figure 3.12 The nitrogen cycle. The nitrogen cycle moves nitrogen from the atmosphere and into soils through several fixation pathways, including the production of fertilizers by humans. In the soil, nitrogen can exist in several forms. Denitrifying bacteria release nitrogen gas back into the atmosphere.

Nitrogen-fixing organisms use the fixed nitrogen to synthesize their own tissues, then excrete any excess. Cyanobacteria, which are primarily aquatic organisms, excrete
excess ammonium ions into the water. Bacteria living within plant roots excrete excess ammonium ions into the plant’s root system; the plant, in turn, supplies the bacteria with sugars it produces via photosynthesis.

Nitrogen can also be fixed through two abiotic pathways. First, N$_2$ can be fixed in the atmosphere by lightning or during combustion processes such as fires and the burning of fossil fuels. These processes convert N$_2$ into nitrate(NO$_3^-$), which is usable by plants. The nitrate is carried to Earth’s surface in precipitation. Humans have also developed techniques for converting N$_2$ gas into ammonia or nitrate to be used in plant fertilizers. Although these processes require a great deal of energy, humans now fix more nitrogen than is fixed in nature. The development of synthetic nitrogen fertilizers has led to large increases in crop yields, particularly for crops such as corn that require large amounts of nitrogen. Regardless of how nitrogen fixation occurs, the end product—NH$_4^+$ or NO$_3^-$—is a form of nitrogen that can be used by producers.

Once producers obtain fixed nitrogen, they assimilate it into their tissues (step 2 of the cycle). When primary consumers feed on the producers, some of that nitrogen is assimilated into the consumers’ tissues, and some is eliminated as waste products. Eventually, both producers and consumers die and decompose. In step 3 of the cycle, a process called ammionification, fungal and bacterial decomposers use nitrogen-containing wastes and dead bodies as a food source and excrete ammonium. Ammonium, in turn, is converted into nitrite (NO$_2^-$) and then into nitrate (NO$_3^-$) by specialized nitrifying bacteria in a two-step process called nitrification (step 4 of the cycle). Nitrite is of minor importance in natural ecosystems, but nitrate can be used by producers.

Because negatively charged particles repel one another, negatively charged nitrate ions do not bind easily to soil particles, most of which are negatively charged. As a result, nitrate is readily transported through the soil with water—a process called leaching. Leached nitrates eventually settle in the bottom sediments of oceans, lakes, and swamps. Under these conditions, or in waterlogged soils, denitrifying bacteria convert nitrate in a series of steps into the gases nitrous oxide (N$_2$O) and, eventually, N$_2$, which is emitted into the atmosphere. This conversion back into atmospheric N$_2$, a process called denitrification, completes the nitrogen cycle.

**EXCESS NITROGEN** Nitrogen is a limiting nutrient in most terrestrial ecosystems, so excess inputs of nitrogen can have consequences in these ecosystems. Adding nitrogen to soils in fertilizers ultimately increases atmospheric concentrations of nitrogen. This nitrogen can be transported through the atmosphere and deposited by rainfall in natural ecosystems that have adapted over time to a particular level of nitrogen availability. The added nitrogen can alter the distribution or abundance of species in those ecosystems.
In one study of nine different terrestrial ecosystems across the United States, scientists added nitrogen fertilizer to some plots and left other plots unfertilized as controls. They found that adding nitrogen reduced the number of species in a plot by up to 48 percent because some species that could survive under low-nitrogen conditions could no longer compete against larger plants that thrived under high-nitrogen conditions. Other studies have documented cases in which plant communities that have grown on low-nitrogen soils for millennia are now experiencing changes in their species composition. An influx of nitrogen due to human activities has favored colonization by new species that are better adapted to soils with higher fertility. The observation that nutrients can have unintended effects on ecosystems highlights an important principle of environmental science: in ecosystems containing species that have adapted to their environments over thousands of years (or longer), changes in conditions are likely to cause changes in biodiversity as well as in the movement of energy through, and the cycling of matter within, those ecosystems.

### 3.3.4 The Phosphorus Cycle

Organisms need phosphorus for many biological processes. Phosphorus is a major component of DNA and RNA as well as ATP, the molecule used by cells for energy transfer. Required by both plants and animals, phosphorus is a limiting nutrient second only to nitrogen in its importance for successful agricultural yields. Thus phosphorus, like nitrogen, is commonly added to soils in the form of fertilizer. **FIGURE 3.13** shows the processes of the phosphorus cycle. Because this cycle has no gaseous component, atmospheric inputs of phosphorus—which occur when phosphorus is dissolved in rainwater or sea spray—are very small. Phosphorus is not very soluble in water, so much of it precipitates out of solution, forming phosphate (PO$_4^{3-}$)-laden sediments on the ocean floor. Humans mine some of these ancient phosphate sediments for fertilizer. The small amount of phosphorus dissolved in water also means that phosphorus is the primary limiting nutrient in many freshwater and marine food webs.
The phosphorus cycle begins with the weathering or mining of phosphate rocks and use of phosphate fertilizer, which releases phosphorus into the soil and water. This phosphorus can be used by producers and subsequently moves through the food web. Phosphorus can precipitate out of solution and form sediments, which over time are transformed into new phosphate rocks.

On land, the major natural source of phosphorus is the weathering of rocks. Negatively charged phosphate ions bind readily to several positively charged minerals found in soil, so phosphorus is not easily leached out of the soil by
water. Producers, however, can extract it from the soil, at which point it can move through the food web in a manner similar to other elements.

**Figure 3.14 Algal bloom.** When excess phosphorus enters waterways, it can stimulate a sudden and rapid growth of algae that turns the water bright green. The algae eventually die, and the resulting increase in decomposition can reduce dissolved oxygen to levels that are lethal to fish and shellfish.

**EXCESS PHOSPHORUS** Because phosphorus is so tightly held by soils on land, and because much of what enters water precipitates out of solution, very little dissolved phosphorus is naturally available in rivers and streams. As a result, phosphorus is a limiting nutrient in many aquatic systems. Even small inputs of leached phosphorus into these systems can greatly increase the growth of producers. Phosphorus inputs into phosphorus-limited aquatic systems can cause rapid growth of algae, known as an *algal bloom*. Algal blooms quickly increase the amount of biomass in the ecosystem (FIGURE 3.14). The algae eventually die, initiating a massive amount of decomposition, which consumes large amounts of oxygen. Thus algal blooms result in *hypoxic* (low-oxygen) conditions that kill fish and other aquatic animals. Hypoxic
dead zones occur around the world, including where the Mississippi River empties into
the Gulf of Mexico.

Two major sources of phosphorus in waterways are fertilizer-containing runoff from
agricultural or residential areas and household detergents. From the 1940s through the
1990s, laundry detergents contained phosphates to make clothes cleaner. The water
discharged from washing machines inadvertently fertilized streams, rivers, and
lakes. Because ecological dead zones caused by excess phosphorus represent
substantial environmental and economic damage, manufacturers stopped adding
phosphates to laundry detergents in 1994 and to dishwashing detergents in 2010.

In addition to causing algal blooms, increases in phosphorus concentrations can alter
plant communities. We have already seen one example in Chapter 2, in which the
“Working Toward Sustainability” feature discussed the deterioration of the environment
in the Florida Everglades. Because of agricultural expansion in southern Florida, the
water that flows through the Florida Everglades has experienced elevated phosphorus
concentrations. This change in nutrient cycling has changed the ecosystem of the
Everglades. Over time, cattails have become more common and sawgrass has
declined. Animals that depended on sawgrass for food or habitat are no longer favored.

### 3.3.5 Calcium, Magnesium, Potassium, and Sulfur

Calcium, magnesium, and potassium play important roles in regulating cellular
processes and in transmitting signals between cells. Like phosphorus, these macro-
nutrients are derived primarily from rocks and decomposed vegetation. All three can be
dissolved in water as positively charged ions: Ca$^{2+}$, Mg$^{2+}$, and K$^+$. None is present in a
gaseous phase, but all can be deposited from the air in small amounts as dust.

Because of their positive charges, calcium, magnesium, and potassium ions are
attracted to the negative charges present on the surfaces of most soil particles. Calcium
and magnesium occur in high concentrations in limestone and marble. Because
Ca$^{2+}$ and Mg$^{2+}$ are strongly attracted to soil particles, they are abundant in many soils
overlying these rock types. In contrast, K$^+$ is only weakly attracted to soil particles and
is therefore more susceptible to being leached away by water moving through the
soil. Leaching of potassium can lead to potassium-deficient soils that constrain the
growth of plants and animals.

The final macronutrient, sulfur, is a component of proteins and also plays an important
role in allowing organisms to use oxygen. Most sulfur exists in rocks and is released
into soils and water as these rocks weather over time. Plants absorb sulfur through their
roots in the form of sulfate ions (SO$_4^{2-}$), and the sulfur then cycles through the food
web. The sulfur cycle also has a gaseous component. Volcanic eruptions are a natural source of atmospheric sulfur in the form of sulfur dioxide (SO₂). Human activities also add sulfur dioxide to the atmosphere, especially the burning of fossil fuels and the mining of metals such as copper. In the atmosphere, SO₂ is converted into sulfuric acid (H₂SO₄) when it mixes with water. The sulfuric acid can then be carried back to the ground when it rains or snows. As humans add more sulfur dioxide to the atmosphere, we cause more acid precipitation, which can negatively affect terrestrial and aquatic ecosystems. Although anthropogenic deposition of sulfur remains an environmental concern, clean air regulations in the United States have significantly lowered these deposits since 1995.

**CHECKPOINT**

- What are the dominant elements that make up living organisms?
- What role does water play in nutrient cycling?
- What are the main similarities and differences among the carbon, nitrogen, and phosphorus cycles?

3.4 Ecosystems respond to disturbance

An event caused by physical, chemical, or biological agents that results in changes in population size or community composition is called **disturbance**. Natural ecosystem disturbances include hurricanes, ice storms, tsunamis, tornadoes, volcanic eruptions, and forest fires (**FIGURE 3.15**). Anthropogenic ecosystem disturbances include human settlements, agriculture, air pollution, clear-cutting of forests, and the removal of entire mountaintops for coal mining. Disturbances can occur over both short and long time scales. Ecosystem ecologists are often interested in how such disturbances affect the flow of energy and matter through an ecosystem. More specifically, they are interested in whether an ecosystem can resist the impact of a disturbance and whether a disturbed ecosystem can recover its original condition.
In this section we will look at how scientists study disturbance. We will then go on to consider resistance and resilience. Finally, we will apply our knowledge to an important theory about how systems respond to disturbances.

### 3.4.1 Watershed Studies

Understanding the natural rates and patterns of biogeochemical cycling in an ecosystem provides a basis for determining how a disturbance has changed the system. Because it is difficult to study biogeochemical cycles on a global scale, most such research takes place on a smaller scale, at which scientists can measure all of the ecosystem processes. A *watershed* is a common place for scientists to conduct such studies. As shown in **FIGURE 3.16**, a *watershed* is all of the land in a given landscape that drains into a particular stream, river, lake, or wetland.
A watershed is the area of land that drains into a particular body of water.

One of the most thorough studies of disturbance at the watershed scale has been ongoing in the Hubbard Brook ecosystem of New Hampshire since 1962. For almost 50 years, investigators have monitored the hydrological and biogeochemical cycles of six watersheds at Hubbard Brook, ranging in area from 12 to 43 ha (30 to 106 acres). The soil in each watershed is underlain by impenetrable bedrock, so there is no deep percolation of water; all precipitation that falls on the watershed leaves it either by evapotranspiration or by runoff. Scientists measure precipitation throughout each watershed, and a stream gauge at the bottom of the main stream draining each watershed allows them to measure the amounts of water and nutrients leaving the system.
At Hubbard Brook, researchers investigated the effects of clear-cutting and subsequent suppression of plant regrowth. The researchers cut down the forest in one watershed and used herbicides to suppress the regrowth of vegetation for several years. An adjacent watershed that was not clear-cut served as a control (FIGURE 3.17). The concentrations of nitrate in stream water were similar in the two watersheds before the clear-cutting. Within 6 months after the cutting, the clear-cut watershed showed significant increases in stream nitrate concentrations. With this information, the researchers were able to determine that when trees are no longer present to take up nitrate from the soil, nitrate leaches out of the soil and ends up in the stream that drains the watershed. This study and subsequent research have demonstrated the importance of plants in regulating the cycling of nutrients, as well as the consequences of not allowing new vegetation to grow when a forest is cut.

Studies such as the one done at Hubbard Brook allow investigators to learn a great deal about biogeochemical cycles. We now understand that as forests and grasslands grow, large amounts of nutrients accumulate in the vegetation and in the soil. The growth of forests allows the terrestrial landscape to accumulate nutrients that would otherwise cycle through the system and end up in the ocean. Forests, grasslands, and other terrestrial ecosystems increase the retention of nutrients on land. This is an important way in which ecosystems directly influence their own growing conditions.
Not every ecosystem disturbance is a disaster. For example, a low-intensity fire might kill some plant species, but at the same time it might benefit fire-adapted species that can use the additional nutrients released from the dead plants. So, although the population of a particular producer species might be diminished or even eliminated, the net primary productivity of all the producers in the ecosystem might remain the same. When this is the case, we say that the productivity of the system is resistant. The resistance of an ecosystem is a measure of how much a disturbance can affect the flows of energy and matter. When a disturbance influences populations and communities, but has no effect on the overall flows of energy and matter, we say that the ecosystem has high resistance.

When an ecosystem’s flows of energy and matter are affected by a disturbance, environmental scientists often ask how quickly and how completely the ecosystem can recover its original condition. The rate at which an ecosystem returns to its original state after a disturbance is termed resilience. A highly resilient ecosystem returns to its original state relatively rapidly; a less resilient ecosystem does so more slowly. For example, imagine that a severe drought has eliminated half the species in an area. In a highly resilient ecosystem, the flows of energy and matter might return to normal in the following year. In a less resilient ecosystem, the flows of energy and matter might not return to their pre-drought conditions for many years.

An ecosystem’s resilience often depends on specific interactions of the biogeochemical and hydrologic cycles. For example, in response to anthropogenic increases in global atmospheric CO$_2$ concentrations, there has been an increase in carbon uptake in terrestrial and aquatic ecosystems. The carbon cycle as a whole can thus mitigate some of the changes that we might expect from increases in atmospheric CO$_2$ concentrations, including global climate change. Conversely, when a drought occurs, the soil may dry out and harden so much that when it eventually does rain, the soil cannot absorb as much water as it did before the drought. This change in the soil leads to further drying and an intensification of the drought damage. In this case, the hydrologic cycle does not relieve the effects of the drought; instead, a positive feedback in the system makes the situation worse.

Many anthropogenic disturbances—for example, housing developments, clear-cutting, or draining of wetlands—are so large that they eliminate an entire ecosystem. In some cases, however, scientists can work to reverse these effects and restore much of the original function of the ecosystem (FIGURE 3.18). Growing interest in restoring damaged ecosystems has led to the creation of a new scientific discipline called restoration ecology. Restoration ecologists are currently working on two high-profile ecosystem restoration projects, in the Florida Everglades and in the Chesapeake
Bay, to restore water flows and nutrient inputs that are closer to historic levels so that the functions of these ecosystems can be restored.

Figure 3.18  **Wetland restoration.** The draining of wetlands can destroy a wetland ecosystem. The damage can be mitigated by using heavy machinery to build new wetlands (inset) that serve the same function.

### 3.4.3 The Intermediate Disturbance Hypothesis
We have seen that not all disturbance is bad. In fact, some level of ecosystem disturbance is natural, and may even be necessary for the maintenance of species diversity. The intermediate disturbance hypothesis states that ecosystems experiencing intermediate levels of disturbance are more diverse than those with high or low disturbance levels. The graph in Figure 3.19 illustrates this relationship between ecosystem disturbance and species diversity. Ecosystems in which disturbances are rare experience intense competition among species. Because of this, populations of only a few highly competitive species eventually dominate the ecosystem. In places where disturbances are frequent, population growth rates must be high enough to counter the effects of frequent disturbance and prevent species extinction. Research shows that when disturbances occur at some intermediate frequency, the populations of major competitors never reach a size at which they can dominate an ecosystem, and populations of other species are never driven too close to zero. As a result, we expect to see the highest diversity of species in ecosystems that experience an intermediate frequency of disturbance.

**CHECKPOINT**

- Why is Hubbard Brook valuable as a study area? What does it teach us?
- What is the difference between resistance and resilience in an ecosystem?
- What is the intermediate disturbance hypothesis?
3.5 Ecosystems provide valuable services

Humans rely on only a small number of the millions of species on Earth for our essential needs. Why should we care about the millions of other species in the world? What is the value in protecting biodiversity?

The answer may lie in the type of value a species has for humans. A species may have **instrumental value**, meaning that it has worth as an *instrument* or *tool* that can be used to accomplish a goal. Instrumental values, which include the value of items such as lumber and pharmaceutical drugs, can be thought of in terms of how much economic benefit a species bestows. Alternatively, a species may have **intrinsic value**, meaning that it has worth independent of any benefit it may provide to humans. Intrinsic values include the moral value of an animal’s life; they cannot be quantified.
Ecosystems, as collections of species and as locations for biogeochemical cycling, can have instrumental value, intrinsic value, or both. The instrumental value of ecosystems lies in what economists call *ecosystem services*: the benefits that humans obtain from natural ecosystems. For example, the ability of an agricultural ecosystem to produce food is an important ecosystem service, as is the ability of a wetland ecosystem to filter and clean the water that flows through it. Most economists believe that the instrumental uses of an ecosystem can be assigned monetary values, and they are beginning to incorporate these values into their calculations of the economic costs and benefits of various human activities. However, assigning a dollar value is easier for some categories of ecosystem services than for others.

In 1997, a team of environmental scientists and ecological economists attempted to estimate the total value of ecosystem services to the human economy. They considered
replacement value—the cost to replace the services provided by natural ecosystems. They also looked at other factors, such as how property values were affected by location relative to these services—for example, oceanfront housing—and how much time or money people were willing to spend to use these services—for example, whether they were willing to pay a fee to visit a national park. Using this method, researchers estimated that ecosystem services were worth over $30 trillion per year, or more than the entire global monetary economy at that time. When calculating the instrumental value of ecosystem services, it is helpful to group those services into five categories: provisions, regulating services, support systems, resilience, and cultural services.

**PROVISIONS** Goods that humans can use directly are called provisions. Examples include lumber, food crops, medicinal plants, natural rubber, and furs. Of the top 150 prescription drugs sold in the United States, about 70 percent come from natural sources. For example, Taxol, a potent anticancer drug, was originally discovered in the bark of the Pacific yew (*Taxus brevifolia*), a rare tree that grows in forests of the Pacific Northwest ([FIGURE 3.20](#)). Within a decade of its approval by the FDA, this single drug accounted for over $1 billion in annual sales. However, there is no way to estimate the potential value of natural pharmaceuticals that have yet to be discovered. Our best strategy may be to preserve as much biodiversity as we can to improve our chances of finding the next critical drug.

**DO THE MATH**

**Raising Mangoes**

As we saw in this chapter’s opening story, farmers in Haiti are being encouraged to plant mango trees because the provisions in the form of fruit are more valuable than the provisions in the form of firewood. A group of Haitian farmers decides to plant mango trees. Mango saplings cost $10 each. Once the trees become mature, each tree will produce $75 worth of fruit per year. A village of 225 people decides to pool its resources and set up a community mango plantation. Their goal is to generate a per capita income of $300 per year for the entire village.

1. How many mature trees will the village need to meet the goal?
   
   Total annual income desired: 
   
   $300/person × 225 persons = $67,500
   
   Number of trees needed to produce $67,500 in annual income: 
   
   $ \frac{67,500}{75/\text{tree}} = 900 \text{ trees}$

2. Each tree requires 25 m² of space. How many hectares must the village set aside for the plantation?
   
   $900 \text{ trees} × 25 \text{ m}² = 22,500 \text{ m}² = 2.25 \text{ ha}$
3. Each tree requires 20 L of water per day during the 6 hot months of the year (180 days). The water must be pumped to the plantation from a nearby stream. How many liters of water are needed each year to water the plantation of 900 trees?

Water needed for 1 tree:

\[
20 \text{ L/day} \times 180 \text{ days} = 3,600 \text{ L of water}
\]

Water needed for 900 trees:

\[
3,600 \text{ L/tree} \times 900 \text{ trees} = 3,240,000 \text{ L of water}
\]

Because provisions are usually sold in the marketplace, their monetary value is fairly easy to quantify. Do the Math “Raising Mangoes” provides an opportunity to use provision values to calculate the costs and benefits of human activities.

REGULATING SERVICES Natural ecosystems help to regulate environmental conditions. For example, humans currently add about 8 gigatons of carbon to the atmosphere annually (1 gigaton = 1 trillion kilograms), but only about 4 gigatons of carbon remain there. The rest is removed by natural ecosystems such as tropical rainforests and oceans, providing us with more time to deal with climate change than we would otherwise have (FIGURE 3.21). As described earlier in this chapter, ecosystems play important roles in regulating nutrient and hydrologic cycles as well.

Figure 3.21 Regulating services. Tropical rainforests play a major role in regulating the amount of carbon in the atmosphere.
Support systems. Pollinators such as this honeybee play an essential role in ensuring the pollination of food crops such as cherries.

**SUPPORT SYSTEMS** Natural ecosystems provide numerous support services that would be extremely costly for humans to generate. One example is pollination of food crops (FIGURE 3.22). The American Institute of Biological Sciences estimates that crop pollination in the United States by native species of bees and other insects, hummingbirds, and bats is worth roughly $3.1 billion in added food production. In addition to providing habitat for animals that pollinate crops, ecosystems provide natural pest control services because they serve as habitat for predators that prey on agricultural pests. Although organic farmers, who rarely use synthetic pesticides, gain the most from these pest controls, conventional agriculture benefits as well.

Healthy ecosystems also filter harmful pathogens and chemicals from water, leaving humans with water that requires relatively little treatment prior to drinking. Without these water-filtering services, humans would have to build many new water treatment facilities using expensive filtration technologies. New York City, for example, draws its water from naturally clean reservoirs in the Catskill Mountains. But residential development and tourism in the area has threatened to increase contamination of the reservoirs with silt and chemicals. Building a filtration plant adequate to address these problems would cost $6 billion to $8 billion. For this reason, New York City and the U.S. Environmental Protection Agency have been working to protect sensitive regions of the Catskills.
RESILIENCE We have already seen that resilience ensures that an ecosystem will continue to exist in its current state, which means it can continue to provide benefits to humans. Resilience depends greatly on species diversity. For example, several different species may perform similar functions in an ecosystem, but differ in their susceptibility to disturbance. If a pollutant kills one plant species that contains nitrogen-fixing bacteria, but not several other plant species that contain nitrogen-fixing bacteria, the ecosystem can continue to fix nitrogen despite the disturbance (FIGURE 3.23). Genetic diversity also provides valuable insurance against the loss of ecosystem services.

CULTURAL SERVICES Ecosystems provide cultural or aesthetic benefits to many people. The awe-inspiring beauty of nature has instrumental value because it provides an aesthetic benefit for which people are willing to pay (FIGURE 3.24). Similarly, scientific funding agencies may award grants to scientists for research that explores biodiversity with no promise of any economic
gain. Nevertheless, the research itself has instrumental value because the scientists and others benefit from the experience by gaining knowledge. While intellectual gain and aesthetic satisfaction may be difficult to quantify, they can be considered cultural services that have instrumental value.

![Figure 3.24: Cultural services.](image)

### 3.5.2 Intrinsic Values of Ecosystems

Many people believe that ecosystems not only have instrumental value, but also have intrinsic value—that is, that they are valuable independent of any benefit to humans. These beliefs may grow out of religious or philosophical convictions. People who believe that ecosystems are inherently valuable may argue that we have a moral
obligation to preserve them. They may equate the obligation of protecting ecosystems with our responsibility toward people or animals who might need our help to survive. People who argue that ecosystems have intrinsic value do not necessarily deny that ecosystems also have instrumental value. Rather, they believe that environmental policy and the protection of ecosystems should be driven by this intrinsic value.

**CHECKPOINT**

- What factors go into calculating the instrumental value of an ecosystem?
- What are the five categories of ecosystem services?
- How do the instrumental and intrinsic values of ecosystems differ?

**WORKING TOWARD SUSTAINABILITY**

*Can We Make Golf Greens Greener?*

For a game that is played outdoors on open green courses designed around the contours of the natural landscape, golf has a surprisingly bleak environmental reputation. Golf courses are highly managed ecosystems that cover over 3 million hectares (7.5 million acres) worldwide—an area about the size of Belgium. About two-thirds of this area consists of closely mowed turfgrass. Closely mowed grass has short leaves that cannot gain enough energy from photosynthesis to grow deep roots. This causes a host of problems: The grass dries out easily and has difficulty obtaining soil nutrients. As a result, the grass is susceptible to challenges from weeds, grubs that feed on grass roots, and fungal diseases that can weaken or kill the grass. Collectively, these are rather formidable challenges that are faced by golf course managers worldwide.

To combat these challenges, golf courses use a disproportionate amount of water, fertilizer, and pesticides. Because humans expect to see green, well-manicured golf courses no matter where in the world they are located, golf courses collectively use 9.5 billion liters (2.5 billion gallons) of water annually to keep their grasses green. Much of this water is used in regions where water is already scarce. In addition, providing the grass with sufficient nutrients requires a large amount of fertilizer. Putting greens require as much nitrogen per hectare as corn, the heaviest nitrogen user of all major food crops. If the course requires irrigation soon after the application of fertilizer, or if it rains, up to 60 percent of the fertilizer can be leached into nearby waterways. To maintain a uniform texture on the greens, golf courses use about six times the amount of agricultural pesticides per hectare as do conventional farms. These chemicals include...
herbicides to remove weeds, insecticides to kill soil-dwelling grubs, and fungicides to control disease.

Since 1991, the Audubon Cooperative Sanctuary Program (ACSP), a partnership between Audubon International and the U.S. Golf Association, has been working to improve the environmental management of golf courses. The ACSP encourages golf course managers to develop courses that perform more like natural ecosystems, with nutrient and water recycling to reduce waste and biodiversity to increase ecosystem resilience. It also educates golf course managers about low-impact pest management, water conservation, and water quality management.

The golf course of the Palisades Country Club in North Carolina was constructed with natural ecosystem services in mind (FIGURE 3.25). To prevent the runoff of nutrients and lawn-care chemicals into nearby waters, the course directs all runoff water through a treatment system. The course was designed to reduce the amount of closely mowed turfgrass. Deep-rooted native grasses surrounding the greens and fairways soak up nutrients and help to direct water underground. As a result, maintenance costs, chemical applications, and time spent using machinery have all declined. Smaller areas of turfgrass also leave space for more native vegetation of various heights, providing better habitats for birds and predatory insects. These consumers keep pest populations low, reducing the need for pesticides. When pesticides are used, they are chosen to protect nontarget wildlife and applied on wind-free days to keep them from spreading beyond where they are needed.

Figure 3.25  Making golf more sustainable. The Palisades Country Club in North Carolina is making its golf course more environmentally friendly by considering the important roles of natural ecosystem processes.
By 2008, more than 2,100 golf courses worldwide had participated in the ACSP. Audubon International found that over 80 percent of the courses in the program reduced the amounts and toxicity of pesticides applied, improved nutrient retention within the course, and used less water for irrigation. The average course in the program saved about 7 million liters (1.9 million gallons) of water per year, and the amount of land area devoted to providing wildlife habitat increased by about 50 percent, from 18 to 27 ha (45 to 67 acres) per 60 ha (150-acre) golf course. Moreover, 99 percent of managers reported that playing quality and golfer satisfaction were maintained or improved.

Even with these changes, golf courses still require large amounts of water, nutrients, fossil fuel energy, and upkeep. Highly managed ecosystems cannot be made input free. However, within these limits, a growing number of courses are attempting to reduce their ecological footprint and make their greens greener.

References

Key Ideas Revisited

- **List the basic components of an ecosystem.**
  An ecosystem has both biotic and abiotic components, all of which interact with one another. An ecosystem has characteristic species as well as specific abiotic characteristics such as amount of sunlight, temperature, and salinity. Every ecosystem has boundaries, although they are often subjective.

- **Describe how energy flows through ecosystems.**
  The energy that flows through most ecosystems originates from the Sun. Ecosystems have multiple trophic levels through which energy flows. Producers use solar energy to generate biomass via photosynthesis. That stored energy can be passed on to consumers and decomposers and is ultimately lost as heat. The low efficiency of energy transfer between trophic levels means that only a small fraction of the energy at any trophic level—aabout 10 percent—is available to be used at the next higher trophic level. Low ecological efficiency results in a large biomass of producers, but a much lower biomass of primary consumers, and an even lower biomass of secondary consumers.

- **Describe how carbon, nitrogen, and phosphorus cycle within ecosystems.**
  In the carbon cycle, producers take up CO₂ for photosynthesis and transfer the carbon to consumers and decomposers. Some of this carbon is converted back into CO₂ by respiration, while the rest is lost to sedimentation and burial. The extraction and
combustion of fossil fuels, as well as the destruction of forests, returns CO$_2$ to the atmosphere. The nitrogen cycle has many steps. Nitrogen is fixed by organisms, lightning, or human activities, then assimilated by organisms. Ammonium is released during decomposition of dead organisms and wastes. Finally, denitrification returns nitrogen to the atmosphere. The phosphorus cycle involves a large pool of phosphorus in rock that can be made available to organisms either by leaching or by mining. Organisms then assimilate it and ultimately transfer it back to the soil via excretion and decomposition.

- **Explain how ecosystems respond to natural and anthropogenic disturbances.**
  Different ecosystems respond to disturbances (both natural and anthropogenic) in different ways. A resistant ecosystem is one that experiences little change in flows of energy and matter after a disturbance. A resilient ecosystem is one that returns rapidly to its original state after a disturbance. Species diversity tends to be highest at intermediate levels of disturbance.

- **Discuss the values of ecosystems and how humans depend on them.**
  Ecosystems have a variety of instrumental values that can directly benefit humans. Ecosystem services include provisions that humans can use directly, such as food and medicine; regulation services that prevent drastic changes in environmental conditions; support systems that provide important services such as pollination and water filtration; resilience that allows ecosystems to continue functioning despite disturbances; and cultural services, including aesthetic value. The intrinsic value of ecosystems derives from the philosophical or religious idea that ecosystems are inherently valuable and that we have a moral obligation to preserve them.

**PREPARING FOR THE AP EXAM**

**MULTIPLE-CHOICE QUESTIONS**

[Notes/Highlighting]

1. Which of the following is *not* an example of an abiotic component of an ecosystem?
   - (a) Water
   - (b) Minerals
   - (c) Sunlight
   - (d) Fungi
   - (e) Air

[Answer Field]
2. Which of the following is not characteristic of ecosystems?
   • (a) Biotic components
   • (b) Abiotic components
   • (c) Recycling of matter
   • (d) Distinct boundaries
   • (e) A wide range of sizes
   [Answer Field]

3. Which biogeochemical cycle(s) does not have a gaseous component?
   • I Potassium
   • II Sulfur
   • III Phosphorus
   • (a) II only
   • (b) I and II only
   • (c) III only
   • (d) II and III only
   • (e) I and III only
   [Answer Field]

For questions 4, 5, and 6, select from the following choices:
   • (a) Producers
   • (b) Decomposers
   • (c) Primary consumers
   • (d) Secondary consumers
   • (e) Tertiary consumers

4. At which trophic level are eagles that consume fish that eat algae?
   [Answer Field]

5. At which trophic level do organisms use a process that produces oxygen as a waste product?
   [Answer Field]

6. At which trophic level are dragonflies that consume mosquitoes that feed on herbivorous mammals?
   [Answer Field]

7. Beginning at the lowest trophic level, arrange the following food chain found on the Serengeti Plain of Africa in the correct sequence.
   • (a) Shrubs–gazelles–cheetahs–decomposers
   • (b) Shrubs–decomposers–gazelles–cheetahs
   • (c) Shrubs–decomposers–cheetahs–gazelles
   • (d) Gazelles–decomposers–cheetahs–shrubs
   • (e) Decomposers–cheetahs–shrubs–gazelles
   [Answer Field]

8. Which macronutrient is required by humans in the largest amounts?
9. Roughly what percentage of incoming solar energy is converted into chemical energy by producers?
   - (a) 99
   - (b) 80
   - (c) 50
   - (d) Between 5 and 20
   - (e) 1

10. The net primary productivity of an ecosystem is 1 kg C/m²/year, and the energy needed by the producers for their own respiration is 1.5 kg C/m²/year. The gross primary productivity of such an ecosystem would be
   - (a) 0.5 kg C/m²/year.
   - (b) 1.0 kg C/m²/year.
   - (c) 1.5 kg C/m²/year.
   - (d) 2.0 kg C/m²/year.
   - (e) 2.5 kg C/m²/year.

11. An ecosystem has an ecological efficiency of 10 percent. If the producer level contains 10,000 kilocalories of energy, how much energy does the tertiary consumer level contain?
   - (a) 1 kcal
   - (b) 10 kcal
   - (c) 100 kcal
   - (d) 1000 kcal
   - (e) 10,000 kcal

12. Research at Hubbard Brook showed that stream nitrate concentrations in two watersheds were ________ before clear-cutting, and that after one watershed was clear-cut, its stream nitrate concentration was ________.
   - (a) similar/decreased
   - (b) similar/increased
   - (c) similar/the same
   - (d) different/increased
13. Small inputs of this substance, commonly a limiting factor in aquatic ecosystems, can result in algal blooms and dead zones.
   - (a) Dissolved carbon dioxide
   - (b) Sulfur
   - (c) Dissolved oxygen
   - (d) Potassium
   - (e) Phosphorus

14. The anticancer drug Taxol was originally extracted from the bark of the Pacific yew tree. This drug is an example of a type of ecosystem service known as
   - (a) cultural services.
   - (b) support systems.
   - (c) provisions.
   - (d) resilience.
   - (e) regulating services.

15. After a severe drought, the productivity in an ecosystem took many years to return to pre-drought conditions. This observation indicates that the ecosystem has
   - (a) high resilience.
   - (b) low resilience.
   - (c) high resistance.
   - (d) low resistance.
   - (e) equal resilience and resistance.

**FREE-RESPONSE QUESTIONS**

1. Nitrogen is crucial for sustaining life in both terrestrial and aquatic ecosystems.
   - (a) Draw a fully labeled diagram of the nitrogen cycle. (4 points)
   - (b) Describe the following steps in the nitrogen cycle:
     - (i) Nitrogen fixation (1 point)
     - (ii) Ammonification (1 point)
     - (iii) Nitrification (1 point)
     - (iv) Denitrification (1 point)
   - (c) Describe one reason why nitrogen is crucial for sustaining life on Earth. (1 point)
(d) Describe one way that the nitrogen cycle can be disrupted by human activities. (1 point)

Neighbors Voice Opposition to Proposed Clear-Cut

A heated discussion took place last night at the monthly meeting of the Fremont Zoning Board. Local landowner Julia Taylor has filed a request that her 150-acre woodland area be rezoned from residential to multi-use in order to allow her to remove all of the timber from the site.

“This is my land, and I should be able to use it as I see fit,” explained Ms. Taylor. “In due course, all of the trees will return and everything will go back to the same as it is now. The birds and the squirrels will still be there in the future. I have to sell the timber because I need the extra revenue to supplement my retirement as I am on a fixed income. I don’t see what all the fuss is about,” she commented.

A group of owners of adjacent properties see things very differently. Their spokesperson, Ethan Jared, argued against granting a change in the current zoning. “Ms. Taylor has allowed the community to use these woods for many years, and we thank her for that. But I hope that the local children will be able to hike and explore the woods with their children as I have done with mine. Removing the trees in a clear-cut will damage our community in many ways, and it could lead to contamination of the groundwater and streams and affect many animal and plant species. Like the rest of us property owners, Ms. Taylor gets her drinking water from a well, and I do not think she has really looked at all the ramifications should her plan go through. We strongly oppose the rezoning of this land—it has a right to be left untouched.”

After more than two hours of debate between Ms. Taylor and many of the local residents, the chair of the Zoning Board decided to research the points raised by the neighbors and report on his findings at next month’s meeting.

(a) Name and describe the ecosystem value(s) that are being expressed by Ms. Taylor in her proposal to clear-cut the wooded area. (2 points)
(b) Name and describe the ecosystem value(s) that Mr. Jared is placing on the wooded area. (2 points)
(c) Provide three realistic suggestions for Ms. Taylor that could provide her with revenue from the property but leave the woods intact. (3 points)
(d) Identify and then discuss the validity of the environmental concerns that were raised by Mr. Jared. (3 points)
MEASURING YOUR IMPACT

1. Atmospheric Carbon Dioxide
   - (a) Describe two anthropogenic influences on the carbon cycle that have resulted in the elevation of atmospheric CO₂ concentrations.
   - (b) Use one of the following carbon calculator Web sites to determine your household carbon emissions. (You may wish to investigate additional Web sites for comparison purposes.)
     www.safeclimate.net/calculator/
     www.myfootprint.org
   - (c) Comment on your calculated carbon footprint estimate. How does your carbon footprint compare with the United States average?