



Focus on the Biota

Metabolism, Ecosystems, and Biodiversity

Key Questions

- What are the characteristics of life on Earth that allow it to interact with physical processes at the global scale in such a significant way that it creates a habitable planet?
- How is the biosphere structured?
- How is energy transferred within the biosphere?

- What is an ecosystem?
- What is biodiversity and how is it measured?
- How is the diversity of interactions between the biota and the physical world related to the stability of the Earth system?

Chapter Overview

In this chapter we highlight the role that life plays in the operation of the Earth system. We begin with a general discussion of life and its unique characteristics, and then explore the varied metabolic pathways different forms of life take to grow and reproduce. Organisms interact at a variety of scales, so we find that populations of organisms group into communities, which at a larger scale interact among themselves and with their environment in ecosystems. The level of diversity of ecosystems can be expressed in a variety of ways. We can simply count the number of species or we can take into account the more complex diversity of interactions that take place between species and between organisms and their environment. This diversity of interactions, a defining characteristic of life on Earth, is important in our understanding of the feedbacks between the biota and the physical world that create a habitable planet, and helps us further understand the complexity of the Earth system.

LIFE ON EARTH

Characteristics of Life

Earth is unique among the planets in our solar system in that it apparently is the only one to support life. Earth more than supports life, it flaunts it. Life is involved in almost every process occurring at the surface of the planet. Some fundamental characteristics of life allow it to have such an influence.

- **Life spreads exponentially.** The rate of population growth depends on the number of individuals reproducing at a particular time. This characteristic leads to the phenomenon of *exponential growth*. If left unchecked, 2 individuals become 4 in one generation, 4 become 8 in two generations, 8 become 16 in three generations, and 16 become 32 in four generations. In nature, however, exponential growth ceases as resources become limiting.
- **Life needs energy.** Photosynthesizers use solar energy, *chemosynthesizers* use chemical energy, and most other organisms utilize the chemical

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energy that is packaged into the material produced by photosynthesizers and chemosynthesizers.

- **Life pollutes.** Every organism needs to metabolize, and when it does so, it releases waste products. These waste products can be of use to other organisms, and they may affect the environment (e.g., the release of the greenhouse gases CO_2 and CH_4 through respiration and decomposition).
- **Life is versatile.** There is considerable versatility in how organisms interact with each other and with the environment. Plants and animals exist in a variety of forms and express various behaviors. But their versatility is modest compared to that of microbes. Microbes express a wide array of metabolic activities that have tremendous impact on the environment and allow them to occupy a wider range of environments than eukaryotes.

All these characteristics of life allow it to interact with the physical processes that occur on the planet in such a way that Earth is a habitable planet. Let's explore this in more detail by developing a classification scheme for life that is based on metabolic rather than genetic similarities, and is structured around the flow of energy through the ecosystem.

Autotrophs and Heterotrophs

Although life can be categorized *taxonomically* (according to species, genera, families, etc.), a classification system that focuses on the ways in which organisms obtain energy and metabolize it is more useful from an Earth systems point of view (Table 1). The most fundamental dis-

inction is between those organisms that grow using a source of energy to reduce carbon dioxide to organic carbon (primary producers or **autotrophs**) and those that require organic matter to grow (consumers or **heterotrophs**). Autotrophs include plants, algae, and a host of microbes that can photosynthesize (e.g., cyanobacteria, purple and green sulfur bacteria) or chemosynthesize (e.g., colorless sulfur bacteria). These autotrophic organisms produce organic matter from inorganic carbon sources, a process that requires energy (i.e., the chemical reactions do not occur spontaneously in nature). In the case of photosynthesis, the sun provides the necessary energy. In chemosynthesis, energy-releasing inorganic chemical reactions (those that occur even without the involvement of organisms *because* they release energy), often involving oxygen and reduced compounds, are the energy source. Chemosynthesis is the mechanism of primary production of the mid-ocean-ridge hydrothermal vent communities that exist at great depths in the ocean where sunlight does not penetrate. The organic material that autotrophs produce is a storehouse of energy, and will decompose *abiotically* (without the intervention of organisms), albeit at a slow rate, releasing that energy as heat. Heterotrophs simply accelerate these chemical reactions that would otherwise proceed at a slower pace abiotically, and in doing so, gain the energy they need to grow and reproduce.

The heterotrophic pathway that releases the most energy is aerobic respiration, which uses molecular oxygen to decompose organic matter through the process of oxidation, converting the organic carbon to carbon dioxide. In

TABLE 1 Metabolic Pathways for Life

General Method for Acquiring Energy	Specific Pathway	Subcategory	Reactants	Byproducts
Autotrophy	Photosynthesis	Oxygenic Anoxygenic	Solar energy, CO_2 H_2O Molecular hydrogen (H_2), reduced sulfur or reduced iron	Molecular oxygen (O_2) Oxidized sulfur (native sulfur or sulfate), iron oxide (solid)
	Chemosynthesis		H_2 , reduced forms of sulfur, nitrogen, iron or manganese	Oxidized sulfur, nitrate, iron and manganese oxides (solids)
Heterotrophy	Aerobic Respiration Anaerobic Respiration		Organic matter O_2 Nitrate, sulfate, iron and manganese oxides	CO_2 , H_2O CO_2 and molecular nitrogen, ammonia, hydrogen sulfide, reduced and dissolved iron and manganese
	Fermentation		Complex organic molecules	Simple organic molecules

Source: K. H. Nealson and D. A. Stahl, *Geomicrobiology, Interactions between Microbes and Mineral* (Chapter 1). Reviews in *Mineralogy* 35, 1997, pp. 5-34.

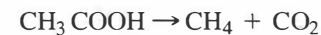
environments where oxygen isn't present (e.g., in muds on the seafloor and lake bottoms, and in the guts of animals), anaerobic heterotrophs, especially bacteria, substitute other oxidized inorganic compounds in lieu of oxygen to decompose the organic matter. Bacteria use such oxidants as dissolved nitrate (through a process known as *denitrification*) or sulfate (sulfate reduction) or particulate metal oxides of iron and manganese. Other heterotrophic organisms (certain fungi such as yeasts and some bacteria) perform fermentation, an important process that breaks down large, complex organic compounds into simpler ones that can be used by other heterotrophs. Fermenters do not oxidize organic matter, but they are able to utilize the energy that is released when complex organic materials are broken apart.

Methanogenic bacteria are an important group of organisms for our consideration of the Earth system, in particular because they may have been very significant in biogeochemical cycling on the early Earth and because they produce an especially effective greenhouse gas, methane (CH_4), through their metabolism. In fact, the word *methanogenic* means methane-producing. Methanogens can be either autotrophic or heterotrophic:

Autotrophic methanogenesis:



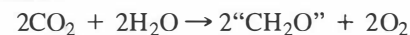
Heterotrophic methanogenesis:



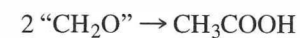
Autotrophic methanogenesis takes advantage of the energy yield of the chemical reaction between carbon dioxide and molecular hydrogen (H_2) when H_2 concentrations are relatively high, a situation that currently occurs in organic-rich muds and may have also occurred on the early Earth surface. Heterotrophic methanogens utilize the simpler carbohydrates (such as acetic acid, CH_3COOH , shown above) produced through fermentation. Both pathways produce methane, and heterotrophic methanogenesis produces both methane and carbon dioxide. Given their global abundance, it is clear that these bacteria can have a significant impact on the greenhouse effect.

Moreover, as James Lovelock pointed out long ago, the combined activity of methanogens (such as methanogenic bacteria) and oxygenic photosynthesizers (such as plants), which produce the organic matter that the fermenters convert to acetic acid, releases both oxygen and methane to the atmosphere. We can represent this chemically:

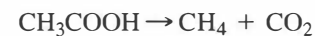
Oxygenic photosynthesis:



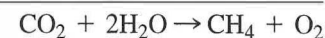
Fermentation:



Heterotrophic methanogenesis:



NET:



The net effect of these coupled processes creates an unstable, highly reactive, far-from-chemical-equilibrium atmosphere that is as strong a signature of life on our planet as any other. Equally amazing is the dynamic stability of this reactive atmosphere. Aerobic life has persisted on Earth for hundreds of millions of years, indicating that the atmosphere has remained oxygen-rich through this interval of Earth history. Strong feedbacks must exist to maintain atmospheric compositions over geologic time intervals. As you will see in the following discussion of ecosystems, the constant and complex interaction between all living things on Earth contributes to the atmospheric conditions that are key to the stability of the Earth system.

STRUCTURE OF THE BIOSPHERE

The metabolic processes we have just described represent the main ways in which organisms interact with other species and with their environment. These interactions are not random. Rather, they make up higher levels of organization that we can recognize and study. The *biosphere* comprises that part of Earth inhabited by organisms; it includes both living and nonliving components. A simple hierarchy has been developed that subdivides the biosphere (Figure 1). The smallest subunit is the *species*, which consists of all closely related organisms that can potentially interbreed. (Note that this definition applies only to species that reproduce sexually.) All the members of a single species that live in a given area make up a **population**. In any area you will tend to find a characteristic assemblage of two or more groups of interacting species, known as a **community**. A community may include any combination of animals, plants, fungi, and microbes. A region with a characteristic plant community (such as a desert or tropical rainforest) is called a **biome**. A community of animals, plants, fungi, and microbes, together with the physical environment that supports it, is referred to as an **ecosystem**. All the ecosystems on Earth in turn make up the biosphere. Although it is usual to discuss biodiversity and extinction in terms of species, it is important to recognize that no one species exists independent of the other species around it. Species coexist and interact with a specific assemblage of other species and with their environment in ecosystems.

ECOSYSTEMS

What Are Ecosystems?

As we have said, ecosystems are subsets of the (global) biosphere, assemblages of animal, plant, fungal, and microbial species that interact with each other and their surrounding environment (see "Species Interactions," below). For terrestrial ecosystems the environment includes the topography, soils, atmosphere, and climate. For aquatic

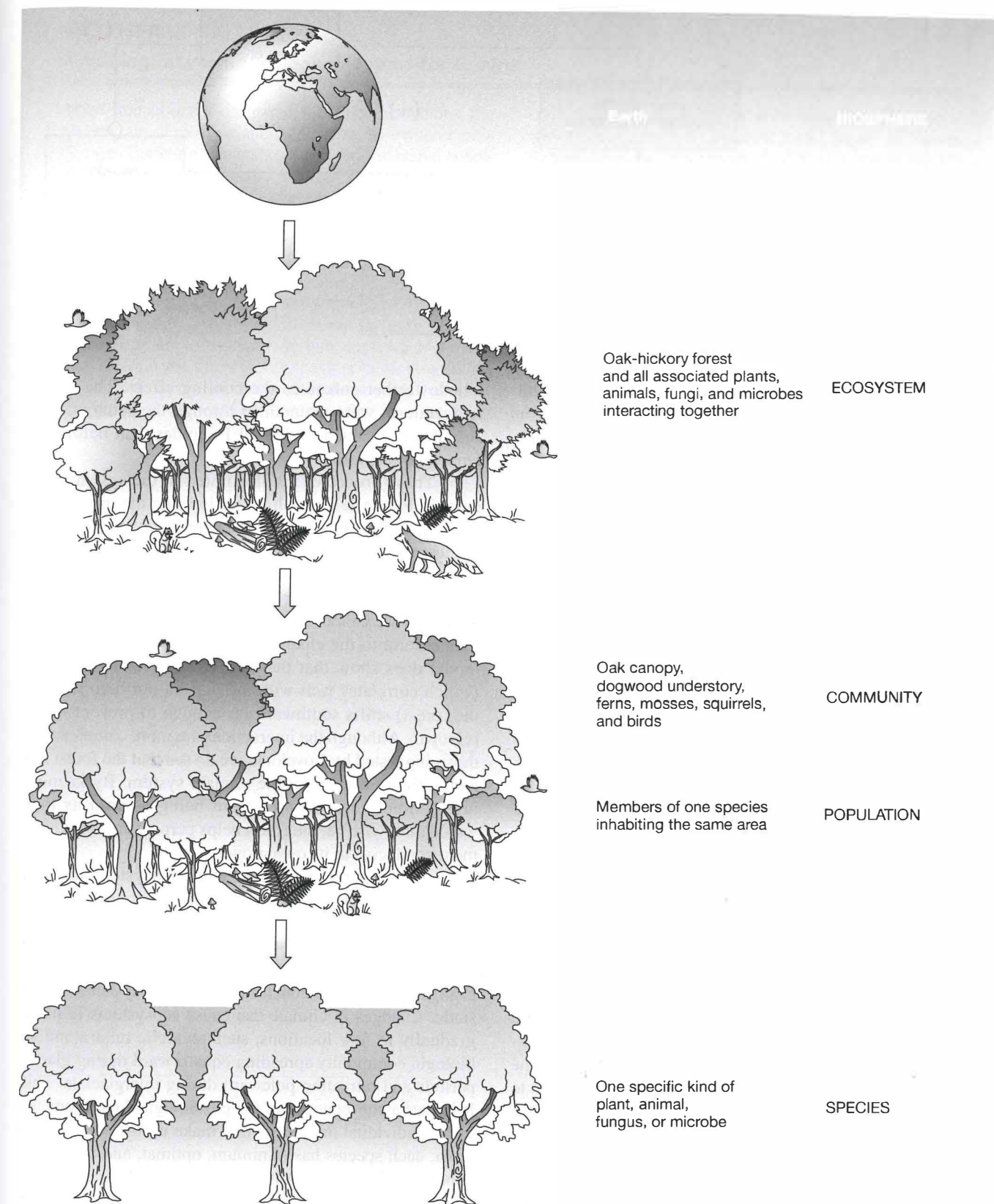


FIGURE 1 Division of the biosphere into ecosystems, communities, populations, and species. (Source: From Nebel and Wright, *Environmental Science*, 4/e, 1993. Reprinted by permission of Prentice Hall, Upper Saddle River, N.J.)

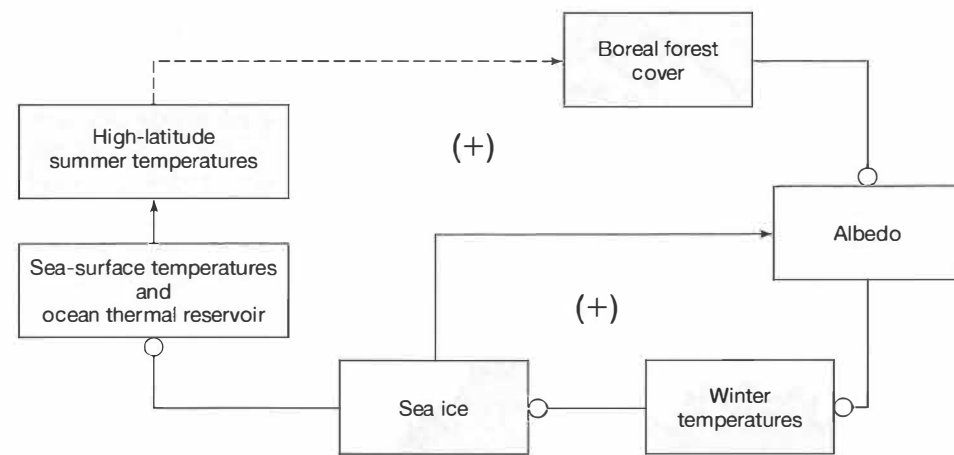


FIGURE 2 Possible feedbacks between the boreal forest and climate.

ecosystems the environment includes the physical and chemical characteristics of the particular freshwater or marine water body concerned. Since each ecosystem is located in a slightly different physical environment, there is a tendency to think of the environment as determining the type of ecosystem that develops. This is true to some degree, but it is not the whole story: The organisms within a particular ecosystem interact with their environment. For example, the type of soil present may help determine which plants will grow, but the plants themselves add organic matter to the soils that changes the soil chemistry, possibly allowing different species to grow there. Certain species might tolerate only particular temperature and precipitation regimes, but those species may be capable of altering local climate, thereby promoting their own growth or the growth of other species.

We illustrate this possibility here with an example of his from the boreal forests of North America and Asia. The coniferous trees in the boreal forest hide the snow-covered ground in winter, reducing the albedo of the forested region. The reduced albedo should result in higher winter temperatures than would occur if the forest were not present. By modifying its local environment to be warmer at its northern edge, the forest may be able to push farther north beyond the point where temperatures would otherwise be too cold to allow the trees to grow. Is there any indication that this might, in fact, be happening?

Scientists at the National Center for Atmospheric Research in Boulder, Colorado, conducted a general circulation model experiment in which they changed all of the forest north of 45° N to bare ground. This is equivalent to moving the border between the boreal forest and the treeless tundra southward. The effect of this change was to produce a large increase in the wintertime albedo, because the white snow cover was revealed by the removal of the forest. The increased albedo caused a large drop in air temperatures, the greatest change in the month of April—up to 12°C (21.6°F) over the land surface. The colder winter temperatures increased the sea-ice cover, and the higher

albedo further enhanced the cooling effect. The colder temperatures were maintained through the summer, with July being as much as 5°C (9°F) colder than before the removal of the forest.

These processes are illustrated in the systems diagram in Figure 2. The solid lines indicate the interactions simulated by the model, including the ice–albedo feedback discussed in several earlier chapters. The dashed line completes another positive feedback loop implied by the model results. The forest cover is not an interactive part of the model, so we cannot see the feedback from the change in temperature to the change in forest cover. However, the model does show that the July 18°C (64.4°F) isotherm (which correlates well with the present northern limit of the forest) shifts southward far enough to prevent forest regrowth. Although the interactions are more complex than those suggested by Lovelock, we do see that the forest has a significant impact on the climate system. By keeping high-latitude temperatures from being as cold as they would otherwise be, the forest helps perpetuate an environment conducive to its own growth.

It is apparent, therefore, that ecosystems are not divorced from their environment; the environment is part of the ecosystem. As the environment changes, the types of organisms in the ecosystem and the interactions among them change, and as they do, the local environment may change. The obvious conclusion is that ecosystems are not static. Changes in climate can cause ecosystems to move gradually to new locations, such as arctic tundra and its biologic community spreading equatorward during glacial periods and retreating poleward during interglacials. This is in part a consequence of the physiological requirements of the individual organisms that make up the ecosystem's biota; each species has minimum, optimal, and maximum conditions for growth. As the environment changes, organisms may find themselves in less than optimal conditions (see "A Closer Look: Physiological versus Ecological Optima for Growth"). More interestingly, new environmental conditions could give rise to a totally new assemblage

A CLOSER LOOK

Physiological versus Ecological Optima for Growth

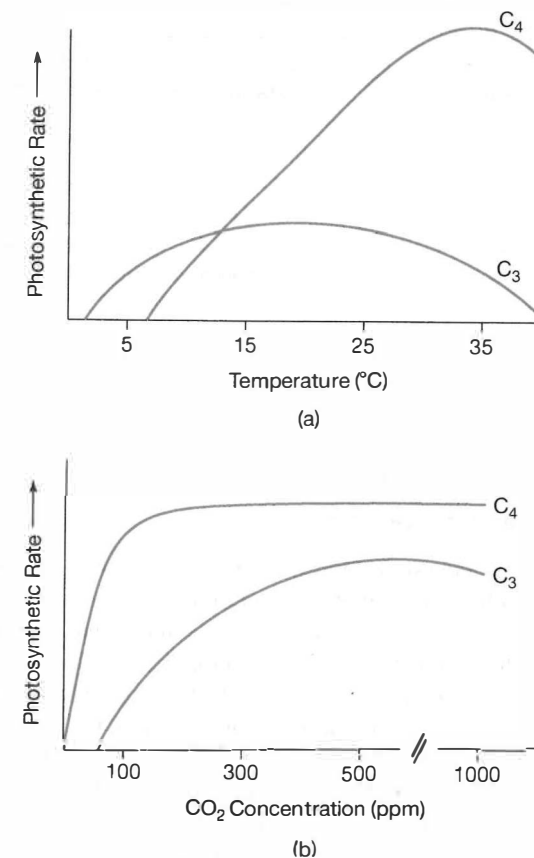
When studied under controlled, laboratory conditions, the growth rate of most organisms responds to environmental change. There are minimal, optimal, and maximal conditions for growth. This relationship can be clearly expressed for the response of photosynthetic rates of plants grown in greenhouses to changes in temperature (Box Figure 1a). This figure also shows a distinction between C₃ and C₄ plants. C₃ autotrophs comprise all the trees, most of the other plants, the cyanobacteria, and all algae; they are called C₃ because an important sugar produced during photosynthesis has three carbon atoms. C₄ plants are relative newcomers to the Earth system, evolving in the last 10–20 million years in response to either lower atmospheric CO₂ levels or drier climates. They include many grasses, corn plants, and pineapples, to name a few. They are called

C₄ because they produce a 4-carbon sugar during their photosynthetic cycle. C₃ plants can grow at lower temperatures, but have lower maximum temperatures for growth than do C₄ plants. C₄ plants, however, are able to very efficiently scavenge CO₂ from the atmosphere (Box Figure 1b), allowing them to spend less time with their stomata (pores) open. (Plants typically obtain CO₂ by opening their stomata.) This ability is a great advantage in arid environments because open stomata also release water vapor to the atmosphere, causing water stress in plants. It has also proven advantageous from the perspective of Earth history: Atmospheric CO₂ levels have fallen over the last several million years, falling ever closer to the break-even point for C₃ plants (~30–70 ppm) where photorespiration (respiration by plants) equals photosynthesis. As atmospheric CO₂ levels have fallen, plants that could more efficiently photosynthesize under these atmospheric conditions have presumably thrived. However, when temperatures drop, as Box Figure 1a shows, the C₃ pathway becomes favorable.

Of course, organisms have many environmental requirements, each of which may exhibit a parabolic relationship under otherwise optimal conditions (as in Box Figure 1), but nature does not provide such ideal conditions. It is important that we understand these relationships both in the laboratory and in nature so that we can establish the coupling and feedback that govern environmental change. Many of the factors that affect growth are interdependent, and can create apparent paradoxes that can only be understood when considered simultaneously. Since *interspecies* interactions are discussed in the main body of the text, let's focus here on interdependencies of *environmental* factors. In laboratory culture, algae exhibit optimal *physiological* growth rate at temperatures in the range of 20–25°C. Thus, one might predict that maximum rates of oceanic primary production would be in the tropical to subtropical ocean. Instead, what one finds are high rates of photosynthesis at high latitudes and in coastal zones irrespective of latitude, as reflected in satellite images of ocean chlorophyll concentration (Figure 10). This paradox is reconciled if we realize that the supply of nutrients to marine ecosystems is generally dependent upon upwelling of nutrient-rich deep waters to the surface. Upwelling is prevalent along west-facing coastlines (because of *Ekman pumping*) and at high latitudes, where the lack of a strong thermocline (pycnocline) allows for deep wind-driven mixing. Thus, the *ecological optimum* for algal growth is closer to 8°C, a compromise between the detrimental effects of colder water and the beneficial effects of enhanced nutrient supply. This fact will prove important to our consideration of the causes of glaciation in Earth history.

Tropical species tend to live closer to their physiological optima, and their temperature ranges (maxima–minima) are narrower than higher-latitude species. This may lead to

(continued)



BOX FIGURE 1 Typical physiological responses of plants grown under greenhouse conditions to changes in some environmental conditions. (a) The response of C₃ and C₄ plants to changes in temperature. (b) The response of C₃ and C₄ plants to changes in the partial pressure of CO₂ in the atmosphere. Note that the scale is nonlinear.

A CLOSER LOOK (continued)

particular vulnerability of tropical species to even small amounts of warming in the future.

Another paradox is the extremely high productivity of tropical rainforests. Perhaps contrary to expectation, tropical soils have severely depleted nutrient concentrations compared to temperate forest soils. How can they sustain such high productivities? The answer is that nutrients are very efficiently recycled in tropical forest ecosystems. Most of the nutrients are stored in the trees themselves. When a tree dies, it falls to the forest floor, which is warm and damp, the ideal conditions for decomposers (fungi and bacteria). Breakdown and release of mineral nutrients is thus quite quick. Moreover, trees in tropical forests have extensive, shallow root systems that rapidly extract nutrients as they are released by the decomposers. As a result, the residence time of nutrients in tropical soils is extremely short (Box Table 1); a typical molecule of nutrient phosphate is retained less than 2 years in a tropical soil, whereas its lifetime in a temperate

forest is closer to 6 years, and in a boreal forest, is over 300 years. The rapid recycling of nutrients in tropical soils draws down the steady-state nutrient concentration but sustains high rates of productivity. However, if the trees are removed, so too are the nutrients, and the soil left behind is infertile. This is one of the serious consequences of deforestation of the tropical rainforest.

Recognition of the distinction between physiological and ecological optima for growth is an important step in developing a deeper understanding of the Earth system. Life, including humans, is influenced by a variety of interacting factors. The overall optimal growth condition thus may be suboptimal for many if not all factors that influence growth. Thus, an environmental change that should increase primary productivity (say, warming of the high-latitude ocean in response to buildup of atmospheric CO₂ levels) may in fact diminish it. The systems approach provides the answers to these seeming paradoxes.

BOX TABLE 1 The Mean Residence Time (in years) of Organic Matter and Nutrients and the Net Primary Productivity (NPP) of Four Biomes

Biome	Organic matter	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	NPP (gc/m ² /yr)
Boreal forest	353	230	324	94	149	455	360
Temperate forest	4	5.5	5.8	1.3	3.0	3.4	540
Chaparral	3.8	4.2	3.6	1.4	5.0	2.8	270
Tropical rain forest	0.4	2.0	1.6	0.7	1.5	1.1	900

Source: From M. B. Bush. *Ecology of a Changing Planet*, 3/e, 2003. Reprinted by permission of Prentice Hall, Upper Saddle River, NJ.)

of species: an ecosystem that has not been seen before. In fact, because ecosystems and the environment interact, it may be possible for a new ecosystem to evolve without any large-scale change in the environment. In this case, the initial environmental conditions support one ecosystem but the interactions change the local environment, so the ecosystem evolves into something new.

Although Figure 1 implies an ordered hierarchy, the levels are not discrete and ecosystems themselves are not discrete units. Each level in the hierarchy interacts with all other levels, and ecosystems overlap each other. One ecosystem gradually merges into another geographically at a diffuse boundary called a transitional ecosystem or **ecotone** (Figure 3). An ecotone may include an entirely different assemblage of species that do not match those in the ecosystems on either side of the boundary (Figure 4). There is also considerable overlap between ecosystems in a structural sense: Several ecosystems may share many common physical attributes. Based on the various plant communities ecosystems support, we can identify distinct

types of terrestrial biomes. The most important are shown in Figure 5.

Species Interactions

Although ecosystems may appear to be very different from one another, they all exhibit a common biotic structure. For example, all ecosystems include autotrophs and heterotrophs. In this type of organization, primary consumers (e.g., zooplankton in the sea or rodents on land) live off the producers (algae, plants), secondary and higher-order consumers (fish, hawks) feed on lower-order and primary consumers (zooplankton, rodents), and the decomposers (bacteria and fungi) and detritus feeders feed on dead organic matter of both producers and consumers. In assisting the chemical breakdown of organic matter, the decomposers and detritus feeders return nutrients to the system that are then reused by the producers.

We can represent which organisms feed on which by means of a **food chain** that links particular organisms in an

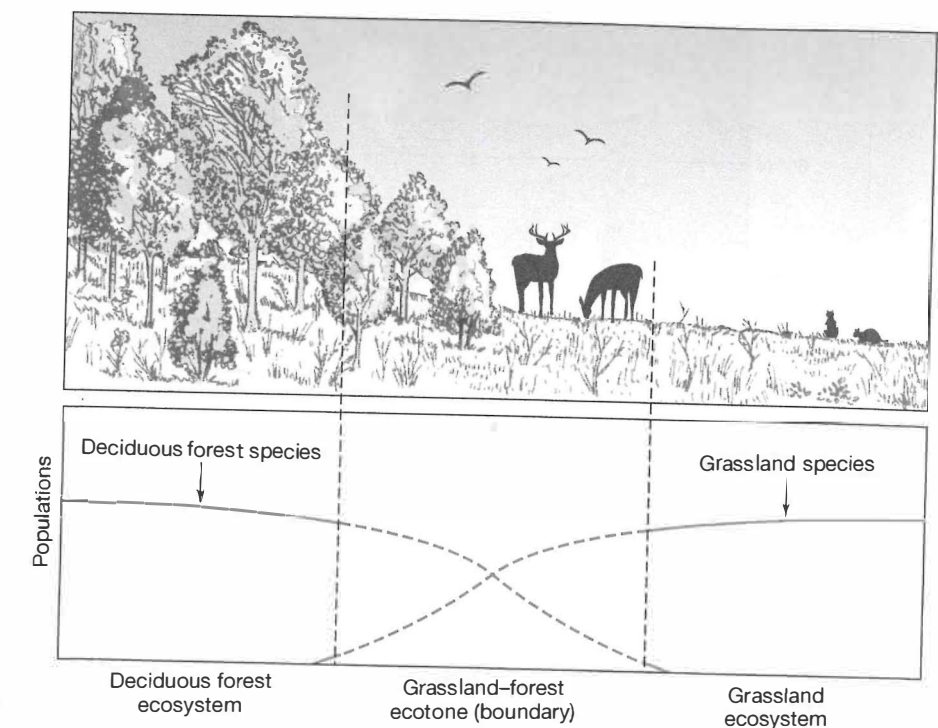


FIGURE 3 Ecosystems and ecotones. (Source: From Nebel and Wright, *Environmental Science*, 6/e, 1998. Reprinted by permission of Prentice Hall, Upper Saddle River, N.J.)

ecosystem. Because one organism may feed on several other types or may be eaten by several different types of organisms, food chains are usually interconnected into **food webs** (Figure 6). Despite the potential complexity of these webs, the overall structure is very simple: Each web consists of a series of feeding levels called **trophic levels**. For example, the following trophic levels range from the bottom up: producers > primary consumers > secondary consumers > higher-order consumers. There are normally no more than four trophic levels in any ecosystem.

How many organisms are there at each level? Rather than looking at the number of individuals, we can simplify the comparison between levels if we talk in terms of **biomass**. Biomass is the total combined weight of organic material in each trophic level. Each trophic level, except for the producers, ingests its food (organic matter) from the level below. The organisms utilize that organic matter for growth and to produce energy. As we move from lower-order to higher-order trophic levels, much organic matter is lost when it is converted to energy. In terrestrial ecosystems, the biomass is

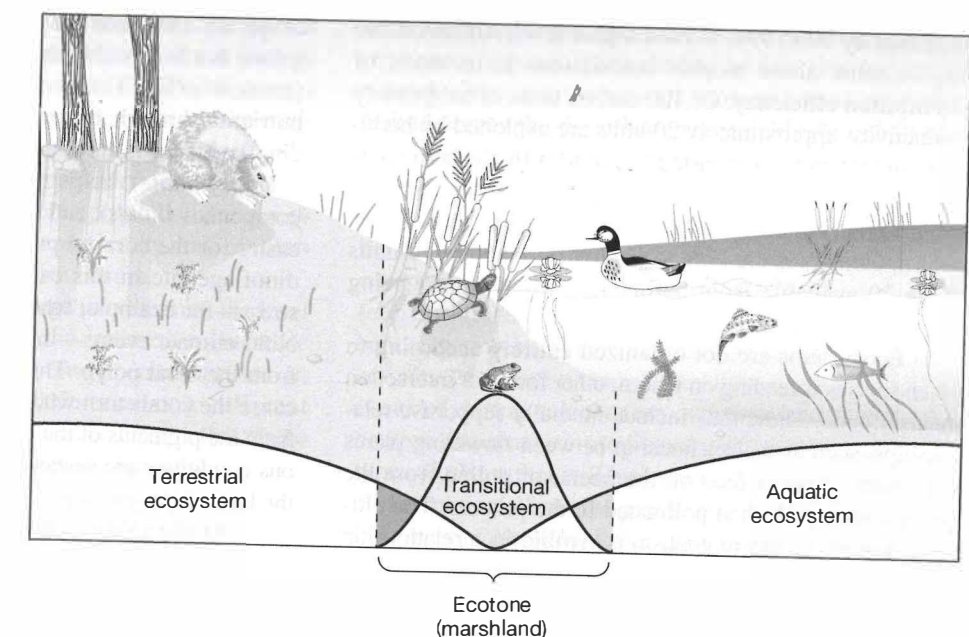


FIGURE 4 An ecotone may create a unique habitat of its own. (Source: From Nebel and Wright, *Environmental Science*, 6/e, 1998. Reprinted by permission of Prentice Hall, Upper Saddle River, N.J.)

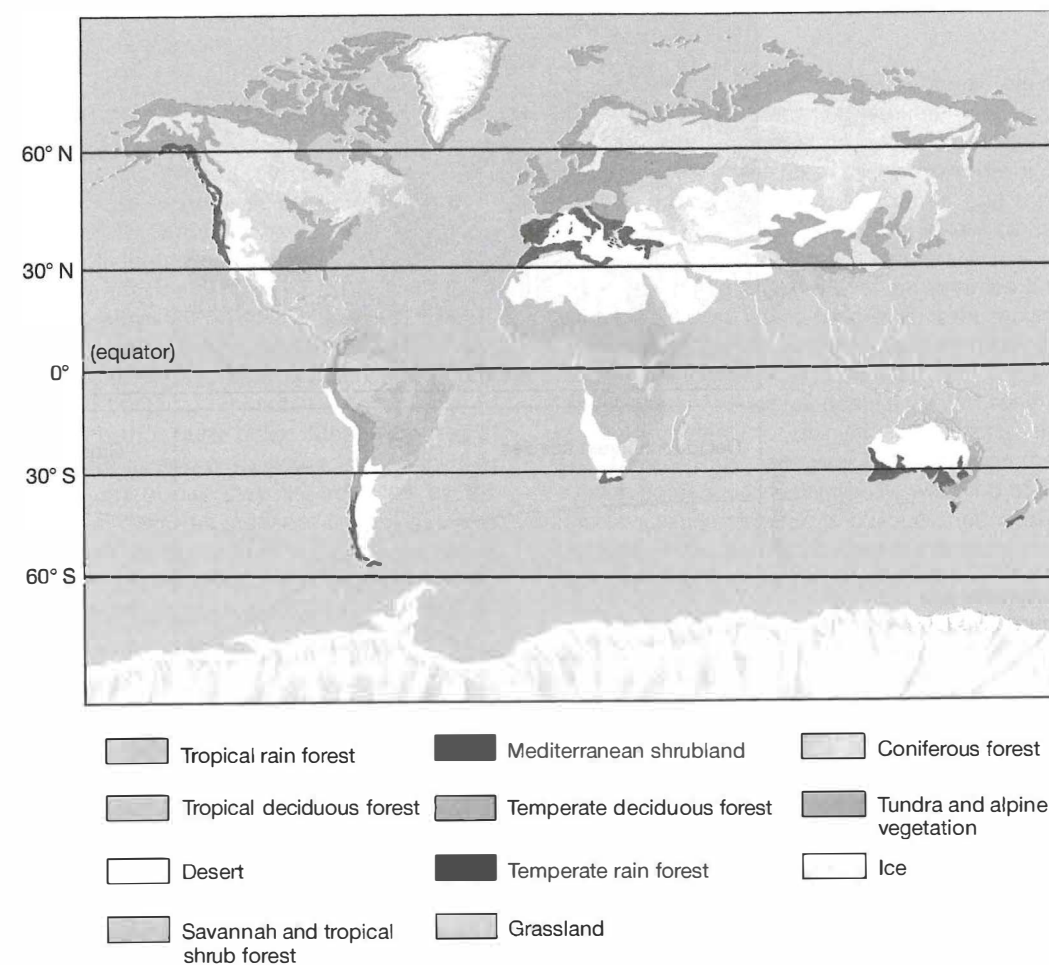


FIGURE 5 [See color section] World distribution of the major terrestrial biomes. (Source: From Audesirk and Audesirk, *Biology: Life on Earth*, 5/e, 1999. Reprinted by permission of Prentice Hall, Upper Saddle River, N.J.)

decreased by 90 to 99% at each higher level. An alternative way to think about trophic interactions is in terms of **exploitation efficiency**. Of 100 carbon units of net primary productivity, approximately 20 units are exploited by herbivores and 80 units are “wasted,” expended by the herbivores without translation into biomass or unutilized and transferred to the soil ecosystem where decomposers take over. In turn, carnivores are able to exploit only about 0.2 units of the 20 available from herbivores, with the rest being expended in their metabolism.

Ecosystems are not organized entirely according to which species is feeding on whom; other forms of interaction are also found. These may include mutually supportive relationships, such as the relationship between flowering plants and insects: Insects feed on the nectar or pollen from the flowers, which are then pollinated in the process. The ultimate example of this mutualism is **symbiosis**, a relationship in which two species benefit from living together in intimate contact. The relationship between corals and plantlike protists known as *dinoflagellates* is a good example of a symbiosis. This symbiotic relationship involves a beneficial

cooperation between the coral animal (*polyp*) and a dinoflagellate that lives within the digestive cavity of the coral polyp (*zooxanthalla*). The coral provides protection, inorganic nutrients through excretion, and carbon dioxide for the dinoflagellate. In turn, the dinoflagellate provides nutrition (*photosynthate*), helps the coral synthesize some organic compounds (*lipids*), and removes carbon dioxide, making it easier for the coral to precipitate its CaCO_3 skeleton. The dinoflagellate in this case is the coral’s *symbiont*. Under stress—for example, when sea temperatures rise during El Niño climate events—the dinoflagellates may be expelled from the coral polyp. This is called a “bleaching” event because the corals turn white; their beautiful coloration comes from the pigments of the dinoflagellate symbiont. If deleterious conditions are sustained, the coral can die as a result of the lack of its symbiont.

At the other extreme are species that coexist in a competitive relationship, although this competition tends to occur less frequently than we might suppose. Most species tend to adapt to a particular habitat and, even where potentially competitive species occupy the same

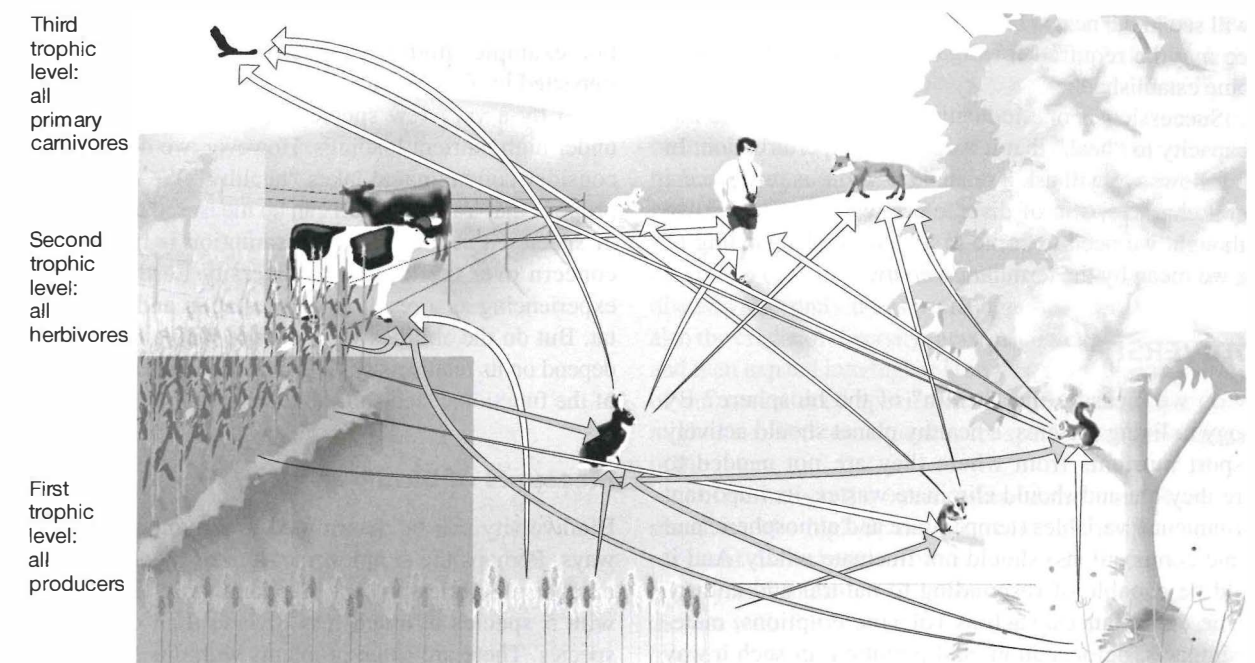


FIGURE 6 A simple food web. Food (energy and nutrients) is transferred from one organism to another along these pathways. (Source: From Nebel and Wright, *Environmental Science*, 6/e, 1998. Reprinted by permission of Prentice Hall, Upper Saddle River, N.J.)

habitat, each tends to develop its own particular *niche*. An animal’s niche describes not only the food it eats, but also where and when it eats, where it lives, where it nests, and so on. Specialization to this degree, in which different species occupy the same geographic location but have different living habits, reduces potential contact and helps reduce competition among species at the same trophic level.

The species in an ecosystem interact with their environment as well as with each other, and different species thrive under different physical conditions. There is usually some optimal range of conditions over which each species is best adapted. The species comes under stress as the environment moves away from that range—for example, as it becomes wetter or drier, warmer or colder, shadier or sunnier, or more or less acidic. At some point, the stress may be great enough that the organism reaches its limit of tolerance for those conditions, and death occurs.

When we throw human beings into the mix, the level of complexity and the nature of the interactions increase substantially. We then must take into account the social, political, and economic interactions among different human societies and also the dramatic effects that these societies can have on the physical environment.

Ecosystem Disturbance and Succession

Natural or human disturbances of an ecosystem that seriously disrupts the existing ecosystem structure—for example, wildfire or deforestation—initiate a response, often of

rebuilding, that in some cases follows a predictable pattern called **succession**. The job of rebuilding can be quite extensive because initial disturbances such as wildfires or deforestation can promote subsequent effects like soil erosion, nutrient loss, or microclimate changes such as aridification from the loss of evapotranspirative pumping of water into the atmosphere. The resulting arid, nutrient-poor environment is not necessarily conducive to the regrowth of the preexisting community. The first species to reinvade a disturbed environment are called *opportunists* or *pioneer* species. They tend to be fast growing, rapidly reproducing, environmentally tolerant species that can spread across the disturbed area quickly. In colonizing a previously disturbed area, these organisms tend to begin the process of repair, improving the soil or modifying the local climate in ways that can result in their replacement by other, slower growing organisms that ultimately have competitive advantages. The establishment of a mature forest can take decades to hundreds of years after disturbance; the forests of New England are still undergoing succession 200 years or more after the original logging that occurred during colonization of America. In general, succession patterns are predictable, at least in terms of the types of plants that will become prevalent at various stages of succession. If many species are equally well suited to the environmental conditions at a particular stage of succession, however, an element of unpredictability may be introduced into the succession pattern. Thus a diversity of outcomes is possible, and this diversity may be reflected in the *biodiversity* of a region subject to disturbance. Indeed,

we will see in the next section that a modest level of disturbance may be required for high-diversity ecosystems to become established.

Succession is one indication that the biosphere has the capacity to “heal,” that it is resilient to perturbation. In what follows we will ask a related question: is resilience a general characteristic of diverse ecosystems? Before we do, though, we need to come to a better understanding of what we mean by the term *biodiversity*.

BIODIVERSITY

How do we measure the “health” of the biosphere? By analogy to living systems, a healthy planet should actively transport nutrients from where they are not needed to where they are and should eliminate wastes. Its important environmental variables (temperature and atmospheric and oceanic compositions) should not fluctuate wildly. And it should be capable of responding to natural and anthropogenic disturbances, such as volcanic eruptions, meteorite impacts, deforestation, and pollution, in such a way as to minimize their consequences.

These characteristics of a stable Earth system are ones that we normally associate with living organisms. Indeed, it is these very characteristics that are most suggestive of an important role for the biota in the regulation of the Earth system. The biota have affected Earth’s long-term climate evolution by modifying its greenhouse gas content. They have also created an oxygen-rich atmosphere. Our oxygen-rich atmosphere is a direct consequence of oxygenic photosynthesis. The evolution of this metabolic pathway has been called the greatest pollution event of Earth history. As a result of the prevalence of oxygenic photosynthesis, anaerobes, previously able to inhabit a diversity of habitats, survived only in environments such as seafloor sediments where oxygen does not penetrate. In these cases, the perturbations to which the biota has responded have been gradually imposed, perhaps over millions of years. But how has the Earth system responded to *rapid* environmental change? Is the resilience revealed over the long term also a characteristic in the short term? The answer, is yes. Earth has been subjected to insults the magnitude of which we are unable to imagine: Meteorites broader than the ocean is deep have struck Earth many times during its 3.5 billion years of inhabitation by organisms. The robustness of the planetary system is revealed by a fossil record displaced but not interrupted and by a geological and geochemical record that suggests that the long-term environmental consequences of these sudden disturbances were small.

How is the diversity of life-forms on the planet—its **biodiversity**, the number of species in an area—related to the health of the Earth system? At the local scale, if we measure “health” in terms of biological productivity, we

might conclude low diversity ecosystems are the healthiest. For example, highly productive lakes that have been impacted by fertilizer additions in runoff tend to be dominated by a very few species that are highly productive under high nutrient loadings. However, we don’t normally consider contaminated lakes “healthy.” We might instead propose that Earth’s health can be measured by the number of species it supports. This assumption is implicit in the concern over the loss of biodiversity Earth is currently experiencing as a result of deforestation and loss of habitat. But do the abilities we associate with a healthy planet depend on its biodiversity? Is global biodiversity an indicator of the functional status of the Earth system?

Measures of Biodiversity

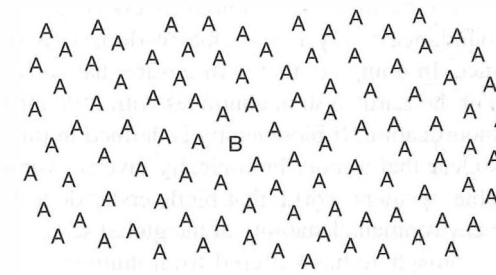
Biodiversity can be determined in a number of different ways. Perhaps the simplest measure of biodiversity is the number of species present in a community. A community with 5 species is much less diverse than one with 100 species. There are some problems with this simple definition, however. One problem has to do with heterogeneity. Suppose there are two communities, both with two species of organisms, as shown in Table 2. According to the simple definition, the two communities are equally diverse. Community I, however, has 99 individuals of species A and 1 individual of species B, whereas community II has 50 individuals of species A and 50 individuals of species B (Figure 7). The chance of encountering species B in community I is quite remote, only 1 in 100; this community is quite homogeneous. In contrast, community II seems more diverse because there is an equal likelihood of encountering an individual of species A and of species B. Community II is thus more heterogeneous.

To capture the importance of heterogeneity, measures of diversity other than simply the number of species have been proposed. The *Simpson’s diversity index* measures the likelihood that two individuals drawn from the same community will be of different species. This likelihood is expressed quantitatively as follows:

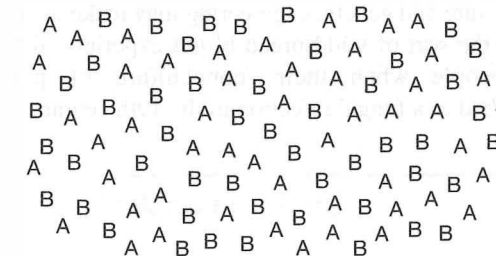
$$\text{Simpson's diversity} = 1 - [(\text{proportion of species A})^2 + (\text{proportion of species B})^2 + \dots]$$

TABLE 2 Diversity of Two Simple Communities

	Number of Individuals, Species A	Number of Individuals, Species B	Simpson's Diversity Index
Community I	99	1	0.02
Community II	50	50	0.50



Community I



Community II

FIGURE 7 Two communities comprising two species (A and B) each. Although equal numbers of species are represented, community II appears more diverse than community I.

The proportion of each species in the community is identical to the probability that an individual chosen at random will be of that species. The probability of choosing two individuals of that species in a row is in the square of the proportion, just as the probability of throwing two “heads” in a row during a coin toss is $(0.5)^2 = 0.25$, or $1/4$. The value of this index for our two simple communities I and II are $1 - (0.99^2 + 0.01^2) = 0.02$ for the homogeneous community I and $1 - (0.5^2 + 0.5^2) = 0.5$ for the heterogeneous community II, as shown in Table 2. When the number of species is large and the composition heterogeneous, the maximum Simpson’s diversity approaches 1.0.

The Simpson’s diversity index is clearly superior to a simple species count in expressing biodiversity. Nevertheless, in most discussions of global biodiversity of the past, present, and future (to some extent, this text included), only the species count is used.

Diversity and Stability

A long-standing debate exists among ecologists about the relationship between diversity and stability. For most communities, diversity increases from the poles to the tropics: Most of the highly diverse communities exist within 10 to 20 degrees of the equator. Why are the tropics so diverse? Tropical climates tend to be stable over a range of time scales. In the short term, the lack of large seasonal variations in solar insolation leads to only small monthly contrasts in temperature and rainfall. Moreover, investigation of the geological record reveals that on long time scales,

tropical temperatures have changed relatively little. Even during the Ice Ages, tropical temperatures fell only slightly while temperate to polar climates cooled substantially. The high diversity and climatic monotony of the tropics have been taken to indicate that environmental stability leads to high diversity—a premise called the *time stability hypothesis*. The persistence of uniform environmental conditions in the tropics presumably allows evolution to proceed without disruption (i.e., lower rates of extinction), leading to higher diversity. Recently it has been suggested that the tropics are also the cradle of diversity: new species evolve in the tropics and then expand into higher latitudes. If so, then higher rates of human-induced species extinction in the tropics today might have dire consequences for species at higher latitudes in the future.

In contrast, the *intermediate disturbance hypothesis* states that the high diversity of tropical ecosystems is the result of disturbances that occur with intermediate frequency and intensity. This hypothesis is in direct contradiction with the time stability hypothesis. Highly diverse tropical rainforests tend to have some species with few or no young trees (indicating that they are dying out) and other species with a very high proportion of young trees (indicating that they are increasing in abundance). This turnover is presumed to be the result of a fairly recent natural disturbance. Regions of rainforest that are known to have been relatively undisturbed over historical time tend to have lower diversities. Also, highly diverse coral reef ecosystems tend to occur at the outer edge of barrier reefs, where these ecosystems are periodically confronted with the damaging effects of waves and storms.

Both hypotheses link the diversity of life on Earth to the stability (or instability) of the environment. Another ecological consideration is the stability of the ecosystem itself: how stable (in time) are its species composition and density (the number of species per unit area)? Stable ecosystems display low variability in species density, respond quickly to perturbation, returning to their original state after the disturbance, can tolerate repeated shocks, and respond sluggishly to persistent forcings. More diverse ecosystems tend to have more stable species densities in the face of environmental variation, because decreases in some species are counterbalanced by increases of others.

DIVERSITY OF INTERACTIONS

Even the more elaborate measures of diversity, such as the Simpson’s diversity index, fail to account for a characteristic of ecosystems that is important to our understanding of the feedbacks between the biota and the physical world: the diversity of interactions. A community consisting of 500 species of ants, with relatively uniform populations of each, along with a few species of plants and predators, is highly diverse according to this index. However, in terms

of the diversity of roles played by these organisms, the community is extremely homogeneous.

Here the infancy of Earth system science is clearly a limitation: No diversity index has been proposed that captures the degree of interaction between biological and physical components of the Earth system. Such a diversity index should increase as the number of couplings among the biota and between the biota and the physical world increases. An ecosystem with 10 interactions and only 20 species is then not as diverse as one with 40 species interacting in these 10 ways. It should also incorporate the attribute of redundancy; the Earth system is more resilient if there are alternative ways of performing important functions, such as photosynthesis or decomposition. If one of these pathways is lost (e.g., through extinction), the others can compensate. The final attribute to incorporate into a

systems diversity index is potential diversity. Species in small abundance today may come to dominate after a disturbance. In doing so, they will ensure that some vital function of the Earth system continues with little interruption or modification. If biodiversity is defined in this way, it seems clear that a more biologically diverse world is a more stable, resilient world, that biodiversity does indeed enhance environmental stability at the global scale.

The biosphere has suffered from unimaginable catastrophes that reduced the species diversity by up to 95%, yet recovered. We also discuss how current practices of monoculture and genetic engineering may make us susceptible to the sort of widespread blight experienced by the Irish people when their monoculture of potatoes succumbed to a fungal infection in the 19th century.

Chapter Summary

1. Some of the characteristics of life that allow it to play an important role in the Earth system are its tendency toward exponential growth, its need for energy, its tendency to pollute, and its versatility.

2. Organisms can be placed into broad groups according to whether they are producers (autotrophs) or consumers (heterotrophs).

a. Autotrophs include those that use solar energy (photosynthesizers) and those that use chemical energy (chemosynthesizers).

b. Heterotrophs, including aerobes (use oxygen), anaerobes (use other oxidants), and fermenters (who do not oxidize organic matter), get energy from the food they consume.

3. Populations of organisms live in communities with other organisms that interact among themselves and their environment in ecosystems. Boundaries between ecosystems are typically gradational ecotones rather than sharply contrasting adjacent ecosystems.

4. The flow of energy (food) through ecosystems is often displayed as a food chain from producers to consumers and decomposers.
- a. Closer inspection of natural communities indicates that the relationships form more of a web than a chain.

b. Exploitation efficiency is quite low; much of the food (energy) available to higher levels in the food chain is not used for growth but rather expended during metabolism.
5. Species also interact in other ways, including some that are competitive but others that are mutually beneficial (symbiosis).
6. After a disturbance, an ecosystem often responds with a predictable succession of organisms, from opportunistic, fast-growing species to slower-growing but ultimately more competitive species.
7. The diversity of life on Earth is a function not only of the number of species, but also of the degree to which the populations of those species are nonuniformly distributed (heterogeneous).
8. Environmental stability seems to lead to high biodiversity in some instances; however, modest disturbance enhances diversity in others.

Key Terms

autotrophs	ecosystem	heterotrophs
biodiversity	ecotone	population
biomass	exploitation efficiency	succession
biomes	food chain	symbiosis
community	food web	

Review Questions

1. What are the characteristics of life that allow it to influence the environment at a global scale?

2. What are the two fundamental groupings of organisms based on their metabolisms?

3. Describe the two mechanisms of autotrophy. Where on Earth might you expect to find one or the other of these two pathways to dominate?

4. Describe the three mechanisms of heterotrophy. Where on Earth might you expect to find one or the other of these two pathways to dominate?

5. Why is a food web often a better description than a food chain of the way in which energy (food) is passed through an ecosystem?
6. How does symbiosis differ from other forms of species interactions?

7. Describe a typical successional sequence following a disturbance of an ecosystem. What are the characteristics of opportunistic species that allow them to rapidly repopulate a disturbed area?

8. What is the advantage of the Simpson's Diversity Index over a simple census of the number of species in quantifying the diversity of an ecosystem?

9. What do we mean by "diversity of interactions"?

Critical-Thinking Problems

1. Figure 2 presents a systems diagram of the feedbacks involving boreal forest cover, albedo, temperatures, sea ice, and the oceans. We used this diagram to show that it is possible for the northern boreal forest to have a significant impact on the larger-scale climate. Using the information you now have about the possible impacts of anthropogenically induced greenhouse climate change, expand on this diagram and discuss the implications in terms of climate and forest cover.

2. In the final section of this chapter we presented some thoughts about what a diversity index useful for Earth system
- scientists might include. Using these thoughts or those of your own, develop a quantitative index, similar to the Simpson's Diversity Index, that reflects the diversity of interactions at the global scale.
3. Using the information from Table 1, design a layered microbial ecosystem that could be self-sustaining with the exception of the import of solar energy from above. All of the inorganic compounds listed in the table are available for your use in building this ecosystem.

Further Reading

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