





SECTION 7

ECOLOGY

by Peter H. Raven and Paul H. Zedler

◀ A chickadee feasts on the achenes of a dried sunflower head in winter. Each of the many flowers of the sunflower head produces a single fruit, an achene, which contains a single seed. Energy from the sun was captured by the sunflower's green leaves and converted into chemical energy stored in sugar and other organic molecules. Much of the sugar, transported to the developing sunflower heads, was then converted into energy-rich storage molecules by the developing seeds. Birds and other animals eat the seeds, leaves, and other plant parts to obtain the fuel necessary for their life processes.



CHAPTER 31

The Dynamics of Communities and Ecosystems

◀ **Ecosystems vary in size** The leaf of this pitcher plant supports a complex community—a small ecosystem—of coevolved organisms, among them bacteria, protists, and invertebrates, all nourished by the decaying insects that have fallen into the liquid within the leaf and drowned. The plant grows in a bog—a larger ecosystem—consisting of animals and other plants, such as the grasses and Venus flytraps seen here.

CHAPTER OUTLINE

Ecosystem Energetics—Trophic Structure

Nutrient and Material Cycling

Interactions between Organisms—Beyond Simple

Trophic Relationships

Development and Change of Communities and Ecosystems

Ecology is traditionally defined as the study of organisms in relation to their living and nonliving environments, but it is best defined as the study of **ecosystems**. Adding the word “system” underscores that our goal is to understand an entity consisting of interacting parts. An ecosystem includes all of the organisms that occur together within the defined boundaries and all of the nonliving environment—the water, chemicals, rocks, minerals, and air.

When we wish to be clear that we are referring to the entirety of the Earth, we speak of the **biosphere**—that is, the global ecosystem. We can, however, narrow our focus and direct our attention to particular parts of the biosphere. Say, for example, that we wish to study the riparian ecosystem of the Lower Colorado River, meaning that we are considering only the ecosystem that occurs along the river. Focusing more closely, we might study the microbial ecosystem in 1 square meter of soil, or the ecosystem in the water-holding leaves of the pitcher plant.

The great challenge in studying ecosystems is their complexity. Everything discussed in previous chapters of the text-

book—cell physiology, energetics, genetics, the taxonomic diversity of plants, anatomy, and physiology—is relevant to the functioning of ecosystems. Although it is true, of course, that the whole ecosystem is the sum of its parts, it is not true that we can understand an ecosystem if we confine ourselves to the study of the individual components in isolation. In other words, ecosystems have emergent properties, that is, qualities and processes that we discover as we study increasingly higher levels of organization.

Ecologists are expected to be able to answer questions such as: Why are grasslands common in some places, and forests in others? Why are there so many more species of plants and animals in the wet tropics than in the Arctic regions? Which ecosystems capture solar energy at the greatest rates, and which have the highest total annual carbon fixation? For complete answers to

CHECKPOINTS

After reading this chapter, you should be able to answer the following:

1. What does the science of ecology encompass, and what is the difference between a population, a community, and an ecosystem?
2. What is a food chain, what types of organisms are found in each link of the chain, and how does energy flow through it?
3. What do ecologists mean by the term “competition,” and how do plants compete with one another?
4. What is mutualism?

these questions, we may need to know about enzyme chemistry and the genetic code, but we will also have to think about such matters as climate, soils, geologic history, animal predators and pollinators, interactions with microbial species, and the evolutionary history of the various species.

It is the goal of ecology to provide an explanation of how ecosystems got to the state they are in and to predict how they will change in the future. Ecologists spend much time studying “natural,” that is, minimally disturbed systems, but they believe that the insights gained have important practical applications for humans. Most believe that we also need to study systems affected by humans and their many activities. This leads to fields such as agroecology, the study of farms and farm landscapes as ecosystems.

Despite the proper emphasis on the entire system, ecologists recognize that to understand the complexity of ecosystems, we need to break them down into parts for analysis. There is no one correct way to do this, but there are approaches that have been proven to be generally useful. One such analytical view is based on the biological hierarchy. The living portion of an ecosystem consists of a set of individual organisms. Individuals are aggregated into populations, where a **population** consists of all individuals belonging to the same taxonomic unit, usually a species, at a particular place within the ecosystem. The set of all populations makes a **community**. Community can also be qualified to indicate subsets of the whole, so that some studies may focus on the bird community, others on the plant community or the microbial community. The aggregate community of all populations, joined with subsystems of the physical environment, form the ecosystem.

As with any attempt to categorize, groupings that may seem clear in theory can be unclear in practice. For example, many herbaceous plants spread by vegetative growth. For some of these, the new sprouts quickly assume an independent existence, but for others they do not. In the latter case, what qualifies as an individual—each separate stem or the local aggregation of stems? A desert bunch grass would seem to be an individual consisting of a collection of stems, yet detailed study of its morphology and physiology reveals that the connections between the individual stems disappear shortly after a new stem is produced. So, what is the individual? For some purposes, the well-defined bunch is the individual, but for other purposes we may want to study the individual stems that make up this collective individual.

So far, we have viewed the ecosystem as a thing that exists in the present. But ecologists not only want to project forward from the present; they also want to know how particular combinations of organisms that exist now have come to be. If we are to fully understand interactions among species, we must know something about their evolutionary history—ecologists must join forces with evolutionists. As we have emphasized throughout the book, evolutionary processes shape organisms and thus also help to determine how they interact. Evolution is therefore inextricably intertwined with ecology in what the famous ecologist G. E. Hutchinson of Yale University aptly called “the ecological theater and the evolutionary play.” In previous chapters, we have considered the fundamental points of evolutionary theory and the major categories of evidence, as well as the mechanisms by which the plot of the evolutionary play moves forward. Here and in the

online Chapter 32, we place ourselves in the ecological theater to observe the actors—that is, all living things—in their interactions with each other and with the physical environment that together constitute the play.

Ecosystem Energetics—Trophic Structure

We have said that an ecosystem consists of a collection of interacting organisms. But what do we mean by “interact”? Of the many varieties of interaction those involving energy provide a useful way to view ecosystem function. As we have seen, living organisms require a constant supply of usable energy, and so we may consider the ecosystem as an energy-capturing and energy-processing system. It can exist only if energy continuously flows through it. We choose the word “flow” intentionally, because ultimately, all of the energy that is captured by living organisms in the ecosystem will be dissipated in the form of unusable heat, as dictated by the second law of thermodynamics (pages 96 to 97 of the textbook). Although energy can be stored in various forms (for example, as the starch in a potato tuber), sooner or later it must leave the system, never to return.

The process that is the engine of the ecosystem—the starting place for the energy flow—is the capture of usable energy from the nonliving environment. Only certain organisms are capable of doing this, the **autotrophs**, or “self-feeders,” of which there are two types: *chemosynthesizers* and *photosynthesizers*. Chemosynthesizers, all of which are microbial, are a fascinating group, both in the contemporary biosphere and as players in the evolution of life on Earth. Today, they are most important in extreme habitats, dramatic examples of which are the hydrothermal vent communities in the deep ocean. There, the complete darkness makes photosynthesis impossible, but the abundance of reduced inorganic molecules offers the opportunity to extract energy through oxidation. Overall, however, chemosynthesizers make only a small contribution to the total energy extracted from nonliving sources.

The predominant autotrophs of the biosphere are the photosynthesizers, a group that includes the familiar green plants of terrestrial ecosystems. These autotrophs use the captured solar energy to synthesize organic materials that serve as a source of energy for the other major group—the **heterotrophs**, organisms that feed on others by consuming parts or all of living or dead organisms. Like autotrophs, heterotrophs are found in all sizes and in an astonishing array of functional types, from heterotrophic bacteria to mushrooms, spiders, whales, and human beings. Even this fundamental division of organisms is not absolute, though, because some organisms can function as either heterotrophs or autotrophs, or both at the same time. The colorful Indian paintbrush, for example, is one of many plants that parasitize other plants, extracting energy and nutrients from them but retaining the capacity to photosynthesize (Figure 31–1).

The concept of **trophic levels** is basic to ecosystem energetics. The first trophic level consists of the autotrophs, also called **primary producers**. In a forest ecosystem, for example, the primary-producer trophic level includes not only trees but also cyanobacteria, algae, lichens, mosses, ferns, grasses, and shrubs. In the open water of oceans (pelagic ecosystems), the primary producers are phytoplankton, mostly single-celled



31-1 Autotrophic and heterotrophic The rosy Indian paintbrush (*Castilleja rhexifolia*) belongs to a widespread genus of 200 species of annual and perennial plants. It can photosynthesize, but it also forms associations with other plants through specialized fungal hyphae called haustoria (see Figure 14-6), which invade the root cells of other photosynthesizers, such as grasses and other herbaceous plants.

photosynthesizers of many types (cyanobacteria, diatoms, and dinoflagellates) that are suspended in the water column.

The next trophic level, the **primary consumers**, consists of heterotrophs that derive their energy by feeding directly on the primary producers. These primary consumers are also, by definition, **herbivores**, or eaters of plants. The next trophic level, **secondary consumers**, includes heterotrophs that feed on the primary consumers. Thus, in a forest, a caterpillar eating leaves is a primary consumer, and a warbler that eats the caterpillars is a secondary consumer. An animal—a kestrel (sparrow hawk), for example—that eats the warblers would be a tertiary consumer. The secondary consumers that eat but are not eaten are (with the exception of parasites, as described below) referred to as **top carnivores**. Studies have shown that ecosystems rarely have more than four to six trophic levels (Figure 31-2).

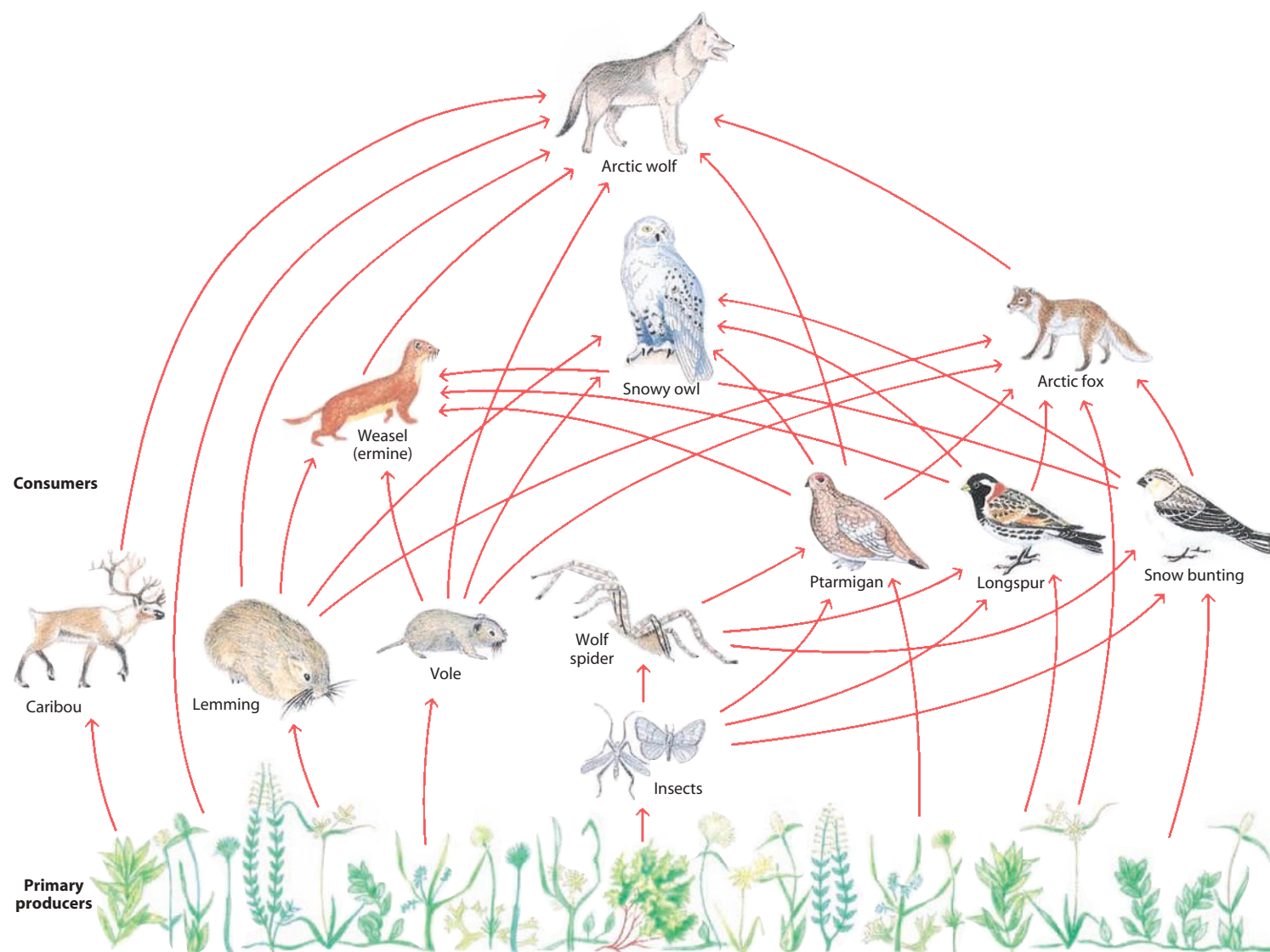
Thermodynamics explains why there are limits on the number of levels. First, all of the metabolically useful energy that flows through the system is captured by the primary producers. Second, at each transfer—from sunlight to plant, plant to herbivore, and so on, up the chain—the second law of thermodynamics tells us that some energy is inevitably lost. Less energy is available to each successive trophic level.

The loss at the primary production stage, from solar energy to measurable growth of plants, is substantial. Generally, less than one percent of the light that falls on vegetation is incorporated into plant **biomass** (total organic matter; see page 94). The highest-yielding systems, such as tropical sugarcane fields, convert as much as 1.6 percent of the incident solar energy to plant matter. Then, in general, only about one-tenth of the energy incorporated in one trophic level can be assimilated into the next. The annual growth of herbivore biomass, therefore, is roughly one-tenth of the annual productivity of the plants, and the carnivores feeding on herbivores—as carnivore biomass, not as individual animals—grow about one-tenth as much as the herbivores.

With such sharp declines in available energy at each step, it is clear that after only a few links in a food chain, little energy remains. So, for example, we could imagine a “super-raptor,” a top carnivore bird that fed only on eagles and hawks, but there is no such bird. Its prey would be so sparse and so dispersed that the super-raptor would require an immense range. It is not an energetically sustainable mode of life.

These energetic basics also help explain why the largest land animals that live now or have lived in the past are not carnivores. A giant herbivorous animal can be massive because its food is all around it. Large size favors the ability to roam over large distances to reach new food sources and to fend off carnivores and protect the vulnerable young. The largest land animal so far discovered is the sauropod dinosaur *Argentinosaurus*, which is estimated to have weighed 80 to 100 metric tons. The largest land mammal is thought to be the extinct *Paraceratherium*, which stood 5.5 meters tall at the shoulder. Both were herbivores.

So far, we have followed the food chain from the primary producers to higher levels of consumers—from plants to top carnivores. But not all the energy present in one trophic level along this sequence can be extracted by the next. In natural terrestrial grazing systems, for example, the vertebrate and invertebrate consumers usually eat only a portion of the plant material available to them. As a classic 1960 paper by Hairston, Smith, and Slobodkin stated, “the world is green.” Why is this so? The persistent greenness of terrestrial ecosystems, reflecting the amount of photosynthesizing tissue that is not consumed, may be due to two nonexclusive relationships: (1) predation and parasitism prevent herbivore populations from increasing to a point where they eat almost everything available, or (2) plants have means of discouraging herbivory, so that at any one time, only some of the green tissue is available and nontoxic. In general, it seems that both of these processes operate. Evidence for the importance of predators comes from situations in which feral goats without predators have decimated native vegetation, as they did in the past on the Channel Islands off the California coast. Likewise, vegetation that has evolved without grazing has been shown to be more palatable to grazers and browsers than vegetation long exposed to them, showing that plants have the capacity to fend off herbivores.



31–2 Food web Diagram of a food web in the Arctic tundra during the spring and summer. The arrows point in the direction of energy flow. This food web is simplified considerably. In reality, many more species of both plants and animals are involved. The fungi, bacteria, and small animals that function as decomposers (not shown here) also play an important role in food webs.

The Earth is green, but a significant amount of dead and discarded organic matter—such as dead roots and leaves, animal carcasses, and feces—contains usable energy. These materials are the food of **decomposers** (also called **detritivores**). The decomposer food chain is at least as complex as the more familiar plant-herbivore-carnivore system. Although some large animals, such as condors and vultures, feed on dead animals and so are, in a sense, decomposers, most of the task is accomplished by small to microscopic organisms. A huge variety of invertebrate groups feed on dead materials—among these are burying beetles, many flies, millipedes, nematodes, earthworms, and sowbugs. Many fungi specialize in the decomposition of dead organic material, and a variety of bacteria extract the last of the usable energy. These many decomposers support a great variety of predatory microcarnivores, such as centipedes, pseudo-scorpions, and some

nematodes, that feed on the decomposers and on each other. Decomposers, especially microbial decomposers, are crucial for ecosystem function, because without them the biosphere would be buried beneath organic debris containing badly needed but unavailable nutrients. Decomposers release these nutrients in usable forms that can reenter the biological cycles. They also are crucial to building soils that retain moisture and nutrients and are well aerated. Composting facilitates the natural decomposition process.

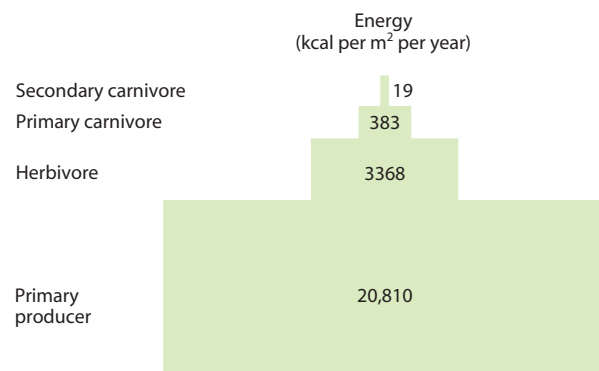
The simple trophic view is useful for doing energy book-keeping. A classic example is Lamont Cole's study of Lake Cayuga, near the Cornell University campus in New York State. He calculated that for every 1000 kilocalories of light energy utilized by algae (phytoplankton) in the lake, about 150 kilocalories are reconstituted as small aquatic animals (zooplankton). Of

these 150 kilocalories, 30 kilocalories are incorporated into small fish (smelt). If we were to eat the smelt, we would gain about 6 kilocalories from the original 1000 kilocalories used by the algae. But if trout eat the smelt and we then eat the trout, we gain only about 1.2 kilocalories from the original 1000 kilocalories. Smelt are much more abundant and constitute a much larger biomass in Lake Cayuga than do the trout. Thus, more of the original energy is available to us, as heterotrophic carnivores, if we eat smelt rather than the trout that feed on smelt. Yet trout are universally considered a delicacy, whereas smelt are less highly prized. The same results apply when we consider the energetics of eating corn and soybeans versus beef. The inevitable loss of energy when we convert plant carbohydrate and protein to animal protein means that there must be significantly less utilizable food in beef than in the crops we use to produce it.

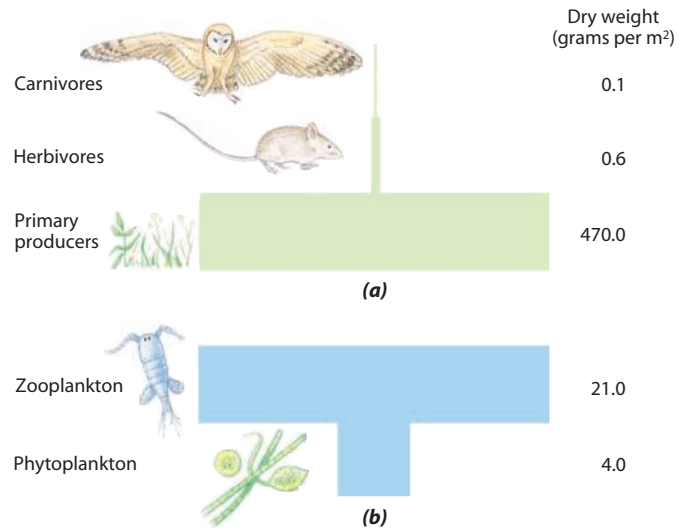
That the most sought-after human foods tend to be from higher trophic levels has profound implications for the future of our species. The poorest populations in densely settled regions today tend strongly toward vegetarianism, because legumes, grains, and vegetables can support a much larger population than a diet high in meat (see the essay “Vegetarians, Amino Acids, and Nitrogen” on page 25). Given the size of the rapidly growing world population, if we are to have reasonable food equity, those of us in richer countries will have to reduce our consumption of meat.

Ecosystems Can Be Described by Pyramids of Energy, Biomass, and Numbers

The basic organizing force imposed by the dissipation of energy as it flows to higher trophic levels is reflected in the “pyramid of energy” (Figure 31-3). Because the energy books must balance, in a system operating in a more or less consistent manner (the so-called steady state), with inputs of energy balancing losses over the course of a year, the energy input to each successive trophic level is less than the energy input to the level below it. The laws of thermodynamics dictate that organisms at each trophic level cannot have more energy available to them than those at the level below, except for short periods of time. As we have noted, approximately one-tenth of the energy incorporated in one trophic level is incorporated into the next.



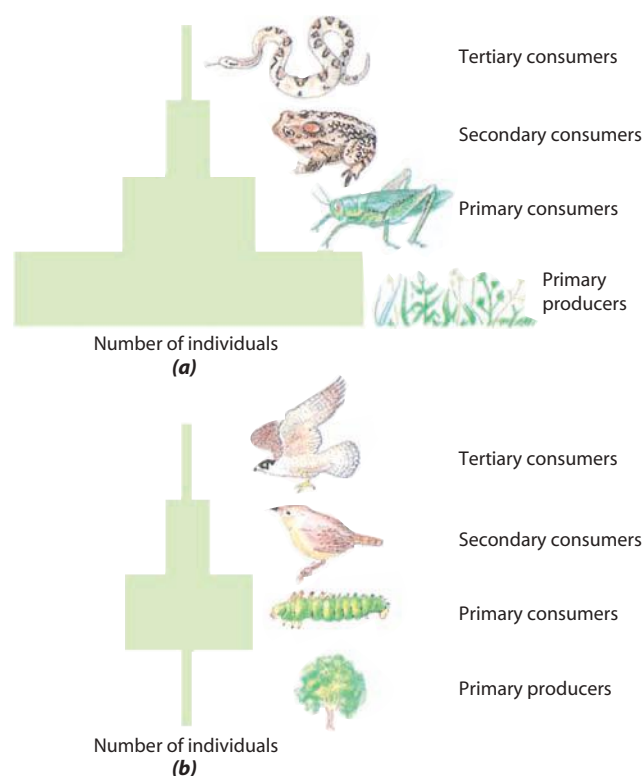
31-3 Pyramid of energy flow In this river ecosystem in Florida, a relatively small proportion of the energy in the system is transferred at each trophic level. Much of the energy is used metabolically and is measured as heat (in kilocalories) lost in respiration.



31-4 Pyramids of biomass The pyramids shown here are for (a) a terrestrial ecosystem, the plants and animals in a field in the state of Georgia, and (b) an aquatic ecosystem, plankton in the English Channel. These pyramids reflect the biomass present at any one time. The seemingly paradoxical relationship between the biomass of phytoplankton and zooplankton in (b) exists because the high reproductive rate of the smaller phytoplankton population is sufficient to support a large zooplankton population.

There is also a “pyramid of biomass,” the mass of living organisms, which is usually expressed as dry weight, because including water introduces too much extraneous variation. Biomass is the cumulative material product of energy acquisition, and at an ecosystem level it varies in rough proportion to the annual net primary productivity. The pattern for the biomass pyramid for terrestrial systems parallels that of the energy pyramid (Figure 31-4a). But the biomass stored in a trophic level at any time represents the balance between the capacity of that trophic level to take in energy and the rate at which energy is lost—through consumption by the next trophic level or by death, passing energy to decomposers. Since biomass is an accumulation based on the rate of gain minus the rate of loss, it is possible for the first trophic level, for example, to have a lower biomass than the next trophic level. This occurs if the rate of gain is high enough to offset whatever the loss is to the next level. This situation is all but impossible for most terrestrial systems, but it is often observed in aquatic systems in which algae, which are dispersed through the water column, grow at a rate that can support a greater biomass of herbivores (Figure 31-4b).

Ecologists sometimes also speak of “pyramids of numbers.” If all organisms were of the same size and required the same amount of energy per unit time per unit biomass, then pyramids of numbers would resemble pyramids of biomass and energy. In fact, however, organisms are very different in size and in energy requirements per unit biomass, with the result that pyramids of numbers can have a variety of shapes (Figure 31-5). It should also be clear that introducing microbial organisms into the pyramid of numbers would produce patterns even more divergent from the energy pyramid.



31–5 Pyramids of numbers (a) In a grassland ecosystem, the number of primary producers (grass plants) is large. (b) For a temperate forest, a single primary producer, a tree, can support a large number of herbivores.

As we have noted, all of the organic materials produced are potentially the food of decomposers. In systems with ample moisture, warm temperatures, and good access to oxygen, such as the tropical rainforests, decomposition is a very active process, with organic debris and dead organisms disappearing rapidly and almost completely. Only a small amount of organic material, that which is resistant to decay, accumulates in the soil. In other ecosystems, however, decomposers can be inhibited by lack of moisture, by low temperatures, or by the lack of oxygen that occurs when systems are saturated with water. In arid regions, decomposition is low, on average, but so is the primary production, and therefore deserts and desert soils have limited accumulation of organic matter.

The tendency for dead biomass to accumulate is most pronounced in wetlands and swamps. Toward the poles, and especially in the vast landscapes of the northern forests and bogs, strong seasonality allows significant growth in summer, while the high water content of the soils and large proportion of land covered with standing water limit oxygen and allow organic matter to accumulate. Peat moss, a traditional fuel in Ireland and a staple of the horticultural industry, is mined from such accumulations. The same process can occur in tropical swamps and wetlands, which have some of the highest rates of annual production of organic matter. Such accumulations of organic matter in the distant past, when buried beneath sediments and subjected to heat and pressure over geologic time, were transformed into the coal, lignite,

oil, and gas that are mined today as the sources of energy that fuel our modern economies.

Note that coal and the other fossil fuels are the accumulated product of past photosynthesis—stored solar energy. For more than 200 years, humans have been heavily exploiting these residues of past productivity. The most readily accessible of these are now depleted, and although new discoveries are being made, it is agreed that they will be both fewer and, on average, more costly to exploit.

Regardless of when fossil fuels will run out, we are using them faster than they are forming. According to one study, our annual rate of consumption of coal of about 4.5×10^9 metric tons is about 60,000 times greater than the historical maximum annual rate of accumulation. Clearly, we need more sustainable energy, including *biological energy conversion*, meaning that we need to use the current production of plants as fuel sources. At one point in human history, most of the energy for heat, light, and industrial processes was derived from burning wood and charcoal. Another traditional source of fuel is the dung of herbivorous animals. These biological sources remain important today, with more than 2 billion people in developing countries relying on biomass for their cooking, heating, and lighting.

Can these traditional sources of energy make significant contributions in advanced industrial societies? Technological innovations can do the equivalent of burning dung by extracting methane from animal waste, as is being done in progressive farming operations to heat farm buildings. A more direct method is to use agricultural waste, such as corn stalks, and burn it in boilers to produce steam to run electric generators. More controversial are methods that require the harvesting of plants (bio-fuels) grown specifically for their energy content. One approach to efficiently capture solar energy is to plant fast-growing trees such as hybrid poplars on marginal agricultural lands. Another is to harvest high-yielding perennial grasses, with varieties of the North American prairie switchgrass (*Panicum virgatum*) among the leading candidates. Another possibility is to harvest algae grown in nutrient-rich solutions.

People who take an ecosystems view of energy-producing schemes that involve biomass tend to be more skeptical about the prospects than those who limit themselves to a narrower, technical view. Using algae, for example, is efficient only if the cultures are stirred, which requires energy. Once harvested, more energy—even if solar energy—is needed to remove most of the water. Different problems confront terrestrial biomass schemes. Assuming that the area of cropland is fixed, then if we divert lands to fuel production, we will need to produce more food per hectare on the land that remains to meet the food needs of an increasing global population. If we are to bring new lands into production, we must consider that many conversions will entail an initial loss of stored carbon as the native vegetation is removed, often by burning. Also, in most parts of the world, the best agricultural lands are already in production, and this means that moving to more marginal lands will mean much lower rates of production per hectare for the energy crops. And finally, of greatest concern to those who value natural habitats, the search for lands to devote to fuel production will place enormous pressures on “unproductive” natural ecosystems. Areas presently supporting species-rich natural systems could be converted to energy plantations of only a few species. As with natural ecosystems,

human ecosystems cannot violate the laws of thermodynamics. The total environmental cost of each energy alternative must be carefully considered.

Looming over any discussion of fuels and energy production are the serious concerns about global climate change. Though experts debate the details, there is overwhelming consensus that human activities are changing our climate. While it is true that the Earth's climate has gone through large swings in the past, the expansion of glaciers being the most recent example, current rates of change are faster than most of these historical cycles—though there have been exceptions, such as catastrophic asteroid impacts. Given that the human population will continue to increase, it follows that if the severe consequences of climate change are to be averted, the per capita use of fossil fuels must drop significantly, and drop farthest in the countries that are the most affluent. It is not clear how this will be accomplished within our current economic and political systems. Many experts believe this drastic readjustment can occur only if we tap every feasible source of renewable, nonpolluting energy production, including wind, water, solar, biomass, and, more controversially, nuclear sources.

Food Webs Provide a More Complete Accounting of Trophic Relationships

The simple producer-herbivore-carnivore type of trophic structure provides a sufficient frame for sketching the basics of energy flow. But to understand the functioning of ecosystems more fully, we need to analyze the energy relationships in more detail. The concept of food webs provides us with one way of doing this. A food web divides an ecosystem into species or groups of species that are functionally similar—for example, the group of nitrogen-fixing herbs. Considering species is logical, since feeding relationships are more similar among members of a species than between different species. The food web, then, is the set of trophic connections among species or functional groups that shows who feeds on or derives energy from whom. For even a small, species-poor ecosystem a few hectares in size, such a complete diagram would contain hundreds of nodes and a mass of interconnecting lines. This explains why food webs have more often been used for simpler systems such as the Arctic tundra illustrated in Figure 31-2. Because of the almost unworkable complexity of complete food webs, especially for species-rich systems, it is common to deal only with the most abundant species and the major lumped groups, such as the bacterial detritivores, which feed on dead organic matter.

Thinking about trophic relations in a food web reveals complications. One is that some species cannot be placed within a single trophic level as defined earlier. Our own species illustrates this. Most humans are **omnivores** that consume almost any energy-containing biological material—meat, animal products (milk, eggs), green plants, decomposers (mushrooms), and partially decomposed plants and plant products (sauerkraut, yogurt, wine, beer). But belonging to different trophic levels is not exceptional among other kinds of organisms. Many fish, for example, begin life feeding on zooplankton but end as large top carnivores, eating other fish, which, in turn, may be carnivores on still other fish. A second complication is that even when a species' feeding is limited to one trophic level, it may switch

among alternative prey sources at that level as these change in abundance.

Parasites, defined as organisms that live in or on other organisms on which they feed but do not usually kill their hosts, are an important category in food webs and the functioning of ecosystems. All parasites are heterotrophs and so could be considered as herbivores or carnivores, depending on the kinds of organisms parasitized. They deserve special mention because their modes of life are usually very different from that of other classes of heterotrophs. Parasites are a heterogeneous group and include the disease-causing viruses, bacteria, other single-celled organisms such as the malaria-causing *Plasmodium* species, many fungi, and a vast array of mostly invertebrate animals, such as insects and roundworms. Parasites are always one trophic level above their hosts. So, although there is no “super-raptor” that feeds exclusively on eagles and large hawks, there are parasites that feed on large raptors.

There are also **parasitoids**. These are animals, mostly small wasps and flies, that develop within a host insect and eventually kill their hosts, eating them literally from the inside out. The insect that emerges from a caterpillar's pupa, for example, might not be a butterfly or moth but a tiny parasitoid wasp, the host having been consumed after forming its pupal case. Parasitoids are different from parasites in that, unlike parasites, the outcome of the interaction is inevitably the death of the prey organism. In contrast, the ideal for a parasite is to allow the host to live, not necessarily as long as it might if parasite-free, but as long as possible.

The characteristics of a food web, the number of species involved, and the number of links connecting them determine important aspects of ecosystems. One favored hypothesis holds that an ecosystem with a greater number of species and therefore more pathways for energy flow should be more stable than a similar system with fewer species. In this context, “stable” means that basic functional aspects—especially energy capture and flow—stay within a certain range and do not show extreme fluctuations or catastrophic, permanent collapse. The logic behind this deduction is simple. If there are multiple pathways for energy to flow through a system, the failure of one pathway—say, one species is nearly exterminated by a pathogen or a climatic extreme—can be compensated for as the energy flow switches to another pathway. If a species is lost or decimated, that part of the food web can be replaced by one or more other parts, and thus the overall web function is maintained. This intuitively simple and appealing idea has been difficult to verify for real systems, but a consensus, based on observation and experimentation, seems to be emerging that the diversity of species has a positive though not always overriding effect on resilience of the ecosystem.

Nutrient and Material Cycling

Ecosystems are energy-processing systems, but to capture and utilize energy, organisms must contain the right amounts and right kinds of molecules and ions. In contrast to energy, which must flow into a system continuously, or nearly so, the material part of ecosystems is recycled. All the nitrogen atoms in our bodies have been used countless times before and will be used many times more. The scale of recycling and the transitions in

the recycling processes depend on the chemistry of the particular element or molecule. The pathways of some of these essential elements, known as **nutrient cycles**, are discussed in Chapter 29. Elements with a significant gaseous phase have regional and global cycles, especially water (page 705), carbon (page 144), and nitrogen (see Figure 29–8). Elements such as phosphorus (see Figure 29–15), calcium, and iron that move mainly in solution or in suspension, attached to or incorporated in organic or inorganic particles, have more local cycles.

In conceptualizing nutrient flows, it is useful to think of the elements occupying compartments that differ in their rate of turnover. In the biosphere, certain atoms that were once part of a living organism are now buried deep beneath the Earth's surface in sedimentary rocks or in the deepest parts of the oceans. Some of these atoms may lie there for millions of years before they are uplifted and released for use by living organisms. Other atoms are in shallow sediments and are unavailable for only thousands of years. Phosphorus (P), for example, which is needed in relatively large amounts by living organisms, varies in its availability. In a terrestrial ecosystem, some phosphorus is in the liquid phase of the soil, where it is available for immediate uptake, and some is locked in organic matter that must be decomposed to release it. Some phosphorus is fixed in chemical complexes, with iron and aluminum in acid soils and with calcium in alkaline soils, and some is present in pieces of intact rock that might take millennia to break down. To understand the supply of phosphorus—or any of the other necessary elements—requires a detailed knowledge of its various chemical forms. For this reason, soil scientists use the term “available nutrients,” meaning nutrients in a form that is available in a reasonably short time. For plants, this usually means within one growing season.

For ecosystems to capture and process energy, and for the system's constituent organisms to approach an optimum growth level, the necessary elements and molecules must be available in sufficient amounts and in the right proportions. This is not usually the case, and most obviously so for water. On large parts of the Earth's land surface, primary productivity is limited by drought and thus there is a limited energy flow, as in the Atacama Desert of coastal Peru and northern Chile, for example (Figure 31–6). Less obvious is that carbon dioxide supplies are commonly below the levels that would allow maximum rates of photosynthesis, although human activities, by increasing global carbon dioxide levels, are reducing this constraint to an unknown extent, while at the same time promoting global warming.

Nitrogen is needed in large amounts by living organisms because of its central role in the chemistry of life—most notably as a constituent of protein. Since it is not abundant in the rocks of the Earth's crust, nitrogen is often deficient in soils. Experiments that add available nitrogen to soils in natural systems generally result in a positive growth response in the plants. Limitation of nitrogen is even greater in agriculture, and a search for nitrogen fertilizers has been a central concern of agriculturalists. A technological breakthrough occurred early in the last century when a process for producing nitrates from atmospheric nitrogen was perfected. This has injected huge amounts of available nitrogen into the global cycle and contributed to disruptions to natural processes, such as the “dead zone” in the Gulf of Mexico at the mouth of the Mississippi River. Nature devised its own



31–6 Arid desert Plant growth is severely limited in the Atacama Desert of Chile and Peru, the driest desert in the world, with a mean rainfall of less than 1 millimeter per year in certain areas; this means that in many years there's no rain at all—the norm. Some weather stations in the Atacama have never recorded rainfall.

way to take nitrogen from the air early in the evolution of life. As discussed on page 693, certain bacteria have the capacity to fix atmospheric nitrogen. Some higher plants—many legumes, for example—have tapped into this capacity by forming mutualistic associations with nitrogen-fixing bacteria living in special structures, known as nodules, in their roots. Plants with this mutualism, as we shall see, can gain a competitive edge in nitrogen-poor environments, and they introduce available forms of nitrogen into the ecosystems of which they are a part (see Figure 29–11).

Classic Experiments on Nutrient Recycling Were Performed at Hubbard Brook

Studies of a deciduous forest ecosystem in the Hubbard Brook Experimental Forest, in the White Mountain National Forest of New Hampshire, were landmarks in the effort to understand nutrient and other material cycles at the level of entire ecosystems. The purpose of these studies was to gain a quantitative understanding of nutrient storage and movement. Mass balance was used as the basic model. Because the inputs and outputs of the system as a whole—and for compartments within the system—must balance, this served as a check on the completeness and accuracy of the accounting. The sites chosen were an important feature of the study. They are underlain by nearly impervious rocks resistant to weathering, and each of the experimental watersheds is drained by a small stream. This meant that the investigators could measure most of the loss of nutrients for each system by measuring the amount of water and its nutrient content as it flowed over a V-notched weir (Figure 31–7). Because the underlying rocks were nearly impervious and weathered only very slowly, the additions and losses of nutrients beneath the



31-7 Hubbard Brook weir Water from each of six experimental ecosystems in the Hubbard Brook Experimental Forest in New Hampshire was channeled through weirs, built where the water leaves the watershed. The water was analyzed for chemical elements. The trees and shrubs in the watershed behind the weir shown here have been cut down. The experiments showed that deforestation disrupted the tight cycling of nutrients by various living components of the ecosystem and greatly increased the loss of nutrient elements from that system.

watersheds were minimal. There were atmospheric inputs, and these were monitored by measuring dryfall (dust, organic particles) and the inputs from rain and snowfall.

The study showed quantitatively what ecologists had always suspected: that forest ecosystems are extremely efficient in conserving their mineral elements. For example, the annual net loss of calcium from the ecosystem was 9.2 kilograms per hectare. This represents only about 0.3 percent of the calcium in the system. Nitrogen, which can enter the system by fixation and as nitrates, nitrites, and ammonium from dryfall and in solution (see Figure 29-8), was actually accumulating at a rate of about 2 kilograms per hectare per year. There was a somewhat smaller net gain of potassium in the system.

One of the boldest aspects of the Hubbard Brook study was the clearing experiment. In an effort to assess how the presence of the living forest influenced nutrient gains and losses, in the winter of 1965–1966, all trees, saplings, and shrubs in one 15.6-hectare watershed were cut down. No organic materials were removed, however, and the soil was undisturbed. During

the following spring, the area was sprayed with an herbicide to inhibit regrowth. With transpiration no longer a significant factor, during the four months from June through September 1966, the runoff of water was four times greater than in previous years. With the primary producers largely shut down and decomposition ramped up, there was a massive loss of nutrients. New losses for both calcium and potassium were about 20 times higher than in the undisturbed forest.

The most severe disturbance was seen in the nitrogen cycle. The microbial decomposers continued to function, leading to the release of ammonia and ammonium ions and, through the microbial nitrification process, nitrites and nitrates. Without plants to absorb them, these highly soluble ions were readily leached, and from 1966 to 1968 the net loss of nitrogen averaged 120 kilograms per hectare per year. The nitrate concentration in the stream that drained the area exceeded levels established by the U.S. Public Health Service as safe for drinking water, and an algal bloom developed. In their entirety, these studies showed how living systems serve to retain nutrients against natural gradients for their dilution and loss.

Interactions between Organisms—Beyond Simple Trophic Relationships

To this point, we have emphasized overall ecosystem function, that is, organisms as producers and consumers. But mass and energy balance provide only the background. Ecology is fundamentally about interactions. This is encapsulated in the often-repeated statement that the basic message of ecology is that everything is connected. No organism—whether in a patch of woodland, a pasture, a pond, a coral reef, or an urban gated community—exists in isolation. The lines in a food web indicate energy relations, but they also define interactions that are often subtle and complex. To grasp this complexity, we need to delve more deeply into the major categories of interaction. We organize our discussion around three major kinds of interactions between organisms: competition, mutualism, and predation.

Competition Results When Organisms Require the Same Limited Resource

Competition is of fundamental importance, because it is the main force that drives natural selection. It is defined as an interaction in which two or more organisms are utilizing the same *required* resource that is available in *limited* supply. “Required” means that without the resource, the organism will eventually die, and “limited” means there is a fixed supply. Not all of the competing organisms can have as much of the resource as would be necessary for their optimal growth and reproduction. The experimental proof of competition is that (1) an organism performs better (grows faster, produces more offspring) when its competitors are removed and (2) the improved performance is shown to be due to the organism’s having obtained resources that would otherwise have gone to its competitors.

Many ecologists make a distinction (not always crystal clear) between *resource competition*, in which the competition can be directly related to a specific resource, and *interference competition*, in which organisms contend for a resource that is only indirectly related to things essential for growth and reproduction,

such as birds competing aggressively for territories. Although the reason for this latter type of interaction may ultimately be related to the need for each pair of birds to ensure an adequate supply of food, the negative interaction may take place with a vigor independent of the abundance of the food resource.

Growth Rate Is an Important Factor Affecting Competition among Plants That green plants are tied to one place and are dependent on the availability of light sets the stage for their competitive interactions. In all cases, where other necessary resources (water and nutrients) are in good supply and the environment is relatively benign, light is a limiting factor and plants compete for it. This is because, in such circumstances, plants are able to produce leaves that intercept very nearly all the direct light. In theory, if plants cooperated or if there were only one species of green plant, all the light could be absorbed by a carpet-like covering of the plants over the surface of the ground. With proper construction of this carpet—for example, providing a way to avoid light saturation of photosynthesis during the middle of the day—there would be no need to raise the photosynthetic surface high above the ground, as is “wastefully” done in forests. But such carpet-like plant growth is restricted to extreme situations—such as alpine tundra, rocky outcrops, and deserts after rare saturating rains—and this is easily explained by competition. Any plant that raises its canopy above that of its neighbors can gain a significant advantage by putting its competitors in the shade.

Competition in terrestrial plants in habitats generally favorable for plant growth (moist to wet tropics and temperate zones) has, over evolutionary time, been largely a struggle for light. The conspicuous winners in the evolutionary contest are the tall woody plants—trees. In these plants, physiological functions, such as photosynthetic rate and water-use strategies, are combined successfully with a growth form that allocates a certain proportion of energy away from light-absorbing leaves in favor of long-lived woody stems. And these woody stems benefit from the extra support of roots and other specialized structures, such as buttress roots (see Chapter 32), needed to resist the effects of wind and gravity. Trees therefore have a good chance of finding and holding their place in the sun when opportunity presents itself.

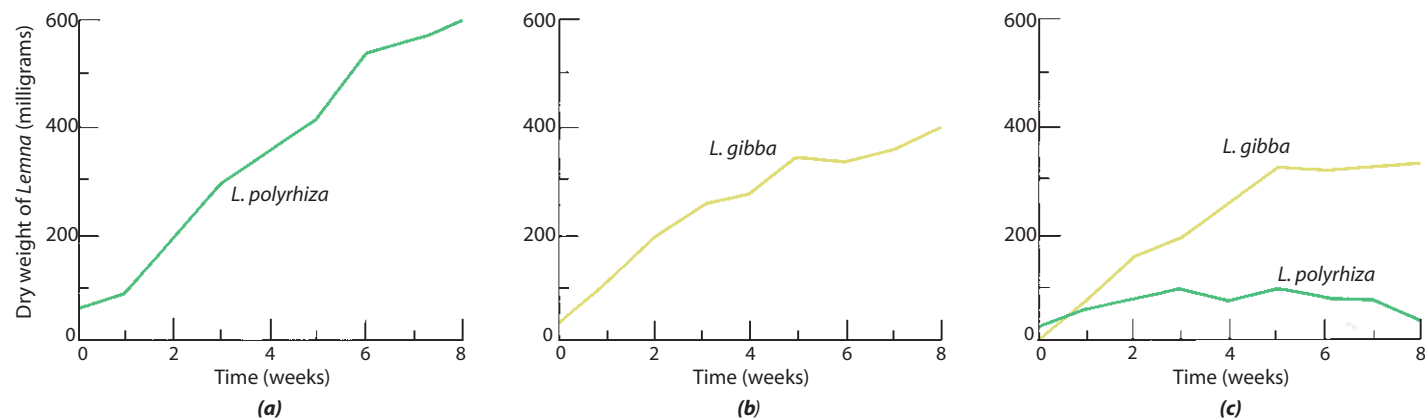
Some plants followed other evolutionary pathways, developing sets of traits that allowed them to utilize the lower light levels of the forest understory or to exploit brief windows of light availability. Spring ephemerals are examples of the latter approach. They comprise a functional group species found in the temperate deciduous forests. Species such as trilliums (see Figure 1–5) begin growth before the trees are fully leafed out and accumulate much or all of their energy during the brief time that the light levels on the forest floor are high. After flowering, these plants go dormant, as expansion of the new tree leaves puts them in the shade. Analogous specialization also exists among trees. Some require high levels of light and can develop from seedling to tree only when other trees are absent or sparse, as after a fire. Other trees have seedlings that can survive with reduced light, growing slowly until something, often the fall of a large tree, opens a gap in the canopy. Since the seedling is already present, it has an advantage over species that disperse seeds to the newly opened site and, to a lesser extent, over species that must germinate

from seeds already present at the site. With the increased light, the established seedling can accelerate its growth and seize a place in the canopy. Species of trees that can tolerate low light are, logically, called *shade tolerant*. Those that cannot are *shade intolerant*.

Where resources other than light are in short supply, the nature of competition is different. In deserts, trees are absent—except where water is locally abundant, as in palm oases and along rivers—and perennial plants are widely spaced. Ecologists have established that in such situations, it is belowground competition for water that is important. Because of the suboptimal water supply, plant canopies are limited and so can capture only a small percentage of the total light. The “nurse effect” seen in deserts provides additional evidence that light is not the crucial factor. This term refers to the situation in which species that ultimately reach a large size often need the protection of an established plant—the nurse—to survive. Larger shrubs in deserts often shelter seedlings and the young plants of other species under their canopies. The seedlings and early growth stages of giant cacti, for example, are generally found beneath the cover of another species. The shrub canopies moderate the heat of the sun and the drying effect of the wind, factors that offset the reduced light and competition for soil moisture and nutrients. It is also possible that growing under a larger shrub may protect the young plants from herbivores. Eventually the sheltered plants will overtop their nurse and survive on their own.

The Principle of Competitive Exclusion Provides a Baseline for Studying Competition It is challenging to measure competition in nature. Although many studies have documented shifts in species composition over time, assigning causes for this by observational studies is difficult. Consequently, much of our knowledge of competition depends on experiments, usually in very simplified settings. Experiments of this kind have been used to justify the theoretical **principle of competitive exclusion**, which holds that two species with similar environmental requirements cannot coexist indefinitely in the same habitat. One or the other must eventually be eliminated. A classic study of competition was conducted with two species of duckweed, *Lemna polyrrhiza* and *Lemna gibba*, both of which are small floating aquatic plants. When grown in individual, pure cultures, *L. gibba* always grew more slowly than *L. polyrrhiza*, yet when the two species were grown together, *L. polyrrhiza* was always replaced by *L. gibba*. The plant bodies of *L. gibba* have air-filled sacs that enable them to form a floating mass over the other species, cutting off the light. As a consequence, in mixed cultures, the shaded *L. polyrrhiza* died out (Figure 31–8).

Competition Favors Specialization If the world were completely uniform and the climate completely stable, the principle of competitive exclusion would suggest that ecological and evolutionary forces would result in the emergence of one or a very few winners for each trophic function. But the world is heterogeneous and changeable, and we find different species dominating in different areas. This can be reconciled with the competitive exclusion principle by invoking **specialization**. As some of the preceding examples suggest, a set of specialized adaptations that make a species dominant in one place generally do not serve it



31-8 Competitive exclusion An experiment with two species of floating duckweed, which are tiny angiosperms found in ponds and lakes. One species, *Lemna polyrhiza* (a), grows more rapidly in pure culture than the other species, *Lemna gibba* (b). But *L. gibba* has tiny air-filled sacs that enable it to float on the surface, and when the two species are grown together, *L. gibba* shades *L. polyrhiza* and is the victor in the competition for light (c).

well in another location. We do not find sugar maple trees in the desert or cacti beneath a spruce canopy in the boreal forest. The alternative to having habitat specialists would be to have highly **plastic** species—say, species that could take the form of a broad-leaved tree in one location and a columnar cactus in another. But despite some striking examples of plasticity—for example, some aquatic plants have two distinctly different leaf types, those submerged and those in the air (page 596)—the capacity of species to alter their characteristics to suit the environment is generally limited. Plasticity has costs.

But the question can be flipped around. The principle of competitive exclusion can be seen to allow different species to grow in different types of habitats, but how can it explain the common situation of multiple species occupying a single habitat? Does a typical one-hectare (2.5-acre) patch of eastern deciduous forest “need” the 10 to 20 species of trees and shrubs found there? And do tropical forests “need” the 100 to 200 species they may have? Does this happen because the redundancy is only apparent, and the various species of primary producers each fill subtly different roles? Or do disturbance factors keep the mixture perpetually on the boil, preventing competitive exclusion from acting? Or is it just that competitive exclusion, very apparent for the *Lemna* species described above, fails to act as strongly in other situations?

A more subtle kind of specialization can be part of the answer. For example, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) coexist in roughly equal abundance and form the dominant tree community in the subalpine zone of the central and northern Rocky Mountains. The greater longevity and size of the spruce are balanced by the faster growth in height of the fir and the broader range of conditions in which fir seedlings will establish. Spruce seedlings are found primarily in forest gaps or associated with a canopy of firs, whereas fir seedlings are more commonly found in the forest. Fir seedlings outcompete spruce seedlings in shaded understories by the simple fact that they survive. Spruce seedlings, however, outcompete fir in sunnier sites, because of their higher growth rates and

greater resistance to drought. Constant disturbance from storms, flooding, and avalanches, among other factors, and the relatively short life span of the fir prevent it from taking over the entire landscape. Patterns of this sort are frequent in plant communities, but they are often not so obvious. The different requirements of the various species mitigate the competition and allow them to coexist indefinitely.

Another explanation for the many species coexisting in a habitat is based on the speed with which a superior competitor replaces another. If two similar species, both well adapted to a particular habitat, differ only slightly in, say, their rates of growth and therefore population expansion, it may take a very long time for the superior species to exclude the other, even if the superior species consistently has the advantage. (If it does not, our explanation would be the same as for the spruce-fir example above.) Where overall growth is slow, the absolute difference in growth is reduced, and thus the time to local extinction of the inferior competitor is longer, perhaps so long that the two can coexist for millennia, even without the intervention of disturbance.

Herbivory is another factor that can limit growth. In the chalk grasslands of England, the grasses were historically kept closely cropped by domestic grazers and rabbits, subduing the grasses and herbs that were most competitive and allowing many other kinds of shorter grasses and herbs to flourish. The situation changed early in the twentieth century when a severe epidemic of the viral disease myxomatosis drastically reduced the population of rabbits. A similar response was seen when domestic grazers were removed. Without intense grazing, the grass cover of the chalk soils became taller and denser as the competitive species were able to reach their full size and extent, and many of the formerly abundant species of flowering plants became rare. Nutrient deficiency and the propensity for drought can have a similar effect. The greatest diversity of species in prairies of the Midwestern United States tends to be found on sandy soils or on thin-soiled prairies on limestone hills. It is assumed that on these more stressful sites, the most aggressive species (in this case, C_4 grasses) are kept in check by limited resources.

But in some places, the biodiversity seems greater than specialization can explain and competitive exclusion should allow. Species-rich tropical forests and the dense shrublands, or *fynbos*, of South Africa have posed a problem for oversimplified views of competition. There seem to be many more species than should be necessary to fill all the essential ecological roles. Attempts to explain the coexistence of species on the basis of balancing specializations, as in the fir-spruce example, have had limited success. Current work suggests that the explanation may lie in recognizing that competitive exclusion describes only a tendency, and that it may be possible for evolutionary processes to generate new species faster than competitive forces can exclude the less fit. The explanation is probably some combination of specialization, environmental variation shifting the competitive advantage, and simply the long times required for extinction.

Some Organisms Produce Chemicals That Inhibit the Growth of Others Plants mostly compete by appropriating resources directly, but there are other modes of negative interaction. In some instances, one (or both) of the competing organisms produces chemical substances that inhibit the growth of members of its own or other species. Competition that seems to be a kind of chemical warfare is most clearly present in microbial interactions. For example, the fungus *Penicillium chrysogenum*, which grows on organic substrates such as seeds, produces significant quantities of penicillin in nature. Penicillin inhibits the growth of gram-positive bacteria, which might otherwise compete directly with the fungus for the same nutrients. Analogous relationships among plants are grouped under the general heading of **allelopathy**.

One can ask if a plant that faces intense competition from other plants might evolve a way to poison its competitors (by allelopathy) rather than struggle directly for the resource in short supply. There is some evidence that this is so. Mahall and Callaway studied root interactions in two species of desert shrubs, burro weed (*Ambrosia dumosa*) and creosote bush (*Larrea divaricata*). Field studies indicated that these two commonly co-occurring species compete for water. In an experimental setting, the roots of creosote bushes were not inhibited by the roots of burro weeds, but growth of the roots of both species slowed when they encountered creosote bush roots. Though the researchers did not identify the specific mechanisms by which this occurred, it is likely that exudates from the roots are detected within and between species. The results suggest an asymmetrical kind of interference competition in which a creosote bush fends off burro weed through growth-inhibiting allelochemicals that diffuse out from the roots. Burro weed, in contrast, is inhibited by its own roots only when they come into direct contact. It seems that creosote bushes tend to divide up the rooting space among themselves, thereby minimizing competition within and between individuals. Burro weed tends to do the same with other burro weed, but only in response to direct contact, and it avoids areas where creosote bush roots are present.

Allelopathic effects are being applied in agriculture. For example, a strip planted with sorghum has two to four times fewer weeds the following year than comparable strips planted with other species. The sorghum plants evidently leave behind allelopathic compounds in the soil that depress the growth of weeds.

Symbiosis Covers a Vast Array of Interactions

Symbiosis, meaning “living together,” is the umbrella term covering the often complex and highly evolved relationships between species that are not competitive, parasitic, or predatory. At one extreme it can be stretched to include interactions such as squirrels depending on trees as locations for their nests. The squirrel-tree association is weak, however. Squirrels can nest in many species or, if given the chance, in the attic of a house. Some forest understory plants depend on the shade cast by trees but may be relatively indifferent to which species provides it. At the other extreme are symbiotic interactions in which the association, at least for one of the species involved, is essential.

Mutualism Is an Interaction in Which Both Species Benefit

Mutualism is a symbiotic interaction in which the growth, survival, and/or reproduction of both interacting species are enhanced. In many examples of mutualism, neither partner can survive without the other, particularly when predation and competition from other plants are taken into account. Several examples of mutualism are discussed in earlier chapters—lichens (see Chapter 14), legumes and the nitrogen-fixing bacteria that live in their root nodules (see Chapter 29), and the close relationships between plants and their pollinators and seed dispersers (see Chapter 20). Here we provide two further examples of mutualism. Both cases appear to have developed as the result of **coevolution**—species mutually evolving to exploit the benefits of cooperation.

Mycorrhizas Are Mutualistic Associations between Roots and Fungi As discussed in Chapter 14, the roots of most vascular plants are associated with fungi, forming compound structures known as mycorrhizas (pages 312 to 315). The mycorrhizal fungi are not simply fungi that happen to grow near plant roots. They are specialized to grow on the roots or actually into the root tissues without causing the damage that would be expected if they were pathogens. In this mutualistic relationship, it is easy to see the benefit to the heterotrophic fungi: they gain access to the proteins, sugars, and other organic products of the primary producer. The advantage to the plant is less obvious but has been revealed through experimentation. The superior ability of the fungi to extract necessary resources from the soil increases the plant's access to nutrients and, sometimes, water. Without the fungi, plants that are obligately mycorrhizal grow poorly or not at all. Other plants, those that are “facultatively” mycorrhizal, are able to grow without mycorrhizas in some circumstances.

Some mycorrhizal associations are highly specific, with one species of fungus forming associations with only a single species or a group of related species of vascular plants. For example, the pore fungus *Boletus elegans* is known to associate only with larch (*Larix*), a conifer. Other fungi, such as *Cenococcum geophilum*, have been discovered living in association with forest trees of more than a dozen genera.

Mycorrhizas are generally considered to be a true mutualism—that is, they benefit both partners. But there are other higher plant–fungal associations in which the mutualism is not so obvious. Some plants have a very high rate of fungal infection in their stems and leaves, where the fungi are clearly not aiding the

absorption of water or nutrients. The general term for this kind of fungus is *endophyte*. The benefit the endophytic fungi seem to confer is that infected tissues are less palatable to herbivores. If this is correct, it can be considered a true mutualism. In other cases, however, the endophytic fungus can turn on its host and act as a pathogen, killing or seriously impairing it. There is much to be learned about such kinds of interaction. To fully understand them will require studying the interactions in real situations—a good example of how a systems view in natural settings is essential.

Acacia Trees and Ants Interact in a Mutually Beneficial Way Many striking examples of mutualism occur in the species-rich tropics. One of them involves species of *Acacia*, a large genus of leguminous trees and shrubs that is widely distributed in tropical and subtropical regions. Certain species of *Acacia* in the lowlands of Mexico and Central America possess traits that were puzzling when first encountered. Like many acacias, these have thorns (technically, they are stipular spines), but the thorns are excessively enlarged, up to 2 centimeters wide at their base. Shaking a branch of one of these acacias quickly reveals a related peculiarity: the thorns are inhabited by ants, which swarm out of the small holes they create in the thorns to attack anything, animal or vegetable, that disturbs their host plant. There are nectaries (sugar-secreting structures) on the acacia petioles. In addition, small protein-rich Beltian bodies (named after the nineteenth-century naturalist Thomas Belt) located at the tip of each leaflet are avidly collected by the ants (Figure 31-9).

Experiments and observations by Daniel Janzen, published in 1964, clarified this strange collection of features. Janzen found that the stings and bites of the worker ants (*Pseudomyrmex*), which swarm over the surface of the bull's-horn acacia (*Acacia cornigera*) when it is disturbed, discourage herbivores. Moreover,

whenever the branches of another plant touch an inhabited acacia tree, the ants girdle the other plant's bark, destroying the invading branches and producing a tunnel to the light through the dense surrounding tropical vegetation. When Janzen removed the ants from a plant by poisoning them or clipping off the portions of the plant that contained ants, the acacia grew very slowly and usually died within a few months as a result of insect damage and shading by other plants. In contrast, plants inhabited by ants grew very rapidly, soon reaching 6 meters or more in height and overtopping the other second-growth vegetation. Ants of the genus *Pseudomyrmex* make their nests only in these particular acacias and are completely dependent on the nectaries and Beltian bodies for food.

Plant-Herbivore and Plant-Pathogen Interactions Involve a Variety of Defense Mechanisms

Predation and parasitism are interactions in which one organism—the herbivore predator, parasite, or pathogen—benefits at the cost of the plant preyed upon. As discussed above, the adage that the “world is green” attests to the fact that plants and the organisms that feed on them generally have achieved a balance, and the result is a more or less continuous plant cover. Herbivory and parasitism are the rule, but healthy plants manage to grow and reproduce despite this. The reason plants are not inevitably overwhelmed by the legions of organisms that attack them is that, over evolutionary time, they have developed countermeasures to protect themselves. Some ecologists like to characterize this process as a coevolutionary “arms race,” with the plant attempting to foil its attackers, and the herbivore or pathogen seeking chinks in the defensive armor that permit attack.

Different plant species have developed different strategies in this evolutionary struggle. Some have defensive structures



(a)



(b)

31-9 Ants and acacias (a) A worker ant (*Pseudomyrmex ferruginea*) drinking from a nectary of a bull's-horn acacia (*Acacia cornigera*). At the right is a large thorn. After cutting out an entrance hole and hollowing out the thorn, the queen will raise her brood within it. (b) A worker ant collects Beltian bodies from the tips of acacia leaflets. Rich in protein and oils, the Beltian bodies are an important food source for both adult and larval ants. The ants kill other insects that attempt to feed on the acacia and girdle plants that come into contact with it.

(spines, for example), but all of them rely to some degree on chemical defenses. These are mostly in the form of compounds commonly referred to as secondary metabolites (pages 30 to 35), and there is a great diversity of them, including terpenoids, alkaloids, saponins, glucosinolates, and many more. The ability of plants to produce these toxic chemicals and retain them in their tissues doesn't completely prevent herbivory or parasitism, but it does make it more difficult. Indeed, these chemicals seem to be the most important factors in controlling herbivorous insects in nature. Scientists working to improve the resistance of crops to invertebrate herbivores are focusing much of their effort on these chemicals.

Tannins Are an Example of a Static Chemical Defense Tannins are distasteful phenolic compounds, repellent to a wide variety of herbivores. In plants that produce them, they are always present in certain plant parts, but their concentration can increase in response to attack. For example, when gypsy moths (*Lymantria dispar*) defoliate oak trees (*Quercus* spp.), the trees produce new leaves that are much higher in tannins and other phenolic compounds. The new leaves are also tougher and contain less water than those they replace. These differences are great enough to inhibit the growth of the larvae feeding on the new leaves, so the overall growth of the moth population is curtailed. The tannins apparently interfere with digestion in the insects by combining with plant proteins, making them indigestible.

Similar effects may be common in other plants as well. For example, when snowshoe hares heavily browse some trees and shrubs, such as paper birch (*Betula papyrifera*), the plants produce new shoots that are much richer in distasteful resins and phenolic compounds than the earlier shoots.

The secondary metabolites ingested by herbivores may, in turn, play a role in the animals' ecological relationships with other animals. For example, some insects, such as the monarch butterfly, store these poisons within their tissues and are thereby protected from their predators (see Figure 2–25). In addition, some sex attractants in insects are derived from the plants on which they feed.

Viewed as a whole, the relationships within a community are diverse and can be subtle. Organisms that coexist within a community often have evolved together. Within the community, they affect one another in an endless variety of ways, a few of which are just beginning to be understood. The kind of coevolution that has contributed to highly developed interactions such as the ants and their acacias has a long evolutionary history. In Chapter 12, we pointed out that both mitochondria and chloroplasts, now integral components of eukaryotic cells, were derived from formerly free-living bacteria that were engulfed by larger, heterotrophic cells (pages 247 to 248). Thus a tree or a human alive today is, in one sense, a highly evolved interacting community, not only because of interactions with mycorrhizal fungi (for the tree) or bacteria in the gut (for the human), but also because of the evolutionary construction of their cellular building blocks.

Plant-Herbivore and Plant-Pathogen Interactions May Be Quite Complex Pea plants (*Pisum sativum*) are largely protected from parasitic fungi by a substance they produce called pisatin. Many strains of the important parasitic fungus *Fusarium*, however, have enzymes

called monooxygenases that convert pisatin into a less toxic compound. These fungi then have the ability to attack peas. Humans also utilize monooxygenases to detoxify certain chemicals that would otherwise be harmful. In such ways, “chemical warfare” between plants and their herbivores is continuously being waged.

The protective chemicals produced by plants often not only are distasteful but may display still other features that deter herbivores. Chromenes, for example, can interfere with insect juvenile hormone (essential to an insect's life cycle) and thus can act as true insecticides. A Mexican sneezeweed (*Helenium* sp.) produces helenalin, which functions as a powerful insect repellent. Pyrethrum is another natural insecticide, which is produced commercially from a species of *Chrysanthemum*. Even the waxy surfaces of leaves, which are difficult to digest, may be important in retarding attacks by insects and fungi (see Figure 2–10). Another example of chemical warfare is the fungal endophytes, discussed above.

Herbivores Can Be Used to Combat Plant Invasions One of the consequences of humans introducing new plant species is that the introduced species can expand to become serious pests. One reason for this is that in its new habitat, the new species will be free of the collection of parasitic and herbivorous organisms that attack it and limit it in its native habitat. For example, a prickly pear cactus (*Opuntia*) was introduced into Australia from Latin America. It spread rapidly from the original planting sites to occupy vast areas, transforming once valuable grazing lands into impenetrable spiny thickets. The economy of great stretches of the interior was severely threatened. The problem was solved when a species of cactus moth (*Cactoblastis cactorum*) native to South America, whose larvae feed on the cactus pads, was deliberately introduced into Australia. It spread through the cactus populations, drastically reducing but not completely eliminating them. The moth can scarcely be found today, even by a careful inspection of the few remaining cactus clumps; yet there is no doubt that it continues to exert a controlling influence over the populations of this plant (Figure 31–10).

The cactus moth story is one of the most famous examples of **biological control**, a technique that has been widely applied to other nuisance plant invaders. For example, control of purple loosestrife (*Lythrum salicaria*; see the Chapter 14 essay “Invasive Plants” on page 217), an aggressive invader of wetlands in the eastern United States, is being attempted by the introduction of European herbivorous insects, of which a leaf-feeding chrysomelid beetle (*Galerucella californiensis*) appears to be the most successful. As with the cactus moth, this species significantly reduces, but does not absolutely exterminate, populations of the nuisance plant. Within a community, the survival of small populations of the herbivores on pockets of the host plant ensures that if the plant starts to spread again, its herbivores will be present to control it.

In introducing new herbivores to areas where they were not naturally present, testing needs to be done to ensure that the introduced organism is specific to the targeted plant, to minimize the chance that it will attack native species. When the control species is a highly evolved specialist, it is assumed that there is no chance of its migrating to other plant species. It seems that this has generally been true, but some researchers have



(a)



(b)

31–10 Plant-herbivore interaction (a) Dense prickly pear cactus (*Opuntia inermis*) growing on a pasture in Queensland, Australia, in November 1926. (b) The same pasture in October 1929, after the cacti were destroyed by the deliberately introduced South American moth *Cactoblastis cactorum*. First introduced in May 1925, the larvae of this moth destroyed the cacti on more than 120 million hectares of rangeland.

documented cases of “escape” and recommend extreme care and exhaustive testing. In the case of the cactus moth, escape onto native species was unlikely, because there are no native cactus species in Australia, but now the moth is spreading rapidly from the West Indies across the southern United States, from Florida westward, posing a real danger to native cactus populations of the same genus.

Development and Change of Communities and Ecosystems

Living systems are dynamic—their continuing requirement for energy ensures that. Changes in the environment that affect the capacity of an ecosystem to accumulate and utilize energy will inevitably cause some degree of change in the system. Hypothetically, the closest approach to stability that can be expected is a constant supply of sunlight (or other source of fixable energy) and no disrupting events such as storms, earthquakes, landslides, or fire. In this case, a **steady state** could be approximated, with energy input equaling energy losses, and all ecosystem components at constant population levels. Some ecosystems can approach this state, but usually for only a limited time, and only when the condition of the system is averaged over areas large enough to include thousands of the largest organisms. The truth of these assertions will be evident to anyone who has tried to maintain an urban lawn in a steady state of green perfection. The most diligent regimen of care will not prevent the system from moving away from the desired steady state in ways that require intervention—mowing for sure, but also weeding, reseeding dead patches, perhaps discouraging moles or gophers.

One of the primary tasks of ecologists is to understand how systems change and to explain why some systems seem to evolve in more or less predictable ways to approach an approximate steady state, while others shift in unexpected ways or undergo cycles of destruction and rebuilding. Our understanding of these patterns can benefit from knowledge of the interactions we have discussed earlier—competition, predation, mutualism, parasitism, and decomposition. To see how this works, we can consider two contrasting but not mutually exclusive views of the ecosystem, which we can characterize as “cooperative” and “competitive.”

We may take the **cooperative model** to the extreme and postulate that a natural ecosystem is structured so that each of its component species gives and receives in equal amounts. In a forest, trees are primarily responsible for collecting and storing solar energy, while the smaller autotrophs use the remaining light that the trees cannot capture. According to the cooperative model, herbivores harvest some of the biomass, but not enough to cause irreparable harm to the photosynthesizers. Carnivores likewise take only their fair share, and decomposers clean up the detritus and release nutrients needed by the primary producers. Evolutionary processes adjust these givings and takings so that each species can get what it needs in perpetuity—an ideal steady state. The **competitive model** is closer to the formula “nature red in tooth and claw.” Each species exists because it has succeeded in an evolutionary and ecological struggle to grab the resources it needs. To do this, it has some allies—for example, its mitochondria and, in plants, its nitrogen-fixing bacterial symbionts—whose own evolutionary pathways have selected for cooperative (that is, mutualistic) tendencies. Typically, however, there are many more competitors and enemies than allies. Competitors are

after the same resources and must be either avoided or pushed aside. Enemies, such as parasites and pathogens, look for any opportunity to attack. That parasites and predators do not usually completely eliminate their hosts is not due to altruism, but because they are prevented from doing so by the imposition of disturbance factors or countermeasures by the hosts.

As often is the case, a middle ground seems the best resolution. Ecosystems exhibit cooperation and mutualism, but also competition and predation in its many variations. A given interaction is not “good” or “bad” but just two species doing what they can to survive. In what follows, you may see a tipping toward one or the other of these extremes—cooperation or competition.

Succession Is Predictable Change in a Community over Time

One of the major insights of the intellectual founders of ecology was that ecosystems often exhibit considerable resilience. Systems can be severely disturbed and yet return to something like their original condition. This predictable process of recovery after disturbance is called **succession**. The destructive activities of humans have provided many opportunities to observe succession in progress. Changes in agricultural economies led to the abandonment of fields, and if these were in or adjacent to natural vegetation, the fields reverted to their pre-agricultural condition. In forested regions, the sequence was from weedy field, to open grass or forb (nongrass) areas, to shrubby grasslands with tree seedlings, to forests of fast-growing trees, and ultimately to forests of longer-lived trees capable of establishing and persisting after the tree canopy was fully developed.

Early ecologists, most notably F. E. Clements, seized upon the process of succession as the centerpiece of ecological theory. According to this view, each part of the Earth had vegetation that developed in response to the climate of that region, and each had a characteristic steady-state system that was the end point of succession. This end point is what Clements called a “climax community.” Clements was emphasizing that a climax community, as the final stage of succession, was stable and self-maintaining unless subjected to very intense external disturbance. This view implicitly led to viewing the global landscape as made up of a set of potential or realized climax community types. Although human activities provided most of the clear examples of the recovery process, it was recognized that succession can also occur naturally. All communities experience disruptions of one kind or another from purely natural sources—fire, flood, windstorms, volcanic eruptions, extreme drought, unseasonal frost, ice storms, and unusual outbreaks of pathogens and herbivores, among others. To Clements, this capacity for healing and the ability to cohere, or hold together, over long periods of time conferred on the ecosystem (not a word he used) the status of a kind of super-organism. In this, he leaned toward the “cooperative” side of theories on the fundamental nature of ecosystems.

Echoes of Clements’s views persist, as in the **Gaia hypothesis**, which sees the biosphere as an organismal system with internal controls that keep it functioning within limits that favor its constituent species. But Clements’s system failed as a comprehensive theory of ecology. The main difficulty was that its emphasis on return to stability in response to disturbance, while

undoubtedly correct to a degree, did not easily accommodate systems such as floodplain forests or Mediterranean-climate chaparral, which are subject to recurring disturbances that keep them in a state of almost perpetual readjustment. Clements’s vision was too simple and too rigid to encompass all the complex ways in which ecosystems change. Successional theory remains just one element in a more general theory that accepts continual adjustment of ecosystems to prevailing conditions. In place of the organism-like concept that succession “heals” an injured climax community, ecologists speak of the more general properties of *resilience* (the ability of a system to return to its original state after disruption) and *stability* (the degree to which a system resists disturbances). The confidence of ecologists in the capacity of nature to heal has been shaken, and many now believe that ecosystems can undergo nearly irreversible change if pushed too far. Ecosystems will recover, but the new system may not be much like the old one.

Primary Succession Mostly Involves Changes in the Substrate for Growth

One source of ecosystem change arises from the physical processes of landscape evolution. This is very apparent in areas of the world engulfed by ice in the last glacial epoch, which, geologically speaking, ended only yesterday. Continental glaciers ground their way across landscapes, engulfing vast quantities of sediments, including giant boulders that were transported for hundreds of kilometers. When the glaciers melted, they dumped some of their burden as an unsorted mixture of rocks, gravel, sand, and fine sediments (till), or as sediments washed out by melting ice. The glaciers overrode and buried preexisting drainage networks and created lake and wetland complexes. The inexorable action of gravity ensures that many of these depressions gradually fill with sediment and organic debris. Sometimes this happens rapidly, sometimes slowly, and sometimes it is forestalled because of limited amounts of sediment from the glacier or because the depression is incorporated into a river system. Where it does occur, it is a kind of slow succession, beginning with the original lake developing marsh along its edges, then the marsh gradually closing in, and ending perhaps with forest cover over an area that 10,000 years earlier was a postglacial lake (Figure 31–11). In glaciated regions, one can see lakes, marshes, and swamps that exemplify the stages of the process, and paleoecologists have confirmed this by obtaining cores from swamps and marshes that were formerly open lakes.

In another example, geologic forces act to lift up rocks faster than the rocks can weather into soil (a volcanic eruption can do it almost instantaneously), and glaciers or other erosive forces can strip away surface debris to expose bedrock. These rock faces are not hospitable for higher plants, and exposed bedrock formed under extreme pressure and heat below the surface is not in equilibrium with the oxygen-enriched physical environment at the surface. Chemical weathering attacks the surface—rapidly for limestones and calcareous shales, and very slowly for resistant rocks such as quartzite. Freezing and thawing and other physical forces cause cracking and spalling. Some plants, especially lichens and mosses, are capable of enduring the extremes of heat, cold, and drought and so can establish on bare rock.



(a)



(b)



(c)



(d)

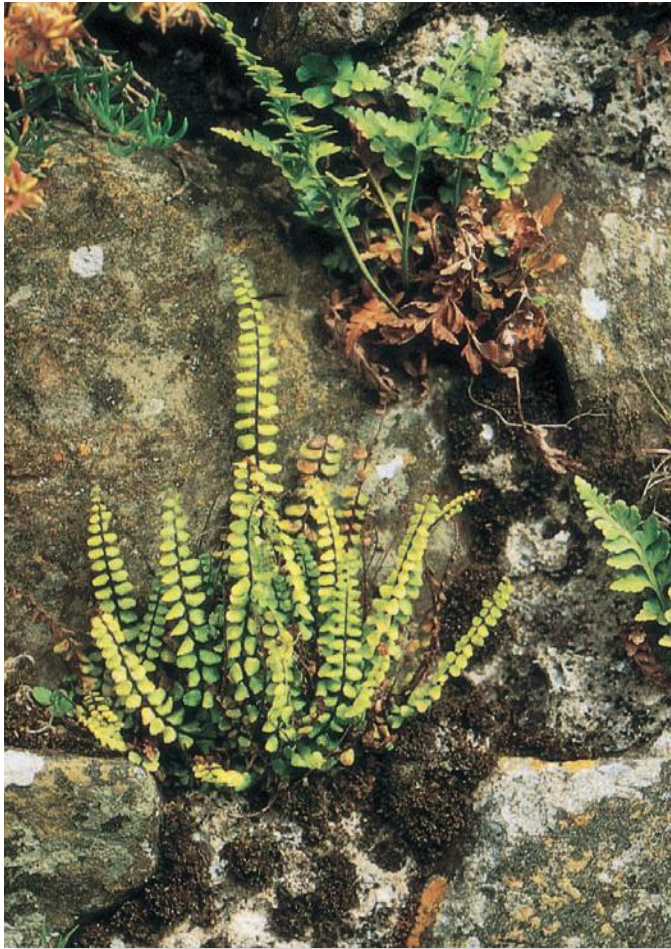
31-11 Succession (a) Emerging vegetation grows along the edge of a pond. (b) Aquatic plants with floating leaves, such as water lily (*Nymphaea odorata*), grow across the surface of a pond and eventually choke out bottom-dwelling plants. (c) Water hyacinths (*Eichhornia crassipes*) play a similar role in warmer climates. (d) Marsh grasses, sedges, and cattails (*Typha* spp.) growing on an old pond bed continue the process of succession.

They also hasten the dissolution of the rock by retaining water and secreting chemicals that erode the rock surface. The mosses, which expand when wet, continually break off little flakes of rock. Eventually, where the forces degrading the rock are not too severe (as is true on most vertical surfaces), soil develops around the bases of the lichens and mosses, providing a substrate that retains enough moisture and rooting space for ferns and flowering plants to become established (Figure 31-12). Their roots penetrate cracks, breaking the rocks down further.

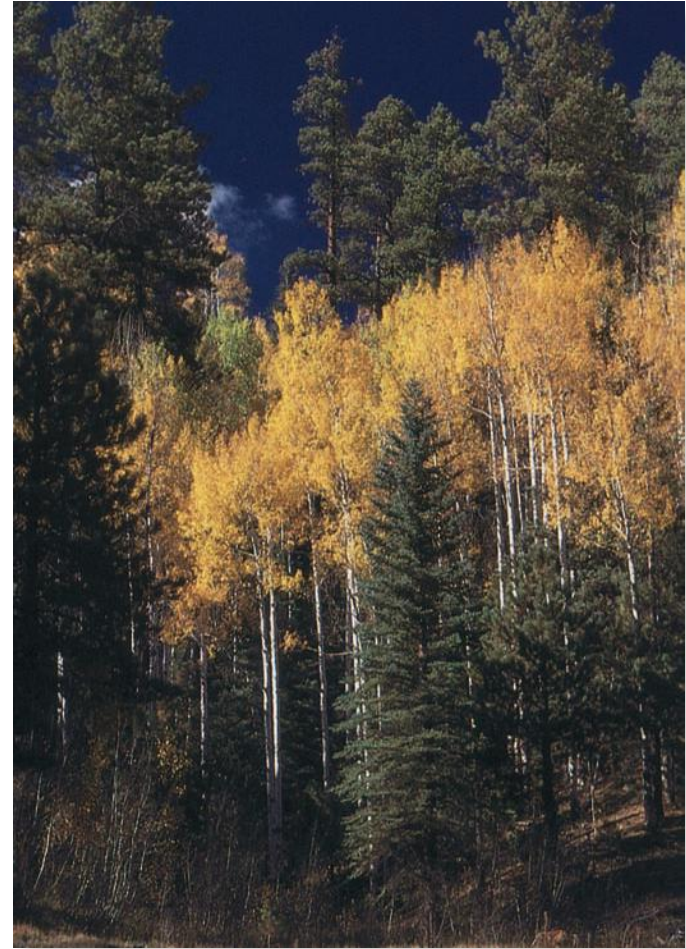
Over time, perhaps after many centuries, the rock may be completely transformed into soil in a process called *soil genesis*. By definition, this soil is a mixture of primary minerals derived from the rock, secondary minerals produced by soil-forming processes, most notably clay particles, and organic matter accumulated from the generations of organisms that have grown in the soil. Eventually there will be vertical differentiation in the soil. Often this is striking, with obvious color and texture differences. Sometimes it is subtle, with slight color change and almost imperceptible transformation between soil and the underlying nonsoil substrate of rock or sediment.

The soil is ultimately occupied by vegetation characteristic of the climatic region and adapted to the kind of soil that has developed. The process by which essentially barren areas are colonized is called “primary succession,” to distinguish it from “secondary succession” in which nearly all of the physical environment and some of the organisms survive the disturbance that disrupted the system. Another example of succession is shown in Figure 31-13.

Volcanic activity provides us with the most dramatic examples of succession on barren substrates. In August 1883, the Krakatau island group in Indonesia was the site of a massive eruption that, among other effects, split the main island (Pulau Rakata), causing half to sink into the sea and covering the remaining half with 60 to 80 meters of ash. The existing vegetation—lush evergreen tropical forest—was completely destroyed. Recolonization on Pulau Rakata began as soon as the volcanic surface cooled. The bird population recovered quickly, with about 30 species of land and freshwater birds present within about 30 years. Recolonization by plants also proceeded rapidly. Three years after the disaster, there was a relatively



31–12 Early stage of succession Lichens have begun to erode the rocks, while ferns and bryophytes are accumulating soil in a small crevice.



31–13 Forest succession Seedling trees of white fir (*Abies concolor*) growing under and replacing quaking aspen (*Populus tremuloides*) in northern Arizona—a stage in forest succession that will lead to the formation of a community of Engelmann spruce (*Picea engelmannii*) and white fir.

well-developed but species-poor beach vegetation, with at least nine species, including herbs, a grass, a vine, and several shrubs. But inland, the vegetation was extremely sparse. A mat of cyanobacteria was observed on the surface of the ash. Several species of ferns were the most common large plants, and they tended to occur in scattered locations. By 1934, more than 270 species of plants were recorded. In the 1980s, 100 years after the eruption, the island was essentially covered with forest, though with fewer species than on adjacent, undisturbed islands.

Similar changes followed the catastrophic eruption of Mount St. Helens in Washington State on May 18, 1980. A massive avalanche of volcanic debris from the top and north side of the mountain poured into the North Toutle River Valley. Within 15 minutes, more than 61,000 hectares of forest and recreational land were devastated by the lateral blast, which leveled forests on much of the area but left dead trees standing in others. In addition, the nine-hour eruption covered the whole area with up to 0.5 meter of ash, pumice, and rock, pulverized by the blast. Much of this debris soon eroded off, and wind-dispersed seeds and fruits blew into the area. Such dispersal was especially

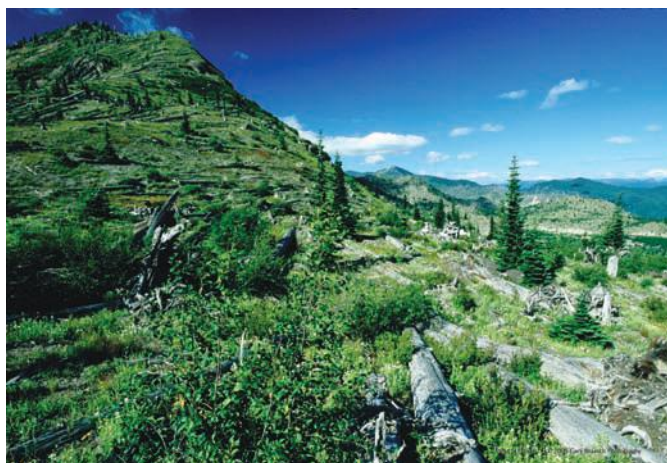
important on volcanic flows and in areas buried by debris avalanches so deep that they killed the plants beneath. Many small nocturnal animals, such as mice and voles, survived in their underground tunnels, and within a few years, frogs and toads reappeared in the lakes and streams. Large terrestrial vertebrates, such as elk, moved back into the area. The pioneer plant species was lupine, a legume that added nitrogen to the soil, which had been sterilized by the extreme heat. Other plants were then able to establish (Figure 31–14).

Succession Blends into Change in General, Particularly in Its Later Stages

Massive disturbance sets in motion the kind of obvious and large-scale changes that clearly deserve to be called succession. But as the ecosystem recovers, it eventually enters a condition in which changes are not so easily detected. When a forest canopy is filled by shade-tolerant species of trees capable of producing seedlings that can establish and survive in the understory, no significant shifts in the dominant species can be expected without



(a)



(b)

31-14 Recovery after devastation When Mount St. Helens erupted in the spring of 1980, shock waves leveled all of the trees in a heavily forested area of about 21,000 hectares, and a deep layer of ash was deposited. These two photographs, taken 23 years apart—in 1982 (**a**) and 2005 (**b**)—show a striking recolonization of the area by conifers, grasses, and other plants.

major disturbance. But this does not mean that change ceases. Rather, it moves to a new mode in which change is dominated by scattered small and medium-sized disturbances that open gaps in the canopy. Because these processes are slow relative to human life spans, and because they occur in scattered locations, it is difficult to grasp the significance of these **gap** processes. Gaps are inevitable in forests, even those closest to the ideal climax condition, according to the inexorable principle that what goes up must come down. If a tree dies in place, it can fall apart bit by bit; but more commonly, at some point the entire tree will come down. If a large tree is blown over, it usually damages adjacent trees and often takes down other trees as it crashes to the ground.

The production of gaps is usually, or at least often, a nearly random process in terms of where it occurs. Severe windstorms can produce much larger gaps that will be spatially clustered. Some bamboos die synchronously over large areas after flowering, responding to an internal clock, and this produces large gaps in the vegetation. Whatever the pattern, the expected frequency with which canopy gaps occur can be represented by “turnover time” (area under study divided by the average area of gaps appearing in a year), which gives the time in years for the entire area to be “turned over” by formation of a gap. This gives a rough idea of the amount of time one would have to wait in one spot before a gap appeared. Ecologists have estimated this time to be between 60 and 250 years in tropical forests and about 100 years in temperate deciduous forests.

When a gap appears, there is an opportunity for seedlings and saplings already in the understory (members of the “seedling bank”) to grow into the canopy. Or new individuals can establish either from seeds already in the soil (in the “seed bank”) or from newly dispersed seeds. Plants originating from the seedling bank have the greatest advantage if the gap is small. If a gap is large enough, there may be sufficient light and perhaps some mineral soil exposed by uprooted trees so that fast-growing invaders can become established and survive to take a place in the canopy.

When this occurs, there will be a recapitulation in miniature of the successional sequence that established the climax forest after a major disturbance many years in the past. But in many instances, one of the shade-tolerant species in the seedling bank will eventually dominate the gap. This latter case is a dynamic that could produce the kind of long-term steady state of composition postulated by Clements to describe climax vegetation.

There is some evidence, however, for the switching of dominance, with species B replacing species A, and in the next cycle, A replacing B. Why should this occur? One explanation is that if species A is abundant at one point, as would be the case for a single large canopy tree, then parasites and predators of that species and of its seedlings and saplings will also be abundant. Species B, less abundant at that point, would not be as afflicted. As a result, probabilities would favor B replacing A—and vice versa in the next cycle. But there is also evidence that replacement in a gap is governed more by chance than by specific qualities of the species available for replacement. According to this so-called neutral theory, it is the local abundance of species that determines which one has the highest probability of invading a gap. Hubbell and colleagues have shown that starting from simple, “neutral” assumptions leads to predictions of species abundance that correspond well with historical data on tropical forests in Panama.

The concept of gap applies beyond forests. In prairies, for example, although no gaps are produced by “grass falls,” similar disturbances are caused by ground-inhabiting mammals, such as badgers, ground squirrels, pocket gophers, and prairie dogs. Digging for food and building burrows, these animals create areas of bare soil that provide habitats for species that will occupy them until overgrown again. These bare soil gaps create local habitats in which annual ragweed (*Ambrosia artemisiifolia*), for example, can germinate and survive for one or more generations before the gap is recaptured by other, dominant perennial species. Large grazers, such as the American bison, can also open up prairie canopies in a variety of ways (for example, buffalo wallows, used for

dust baths) and provide similar opportunities for gap-exploiting species. Before pervasive human disturbances, gap processes of this kind were probably the major type of change in grasslands. Many of our widespread weedy species most likely originated from species that inhabited small disturbed patches opportunistically, before human disturbance made habitats of this sort widespread.

Another way to create gaps in communities is by burning them, and fire is one of the most significant forms of natural disturbance affecting plant communities (Figure 31–15). We say “natural” because there is no doubt that fire from lightning was a factor before humans learned to rub two sticks together. But after they did gain this knowledge, humans used it extensively. For this reason, it is difficult to know what world vegetation might have looked like before humans began to burn it regularly. We know relatively little about the patterns that early humans created, but their activities certainly had widespread effects.

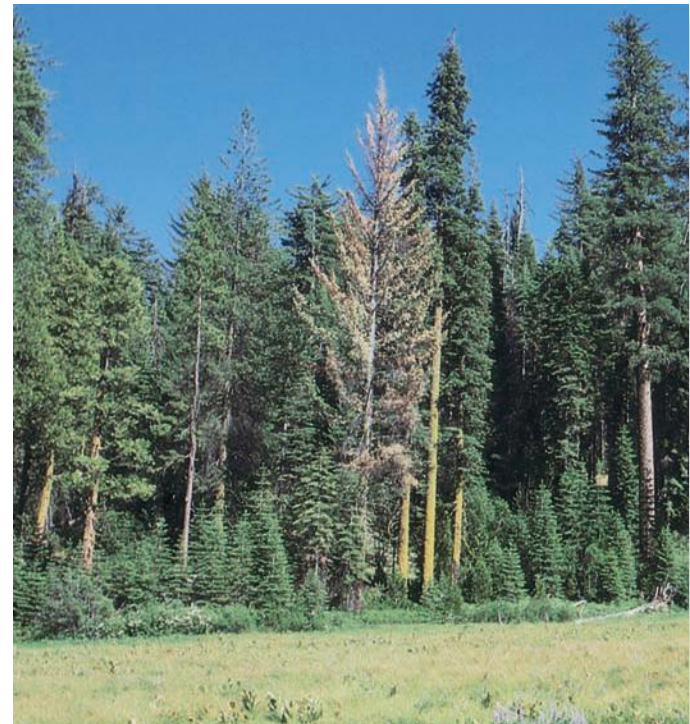
When European settlers first arrived in California, for example, they found magnificent forests of sugar pine (*Pinus lambertiana*) along much of the length of the Sierra Nevada. Although some of these forests were preserved on public lands, sugar pine populations overall decreased, and in many places were replaced by other species, such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*). Why did this change take place?

Sugar pine was a member of a successional stage in the forests of this region that was maintained by periodic fires. These fires were greatly reduced in number and scope after the influx of settlers to the area. Without low-intensity lightning-set fires periodically racing through the groves, a thick growth of brush and smaller trees grew up, evidently creating conditions so shady that sugar pine seedlings could not compete effectively. Many attribute this kind of change to past policies of strict fire exclusion and advocate a program of controlled burns or letting occasional wildfires burn themselves out, or both (Figure 31–15b). In recent decades, however, the western United States has been plagued by large destructive fires that in some places have seriously depleted the populations of pines, sugar pine included. It remains to be seen how long it will take these forests to recover, especially considering that climate scientists predict that human-driven climatic changes promise to make large fires more common.

For Tecate cypress (*Cupressus forbesii*), which grows in the coastal mountains from Orange County, California, south into Baja California, too much fire can be a problem. This species is a “closed-cone conifer,” meaning that it has **serotinous** cones that do not open at maturity but require the heat of a fire for seed release. Since even the largest individuals are also very sensitive to heat, and their canopies are highly flammable and usually close to the ground, a wildfire generally kills all the



(a)



(b)

31–15 Recolonization after forest fire (a) When fire sweeps through a forest, recolonization—with regeneration from nearby unburned stands of vegetation—is initiated. Some plants produce sprouts from the base, others seed abundantly on the burned area. In one group of pines, the closed-cone (serotinous) pines, the cones do not open to release their seeds until they have been exposed to fire. (b) Sugar pines (*Pinus lambertiana*), seen here in Yosemite National Park in California, require periodic fires to reduce the brush and smaller trees that compete with the sugar pine seedlings for light. Limiting or preventing fires has allowed other species, such as the white fir (*Abies concolor*) seen here growing at the base of the stately sugar pines, to replace them.

established plants, and regeneration is entirely dependent on establishment from seeds stored in the cones. If fires occur after the plants have accumulated a crop of seeds sufficient to replace the individuals killed, all is well. But if a fire occurs before seed production has started or before enough seed has accumulated, the population can be virtually wiped out in a single fire. This kind of catastrophic decrease has occurred in several stands of Tecate cypress, especially along the United States–Mexico border regions, where fires have been more frequent than was historically the case.

Humans can cause damage by allowing either too many or too few fires. The challenge in going forward is to adjust, to the extent that we can, the recurrence time of fires for each vegetation type. But a problem is that many fires are the result of arson or careless use of fire, and so limiting fire occurrence becomes mostly a social problem rather than a strictly ecological one.

The recent episode of regional dieback in pinyon (mostly *Pinus edulis*) and juniper (mostly *Juniperus monosperma*) provides a dramatic example of how change can involve processes that do not conform to a simplistic view of succession. Pinyon-juniper woodlands cover millions of hectares of land in the southwestern United States. In the early years of this century, and especially in 2002, this region experienced severe droughts. The stress caused by a lack of soil water was the cause of severe tree mortality across the region. In some places, 100 percent of the pinyon and juniper trees died; in many places, mortality exceeded 50 percent. Attack by insects, especially the pinyon ips bark beetle (*Ips confusus*), facilitated by the weakened defenses of the trees, seems to have been the final blow that killed many of the trees. No one doubts that many decades, perhaps centuries, will be required for the stands to recover, assuming that no droughts of similar severity recur. But unlike the series of successional stages expected in, say, a deciduous forest that has been burned or blown down, the process will mostly involve the slow reestablishment of pinyons and junipers surviving here and there on the site. There are also serious questions about whether global climate change will prevent full recovery, because droughts as severe or even more severe are expected to occur in the future. If this happens, much of the area formerly dominated by pinyon and juniper will convert to a more drought-resistant kind of vegetation.

Restoration Ecology Reestablishes Natural Communities

In much of the discussion above, we have dealt with “natural” communities, meaning ecosystems in which human influence can be ignored. Ecologists have been criticized for this. Many people take the view that the global ecosystem is to humans as an automobile is to its driver. Like the automobile, the global ecosystem is a human construct. We, the human species, are in control and can direct the global machine where we like. There is no doubt that science and technology have made amazing advances that permit us to shape the environment to serve our species. But there are plenty of signs that we may be approaching limits in our ability to maintain our present system—of which the eventual depletion of readily available fossil fuels is the most stark and undeniable. The precautionary principle suggests that we should be careful about overestimating our ability to control. This is the basis for the argument that we should allow natural processes maximum freedom, and natural systems maximum

scope. We know that a good-sized tropical rainforest or prairie will function in a more or less predictable manner in perpetuity, with little or no management. Both will contribute to global balances of water and carbon and will be capable of recovering from unusual disturbances without assistance. The greater the proportion of our landscapes that exists in such self-maintaining states, the easier our task becomes for managing the lands that we use intensively, such as our annually plowed croplands and our concrete cityscapes.

This is an argument to save as much of the surviving natural lands as possible. But this is not our only option. We can also convert disturbed lands back toward the natural systems they once supported. In recent decades, the science of **restoration ecology** has arisen to explore the best ways of doing this. It is often not a simple matter to recreate natural communities once they have been destroyed; yet the process is one of great significance to an increasingly overcrowded world. A well-known example of restoration ecology was developed at the University of Wisconsin Arboretum in Madison (Figure 31–16). Beginning in 1934 on damaged agricultural land, an effort was made by its first research director, Aldo Leopold, to recreate all of the natural communities of Wisconsin. Among these were a tall grass prairie, a dry prairie, and several types of forest communities. While restoration can be a costly and uncertain process, it provides a way of going on the offensive in the struggle to ensure the survival of native ecosystems and the plants and animals within them. The Arboretum’s restored Curtis Prairie, for example, now supports more than 200 species of native plants, many of them rare in the area.

Although the main rationale for restoration ecology is preservation of native biodiversity and the ecological services they provide—clean air and clean water, among others—restoration also provides us with opportunities to learn how ecosystems function. An example of this is the early work on the Curtis Prairie, which provided insights into the importance of fire for prairie ecosystems. In many parts of North America, the persistence of prairie depends on recurrent fires. Before European colonists moved in large numbers into these landscapes, the prairies were burned by fires, some natural and some deliberately set by Native Americans. If periodic burning does not take place, a prairie may be taken over by trees or shrubs, with the sun-requiring prairie flora largely shaded out. In fact, a prairie may be regarded as an ecosystem that “uses” fire to maintain itself against encroachment by non-prairie species. Although fire played an important role in the management of vegetation in many areas even after settlement, the ecological significance of this was not understood until relatively recently. Attempts to restore prairies, such as the Curtis Prairie, have played a key part in clarifying this role.

In a parallel way, our understanding of the role of fire in the forest ecosystems of the mountains of the western United States has also advanced in recent decades. Some forest types—lodgepole pine, for example—function like the Tecate cypress and are periodically destroyed by fire, but they recover quickly from seed. Of interest from the restoration point of view, however, are the forest systems dominated by ponderosa pine and ecologically similar species. Historically, these systems were quite open, with mostly large trees and an understory of grasses and low shrubs. Fires were frequent, but they burned in the flammable understory while the thick-barked trees were typically left



(a)



(b)

31–16 Habitat restoration (a) Late summer on a restored prairie in Wisconsin, with purple blazing star (*Liatris pycnostachya*), white flowering spurge (*Euphorbia corollata*), and yellow pinnate prairie coneflower (*Ratibida pinnata*). (b) A controlled burn is carried out in a prairie-restoration program in early August at a preserve in southwest Washington State.

without permanent harm. When the U.S. Forest Service decided that fire was a threat that had to be suppressed, populations of shade-tolerant species, such as white fir, expanded and created very different fuel conditions. Instead of just low grasses and shrubs in this ecosystem, the invading trees are present as small seedlings, sapling-sized individuals, and trees that reach into the canopy. In these conditions, fires now tend to “crown,” spreading up into and then across the tree canopies to cause raging infernos that kill the trees. Unlike the closed-cone conifers, ponderosa pines have little seed reserve to reoccupy burned-over lands, and recovery is patchy.

Foresters now generally agree that there is a need to “restore” these systems, where “restoration” means returning the forests to the historical pattern, with frequent understory fires. The challenge to this kind of restoration is that it cannot simply be done by allowing fires to burn, because with the present forest structure, it is difficult, perhaps impossible, for fires to remain confined to the ground layers. Thus it may be necessary to artificially thin the forests by removing small-diameter trees to promote the growth of grasses, forbs, and small shrubs and to allow understory fires to spread. Restoration means not only the planting of missing species, as was done to recreate prairie in the University of Wisconsin Arboretum, but also the removal of species, and the reintroduction of periodic understory fires.

What Have We Learned?

Ecology has raised awareness of important principles that are crucial to human management of our global home. The first principle is dynamism. Change is inevitable, and there has never been, and never will be, a true equilibrium. Theory and observation also tell us that not all change is gradual and, most definitely, not always favorable to humans.

The second principle central to managing our environment is that of diversity and complexity. The more we study, the more layers of complexity we uncover. We don’t fully understand why

there are so many species, but in keeping with the dictum of Aldo Leopold, that “to keep every cog and wheel is the first precaution of intelligent tinkering,” it would seem foolish to let them disappear before we do.

The third principle is connectedness. The global ecosystem and its local subsystems depend on flows and cycles. Every species is connected through multiple interactions with other species, and many of these relationships are mutually beneficial ecologically, if not always for the individual organism. (Both beefsteak and broccoli are obtained by the death of an individual, which requires that we also cultivate and sustain the populations from which we sacrifice individuals.)

The fourth principle is that abstract theory and models, even complex ones, cannot capture everything about ecosystems. Our knowledge is partial, provisional, and, like ecosystems themselves, constantly evolving; and it requires that we venture out and learn more about nature in order to advance it.

SUMMARY

An Ecosystem Consists of a Biotic Community and Its Environment

Ecosystems are self-sustaining systems that include living organisms and the nonliving (physical) elements of the environment with which they interact. Communities consist of all the organisms that live in a particular area.

The Living Components of an Ecosystem Are the Primary Producers, Consumers, and Decomposers

The living elements of an ecosystem belong to two major groups: autotrophs (primary producers) and heterotrophs (consumers). Among the heterotrophs are the primary consumers, or herbivores; the secondary consumers, or carnivores and parasites; and

the decomposers. The organisms found at these levels are members of food chains or food webs.

The Flow of Energy through an Ecosystem Affects the Mass and Number of Its Component Organisms

Energy flows through ecosystems, with 1 percent or less of the incident solar energy converted into chemical energy by green plants. When these plants are consumed, about 10 percent of their potential energy is stored at the next trophic level; a similar degree of efficiency characterizes each transfer up the food chain. The amount of energy remaining after several transfers is so small that food chains are rarely more than four to six links long. In most ecosystems, more energy, biomass, and individuals occur at lower trophic levels, giving rise to “pyramids” of energy, biomass, and numbers.

Hubbard Brook Has Provided an Outdoor Laboratory for Studying Nutrient Cycling

The properties of ecosystems have been studied experimentally on a large scale at Hubbard Brook, in New Hampshire, where it has been shown that undisturbed natural communities control the cycling of nutrients, but the control tends to be lost when the ecosystem is disturbed.

Competition Results When Organisms Require the Same Limited Resource

Competitive interactions occur between plants that grow in close proximity. The principle of competitive exclusion states that when individuals of two different species occur together and compete for the same limiting resources, ultimately, only one species will survive. Nevertheless, most communities contain many species. This can be explained in part by specialization to avoid intense competition or the slow action of competitive exclusion when plants are well matched and disturbances frequently readjust the conditions, or both. For plants, competition for light is of special importance. In the course of evolution, plants have also developed chemical weapons to inhibit nearby competitors.

Mutualism Is a Relationship That Benefits Both Species

In mutualism, two species interact to the benefit of both. Examples include lichens, mycorrhizal associations between fungi and the roots of plants, and the relationships between flowering plants and their pollinators and fruit and seed dispersers. The bull’s-horn acacias of Latin America provide an example of apparent mutualistic coevolution of ant species and a plant.

Plants Have a Variety of Physical and Chemical Defense Mechanisms against Herbivores

Plants counter the effects of herbivores, which limit the reproductive potential of the plants, through the evolution of spines, tough leaves, and similar structures or structural alterations, and, most important, chemical defenses. An insect or other herbivore that has overcome a plant’s chemical defenses not only has a new and

often largely untapped food resource at its disposal but also can utilize the toxic substances produced by the plant to gain a degree of protection from its own predators.

Succession Is the Change in a Community over Time

Succession is the process of orderly and more or less predictable change in the structure and species composition of ecosystems following disturbance (secondary succession) or proceeding as a habitat evolves, due to biotic and physical forces (primary succession). In the course of succession, the kinds of plants and animals inhabiting the area change continuously, some being characteristic of only the early stages of succession. The creation and refilling of gaps caused by natural disturbances plays a key role in the process of succession and in the maintenance of species diversity in various forest communities. At one time, ecologists viewed succession as resulting in a stable climax community, but now they speak of resilience (a system’s ability to return to its original state after disruption) and stability (the degree to which a system will resist disturbances). The current thinking is that ecosystems can also undergo catastrophic change when profoundly disturbed, so that their recovery leads to a different ultimate state. Fire is the most common natural disturbance that initiates successional change, but it has been used by humans presumably since they mastered the ability to start fires. Volcanic eruptions, such as those of Krakatau in 1883 or Mount St. Helens in 1980, provide dramatic examples of successional processes.

QUESTIONS

1. Why are food chains generally limited to four to six links?
2. In general, ecosystems can be described by pyramids of energy, biomass, and numbers. Explain.
3. Comment on the importance of plants in the retention of nutrients in forest ecosystems.
4. Explain the role of growth rate in the competition among plants.
5. According to the principle of competitive exclusion, two species with similar environmental requirements cannot coexist indefinitely in the same habitat. How might competitive exclusion be avoided?
6. The diversity of species is greater in an environment where disturbance is continuous than in a more stable environment. Why?
7. In what way does the ant-acacia system resemble a lichen?
8. Explain the role of tannins in the defense of plants against herbivores.
9. Disturbance and succession are two important factors that account for the full extent of the diversity of life on Earth. Explain.
10. What role do gaps play in succession?
11. How does a plant community change over time?
12. List the important ways that humans have affected local and global ecosystems, including modifying disturbance types and cycles. Will such effects grow or diminish over the coming years?

PHOTO CREDITS

Chapter Opener MJ Cooper/www.fotosearch.com; **31.1** Brand X Pictures/www.fotosearch.com; **31.6** Tifonimages/Shutterstock; **31.7** G. E. Likens; **31.9a** N. H. Cheatham/DRK Photo; **31.9b** Michael Fogden/DRK Photo; **31.10** Australian Department of Lands; **31.11a** Fred Bavendam/Peter Arnold, Inc.; **31.11b** Wendell

Metzen/Peter Arnold, Inc.; **31.11c** James H. Carmichael/Bruce Coleman, Inc.; **31.11d** L. West/Bruce Coleman, Inc.; **31.12** Jane Burton/Bruce Coleman, Inc.; **31.13** Bruce Coleman, Inc.; **31.14** Gary Braasch; **31.15a** J. Dermid; **31.15b** E. S. Ross; **31.16a** Keith Wendt/UW Arboretum; **31.16b** Bruce Richter/University of Wisconsin–Madison.