Chapter 12

Ecosystems: the flux of energy and matter

12.1 Ecosystem ecology

Ecosystem ecology is the study of the interactions of organisms with the transport and flow of energy and matter. Ecologists who study ecosystems ask questions such as: What are the feeding relationships among the organisms in an ecosystem? How many different types of feeding relationships can be supported in a system? Why are some systems more productive than others? How much carbon and nitrogen are stored in the plants in an ecosystem? How rapidly do nutrients cycle through the living organisms in an ecosystem? How much of a particular nutrient is lost from the system each year?

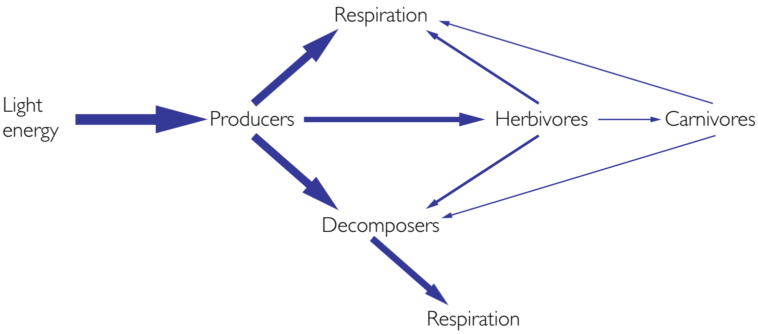
12.2 The trophic–dynamic concept of ecosystem structure

A conceptual framework developed to explain the dynamics of energy and matter flow in aquatic ecosystems was developed in 1942 by Raymond Lindemann at the University of Minnesota. This model is called the trophic–dynamic model, and it describes the relationships between different organisms in an ecosystem by following feeding relationships among them. The organisms in an ecosystem are divided into different trophic levels, with the first trophic level containing the primary producers, the second trophic level containing the primary consumers, the third trophic level containing the secondary consumers, and on to the top consumers in the system. The model is an oversimplification, but it serves to illustrate the flow of energy and matter in ecosystems (Fig. 12.1).

Energy flows one way in ecosystems, with energy input from the sun being captured by primary producers, and large losses of energy between each trophic level, owing to respiration and inefficient energy transfer (Fig. 12.1).

Because of losses to respiration, and inefficiencies in harvesting, assimilation and digestion, the amount of energy in any trophic level is not completely available to the next highest trophic level. This observation has been used to explain the limits to trophic levels in ecosystems. Rarely are there more than four or five trophic levels in an ecosystem, and the number of individuals in top trophic levels is usually limited. Ecologists often illustrate this pattern through the use of pyramid plots, where the total amount of energy in each trophic level is plotted in a series of stacked boxes, starting with the first trophic level on the bottom (Fig. 12.2). A trophic pyramid constructed using energy is never inverted, consumers cannot use more energy than is available in their food. However, pyramids constructed with biomass can sometimes be inverted, and

Fig. 12.1 A diagrammatic representation of the trophic–dynamic concept of ecosystem structure. Light energy is captured by plants and used to build their bodies. Much of this energy is lost to respiration, but a portion is passed onto the next trophic level, represented by herbivores. A portion of the energy in herbivores is then passed on to carnivores. When individuals in any trophic level die, they are broken down by decomposers, which recycle nutrients back into the system for uptake by other organisms.



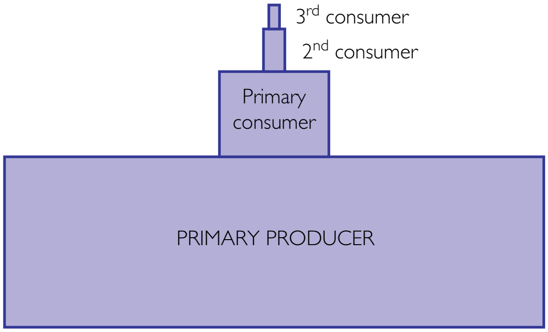


Fig. 12.2 A diagram of the amount of energy in four trophic levels of an idealized ecosystem. Each higher trophic level contains less energy due to losses to respiration within each level and inefficient transfer of energy between levels.

those constructed using numbers of organisms are often inverted—for example, there are many insect herbivores on a single oak tree.

12.3 Differences in efficiency of energy transfer among ecosystems

Once solar energy is used to fix atmospheric carbon dioxide into plant material, there are differences among ecosystems in its availability to higher trophic levels. This is because primary producers can take many different forms, from algae to trees, and have differences in the allocation of carbon to structures, which differ in digestibility. For example, woody plants allocate a significant proportion of their carbon to woody stems. Wood is not easily digested by animals, usually requiring that they have a symbiotic association with micro-organisms capable of digesting wood. In contrast, phytoplankton in aquatic systems can be largely digested by zooplankton grazing on them. In addition, in forest ecosystems, the age of a forest, or successional stage, will affect the proportion of biomass allocated to wood, leaves or other parts of the plants. During earlier stages of succession, the community will have a higher number of herbaceous species, and allocation to leaf material will be high. As a forest stand matures, a higher percentage of carbon will be tied up in woody material, and there is a rise in the respiration costs of supporting this tissue.

After allocation by plants, carbon and nutrients may be harvested by herbivores. The **exploitation efficiency** of these herbivores will be determined by the ratio of the amount of plant production they ingest to the total plant production. This ratio will be dependent on the plant life form. It could be as low as a few per cent in northern evergreen forests, but as high as 60% in African grasslands. Of the total ingested, not all will be digested. Plant material that is high in tannins, phenolics, hemicelluloses or lignin will be harder to assimilate than tissues low in these compounds. Once assimilated, the conversion into consumer biomass will depend on the respiratory demands of the consumer. Thus, endothermic consumers spend a much greater proportion of their assimilated energy on respiration than do ectothermic consumers. An endothermic animal eating low-quality plant food may have a net **production efficiency** of less than 1%, while an ectothermic carnivore that eats a high-quality animal prey may have a value as high as 30%.

12.4 Nutrient cycling and decomposer trophic levels

Detritus, or dead organic matter, is another major energy pathway in most ecosystems. Breakdown of **detritus** is a central process in the nutrient cycles of ecosystems. The productivity of open ocean habitats is often tied to the amount of decomposition and release of nutrients by bacteria in the upper layers of the water, before dead organisms can sink below the zone of light penetration. The turnover rate of detritus is often used as a measure of nutrient cycling, and forms the basis for the high productivity of some tropical communities found on nutrient-poor soils (Table 12.1). The turnover rate will depend on the structure and chemical make-up of the detritus, temperature, moisture and decomposer community. Often, large arthropods are needed to break dead plant material (litter) apart, allowing bacteria and fungi greater surface areas to attack the tissue.

As a rule of thumb, the pattern and rate of nutrient movement are more important to ecosystem function than are the absolute amounts of nutrients in the system. Nutrient movement between plants, animals, decomposers, detritus and soil will depend on the different storage pools of nutrients, and the turnover rates of these pools. Nutrient storage pools include the living organisms in an ecosystem, detritus and soil. Because decomposer activity is affected strongly by temperature and humidity, moist, warm areas generally have faster

Table 12.1 The half-life (time taken for half the material to be broken down) and rate of production of litter for three different forest communities.

Community	Half-life (years)	Litter production rate ($g\ m^{-2}\ year^{-1}$)
Tropical rainforest	0.1	1200
Temperate deciduous forest	1	800
Northern coniferous forest	7	600

turnover rates than colder, drier ecosystems. However, leaf structure (evergreen or deciduous), plant life form (woody or herbaceous), and soil structure also influence nutrient cycling. Leaf tissues that are high in lignin content may be hard to break down, and nutrients may not be released from this pool very fast. Many evergreen trees keep their leaves for several years, maintaining nutrients in their biomass and not releasing them to the system. The soil pool is influenced by soil structural properties such as the proportion of clay, sand and silt particles. Water in sandy soils drains easily, leaching nutrients away with it. High clay and organic contents increase the water and nutrient-holding capacity of soil. The presence of peat bogs, coal swamps and fossil fuel deposits shows that decomposition has lagged behind productivity many times and in many ecosystems during the Earth's history. The result is that much dead organic material has remained undecomposed for thousands, or even millions, of years.

12.5 Food chains and food webs

The path of energy and matter from one trophic level to another is often outlined by constructing food chains. A food chain is simply a listing of which organism eats a different organism in the ecosystem. Food chains are greatly simplified, however, and usually the eating relationships are more accurately depicted as a food web (Box 12.1). An ancient mathematical problem from Egypt, dating back to approximately 1700 BC, sums up the effect of a food web on the rate of energy and matter transfer in an ecosystem. This problem is stated as: In each of seven houses are seven cats; each cat kills seven mice; each mouse would have eaten seven ears of wheat; each ear of wheat would have produced 3.5 pecks of grain. How much grain is saved by the seven houses' cats? The cats would have saved over 8000 pecks of grain, equivalent to about 16 tonnes. But the cats weigh only a few kilograms. We can account for the difference by observing that at every stage in the food chain, the transfer of energy is not completely efficient. For example, when the mice eat the grain, some of the energy contained in the wheat is dissipated as heat (Fig. 12.2).

12.6 Productivity, species richness and disturbance

Chapter 2 discussed the distribution and primary productivity of the major biomes in the world. Productivity in different biomes ranged widely, from less than 50 g to over 3000 g of carbon per square metre per year. There is a broad correlation between productivity and the availability of resources (Fig. 12.3), both within ecosystems and among ecosystems. Generally, as resources such as light and nutrients increase, plant productivity increases. This, in turn supports greater productivity in higher trophic levels.

The relationship between resource availability and species richness is not always positive. Studies from a variety of ecosystems have shown a peak in species richness at intermediate levels of resource availability. What are the bases of this relationship? Many ecologists think that at low levels of resources, only a few species can survive, so species richness is low. These are usually stressful environments, where adaptations to the physical environment are most important. Only a few species have these adaptations, leading to lower species richness in low-resource environments. As the level of limiting resources increases, more species can survive and species richness increases. However, with high levels of resources, competition becomes an important force, and competitive dominants may eliminate less competitive species, resulting in a decrease in species richness.

Predation and herbivory often interact with competition and resources to determine the final biodiversity in an ecosystem. If a predator or herbivore can reduce

Box 12.1 The food web in the pitcher of a carnivorous plant, *Sarracenia purpurea*

The pitcher plant, *Sarracenia purpurea,* occurs in low-nutrient bogs. It derives its name from the vase-shaped pitcher that it forms from modified leaves. The pitcher contains rainwater that some flies, mosquitoes, mites and midges are able to live in, while other insects are trapped in the rainwater and drown. The plant is able to absorb nitrogenous compounds that are released from the breakdown of drowned insects. Insect detritus from the feeding of the larvae of the midge *Metriocnemus knabi* and the small fly *Blaesoxipha fletcheri* is broken down by bacteria and yeast in the pitcher. Algae, yeast and bacteria in the pitcher are then fed upon by various protozoa and the rotifer *Habrotrocha rosa*. The top trophic level is represented by larvae of the pitcher plant mosquito, *Wyeomyia smithii*, which feeds on algae, bacteria and yeast as well as protozoa and rotifers. This example shows that interactions among microbial community members are just as complex as those observed in plant and animal communities (Cochran-Stafira & von Ende 1998).

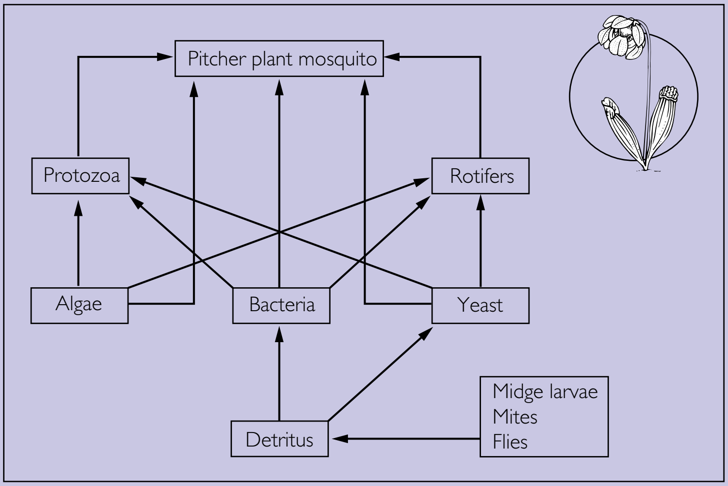


Fig. 1 The food web found in the pitcher of *Sarracenia purpurea*. (From Cochran-Stafira & von Ende 1998.)

the population of a dominant competitor, weaker competitors may be able to coexist, increasing species diversity. The interaction between nutrients, grazing and plant species richness was reviewed by Proulx and Mazumder (1998). They looked at 30 different studies containing 44 comparisons of plant species richness, nutrient availability and grazing in lake, stream, marine, grassland and forest ecosystems (Fig. 12.4). They found that all 19 comparisons from nutrient-poor ecosystems showed lower plant species richness under high grazing compared to low grazing. Only two of the 25 comparisons from nutrient-rich ecosystems showed a decrease in plant species richness when levels of grazing were high, while 14 showed increases in plant species richness. The authors concluded that high levels of grazing reduce species richness in nutrient-poor ecosystems, because resources are so limiting that plants cannot regrow fast enough to replace tissues lost to herbivory. Moreover, in nutrient-rich ecosystems, a high level of grazing allows the increase of less palatable plants, which may have been competitively excluded under low grazing pressure.

12.7 Top-down versus bottom-up control of trophic levels

Ecologists have debated whether, and under what conditions, one trophic level might control the numbers and diversity of organisms in other trophic levels. One viewpoint is that bottom-up control, or the supply of resources, is the dominant factor. This view holds that the amount of resources available to a trophic level

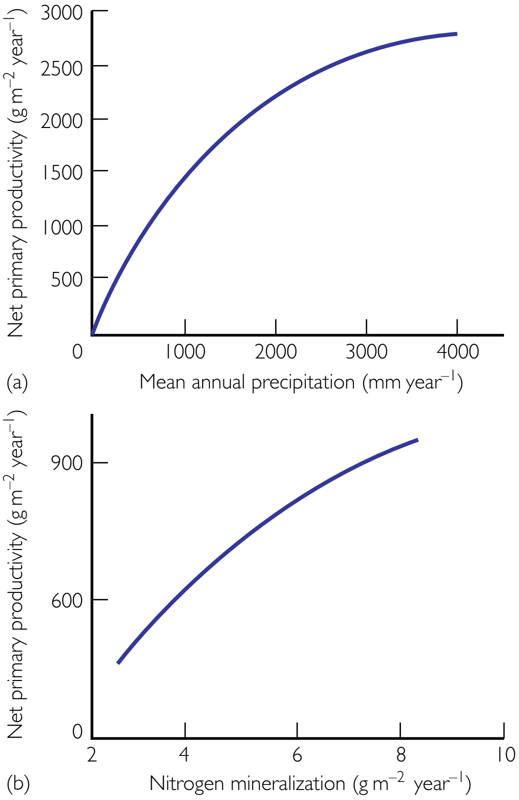


Fig. 12.3 (a) Patterns of terrestrial net productivity as a function of mean annual precipitation. (Adapted from Lieth 1973.) (b) Relationship between productivity and nitrogen mineralization for different ecosystems of Blackhawk Island, Wisconsin, USA. (Adapted from Pastor *et al.* 1984.)

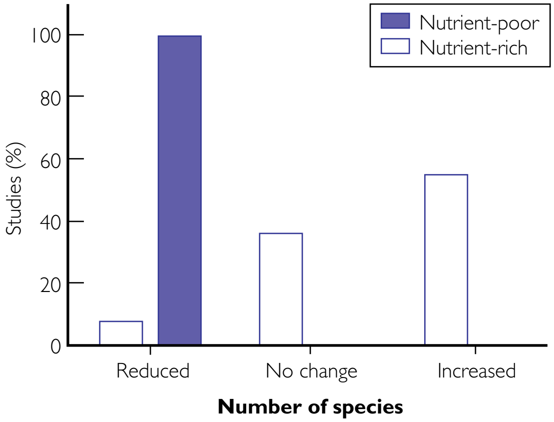


Fig. 12.4 The per cent of studies showing a decrease, an increase or no change in the number of plant species under high grazing compared to low grazing. The responses of nutrient-poor ecosystems differ compared with those of nutrient-rich ecosystems. (Data from Proulx & Mazumder 1998.)

controls the productivity of that trophic level. Because of the over-riding importance of resources, the next highest trophic level has little influence. For example, the amount of nitrogen in the soil may control plant productivity in a particular ecosystem, and the amount of herbivory by consumers does not significantly reduce plant productivity. In this view, nutrient-rich ecosystems will sustain high plant productivity, which will in turn support a large number of herbivores.

Other ecologists maintain that consumption by a higher trophic level (top-down control) is the dominant factor determining the productivity and diversity of the next lowest trophic level. For example, predators may eat so many herbivores that the herbivores never develop high enough population levels to have significant effects on the plants in a system. Top-down control of the ecosystem structure is called a **trophic cascade**, because the effects extend through several trophic levels. In this view, trophic levels alternate between limitation by consumers and limitation by resources. For example, in a three-level trophic system, predators control herbivore populations, allowing plants to be controlled by resource levels such as water or nitrogen. In a four-level system, the fourth trophic level (top consumers) would control populations of the secondary consumer to the extent that the secondary consumer would not exert control over primary consumers. Because of less control by secondary consumers, primary consumers would then develop large populations that would limit the primary producers (Fig. 12.5).

There is evidence to support both views, and aquatic systems may be fundamentally different from terrestrial systems. Rates of herbivory are generally greater in aquatic ecosystems. For example, aquatic herbivores can remove about 51% of primary productivity, three times the average amount removed by terrestrial herbivores.

Thus, aquatic herbivores have a greater ability to control primary productivity, unless they themselves are kept in check by their predators. Several manipulative studies in temperate lakes have shown cascading effects of top trophic levels on lower trophic levels (Carpenter & Kitchell 1988). Generally, these studies have shown that both abiotic and biotic factors are

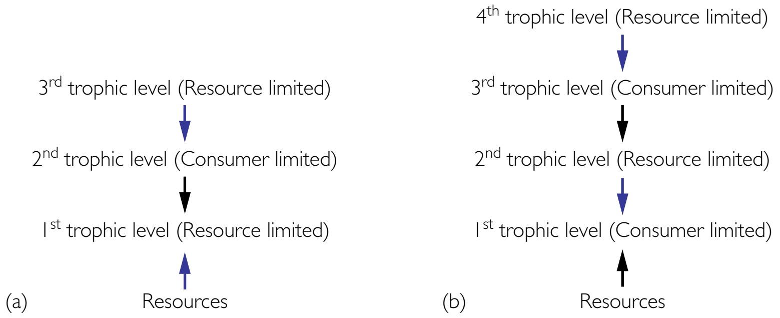


Fig. 12.5 Two trophic cascades, differing in the number of trophic levels. (a) The controls operating on different trophic levels for a system with three trophic levels. (b) A four-level trophic system. Purple arrows indicate that one trophic level exerts a dominant force on another, and black arrows indicate a lack of control.

important in a lake's productivity. The availability of nitrogen, or phosphorus, or both, will set the maximum potential level of productivity, but then the food web composition of the particular lake will set the actual amount of productivity. For example, in a lake with three trophic levels, the productivity of phytoplankton (algae), zooplankton (small animals that graze on the algae) and planktivores (small fish that eat the zooplankton) is near the limit set by nutrients. This is because the planktivores keep zooplankton populations low, which allows phytoplankton populations to increase. In contrast, in a lake with similar nutrient levels, but with four trophic levels, phytoplankton, zooplankton, planktivores and piscivores (larger fish that eat planktivores), primary productivity is usually further from the limit set by nutrients. This is because of the control of planktivores by piscivores, which allows larger zooplankton populations, which reduces phytoplankton numbers through grazing.

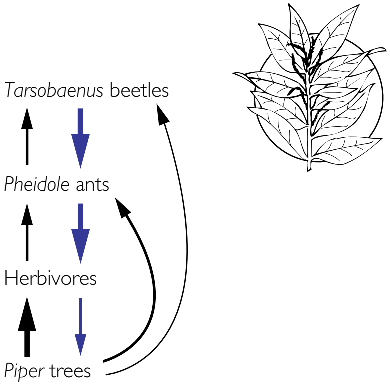


Fig. 12.6 Illustration of the feeding relationships in a tropical forest system consisting of a small tree, *Piper cenocladum*, its herbivores and their predators. Black arrows represent the effects of lower trophic levels on the levels above them, and purple arrows represent the level of control exerted by higher trophic levels on lower levels. Because the plant provides nest sites and food bodies for both ants and beetles, arrows are also drawn between these organisms. (From Letourneau & Dyer 1998.)

There are fewer studies of top-down effects in terrestrial systems. Often, it is hard to manipulate large terrestrial systems and exclude top predators. Another complication is that top predators often feed from more than one trophic level. However, Letourneau and Dyer (1998) examined a system with four trophic levels in a lowland tropical forest in Costa Rica. This system was made up of a small tree, *Piper cenocladum*, and insects in three trophic levels associated with this tree. There were a variety of insect herbivores in the second trophic level, such as moth larvae, weevils, leaf-cutting ants and beetles, that fed on the tree's fruits, leaves and branches. The third trophic level consisted of predators of these insects. The study focused on an ant species, *Pheidole bicornis*, that lives on the tree. These ants live in hollow petioles and stems, feeding on food bodies produced by the tree, as well as on other insects. The relationship between the tree and the ant is mutualistic: the ant provides herbivore protection for the tree, and the tree provides a home and food for the ant. The fourth trophic level had many members, but the study focused on a predatory beetle, *Tarsobaenus letourneae*, that specializes on the ants. Beetle larvae live inside hollow petioles with the ants. They kill adult ants and feed on both ant larvae and plant food bodies (Fig. 12.6).

To manipulate resource levels, Letourneau and Dyer transplanted cuttings of *Piper* trees to forest plots differing in light and nutrient levels. They also manipulated the abundance of the top predator. If top-down effects were important, then high numbers of *Tarsobaenus* beetles should reduce the number of *Pheidole* ants, which should raise the number of herbivores, which would reduce the growth of the trees. If bottom-up forces were dominant, then high light and nutrients should increase plant productivity, which would increase herbivore, ant and beetle numbers.

Observations from the different treatments showed that additions of beetles reduced the abundance of ants by five times, compared with systems without beetles. This resulted in a three-fold increase in herbivory on *Piper* leaves, and a two-fold reduction in leaf area of the plants. Thus, the fourth trophic level had a strong cascading effect on levels below it. Not all of the effects were immediate. While ant numbers were reduced within a few months of the addition of beetles, it took over a year before effects on the plants could be seen.

Light and soil nutrients had only small effects in these experiments, demonstrating that bottom-up effects were mitigated by the strong effects of the top predator. This study and others have now shown that the important question in bottom-up versus top-down control of trophic structure is not: Which control is most important? but rather: Under what circumstances is one more important than the other?

12.8 Ecosystem engineers

In 1997, C.G. Jones, J.H. Lawton and M. Shachak coined the term '**ecosystem engineer**' to describe organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in the environment. It is important to distinguish ecosystem engineers from the trophic and biotic interactions that occur in ecosystems. The utilization of living or dead tissues as food by a consumer or decomposer, or the direct uptake and utilization of an abiotic resource (light, water, nutrients) by an organism, are not engineering. The large effects caused by a keystone species (which influences community structure through competition or predation, see Section 11.2.2) are also not included in the concept of an ecosystem engineer. Rather an ecosystem engineer, by its physical presence or activity, determines the nature of the ecosystem.

For example, trees in a forest are ecosystem engineers. Their tissues are eaten by animals and microbes, and trees compete with each other and other plants for light, water and nutrients. Nevertheless, these interactions are not what make them engineers. Rather, it is their physical structure, including branches, bark, roots and leaf surfaces that provide shelter, resting locations and living space for myriad other organisms. Small ponds full of organisms form where water gets channelled into crotches between branches, soil cavities form as roots grow and die, and leaves and branches cast shade, reducing the impact of rain and wind, moderating temperature and increasing humidity. Dead leaves fall to the forest floor, altering raindrop impact, water runoff and heat and gas exchange. In the soil, dead leaves make barriers or protect seeds, seedlings, animals and microbes. Dead trunks, branches and leaves fall into forest streams, creating debris dams and ponds. Roots bind around rocks, stabilizing substrates and moderating the effects of storms. More species are probably affected by these processes than a tree affects directly through food or competition.

Many other species are also ecosystem engineers. In fact, ecosystem engineers occur in virtually all ecosystems. Examples include organisms that make large physical structures like corals, sphagnum bogs, kelp forests or a sea grass flat. Other, more subtle examples include microphytic crusts in deserts made up of cyanobacteria and fungi that secrete polysaccharides. These chemicals bind the desert soil and stabilize it, preventing erosion, changing runoff patterns and controlling site availability for seed germination. Other examples of engineers include animals that build or destroy massive, persistent structures; or animals that build burrows or disturb soil, such as earthworms, gophers, pack rats, mole rats, alligators, termites and tilefish. Puffins that burrow on islands can create erosion of the soil surface. Large animals like elephants, bison and grazing ungulates may serve as engineers. Not all species in the area benefit from this engineering. With the damming and flooding of areas by beavers, some terrestrial organisms are eliminated, and stream organisms that are not adapted to the still water of the pond may be displaced.

Food webs and engineers can interact to change the physical state of the environment. For example, diatoms in the Bay of Fundy secrete carbohydrates that bind sand particles. This stabilizes sand movement. Diatoms are thus engineers. They are grazed upon by small animals called amphipods. If grazing is too intense, diatom populations decrease, and sand stabilization is reduced. Sandpipers are shore birds that are predators on amphipod crustaceans. When sandpipers are present, they can control amphipod populations, which in turn increases the diatom population and sand is stabilized. When sandpipers are not present, amphipod populations increase, diatoms decrease and the sand is not stabilized.

12.9 Biogeochemical cycles

The cycling of nutrients from non-living to living components and back is one of the most important of ecosystem functions. Because this cycling involves living organisms (biology), geological processes (water movement, mountain building, erosion and soil properties) and chemical transformations, these cycles are termed **biogeochemical** cycles. Biogeochemical cycles can be divided into atmospheric or sedimentary cycles, depending upon whether the atmosphere and oceans are the primary storage pools for the nutrients, or whether sedimentary strata and other rocks are the major repository.

12.9.1 The hydrological cycle

The hydrological cycle involves the movement of water. Without the hydrological cycle, other biogeochemical cycles could not exist, ecosystems could not function, and life on Earth could not be maintained. Water moves either as vapour or as liquid in the atmosphere, oceans, streams and rivers. Energy from the sun powers the evaporation of water into the atmosphere (Fig. 12.7). This atmospheric water turns over rapidly (every 10–11 days), condensing on dust or other particles in the air and falling as precipitation over the land or ocean. Although 84% of the total evaporation of water vapour into the atmosphere occurs from ocean surfaces, only 77% of the total annual precipitation occurs over oceans. The 7% difference between ocean evaporation and precipitation is made up by river, stream and overland flow of water back to the ocean.

After precipitation falls on land, part of it is intercepted by vegetation and other surfaces. This water usually evaporates back into the atmosphere. Water that is not intercepted falls on soil surfaces, where it either infiltrates into the soil, or runs off the surface of the soil. The infiltration rate is affected by the soil type, degree of slope, vegetation and characteristics of the precipitation. A short, intense rainfall will not penetrate into the soil as effectively as a longer, less intense rainfall. Once water infiltrates into the soil, some will be held in the air pores between soil particles and some will percolate down into groundwater. Groundwater can be held in deep aquifers below the soil, or it may make its way to streams and rivers, to be carried away from the ecosystem. The water held in the air pores of the soil will be

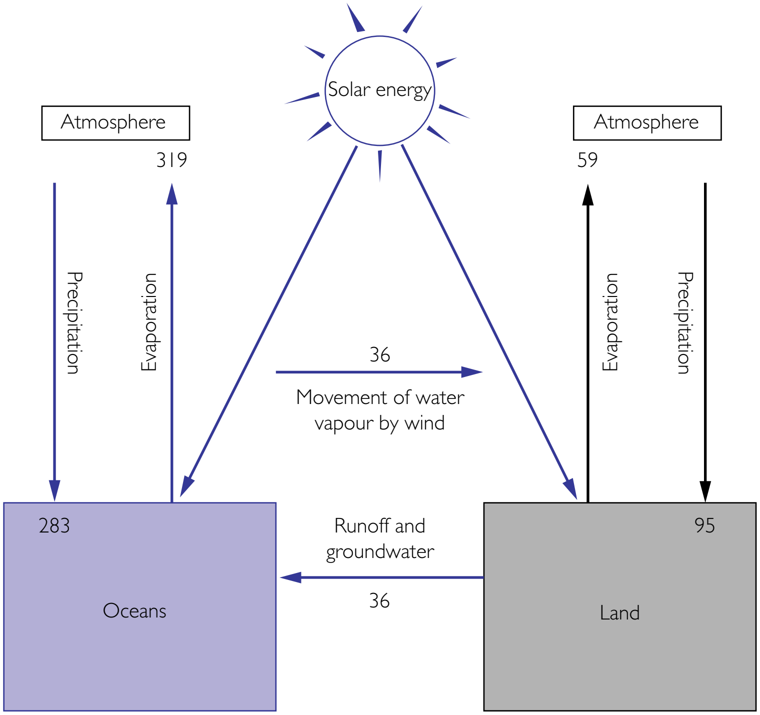


Fig. 12.7 The hydrological cycle. Numbers in the diagram represent 10^{18} g of water per year. The excess of evaporation over the oceans results in movement of water vapour from the ocean to the land. Excess precipitation over land results in the flow of surface and groundwater systems back to the oceans, completing the cycle.

taken up by plants through their roots, and lost from their leaves through transpiration. This soil water contains dissolved nutrients such as nitrogen and phosphorus. If nutrients dissolved in soil solution are not taken up by plants, they can be leached from the system. Thus, transpiration is a nutrient conservation pathway, it keeps nutrients in the ecosystem by taking them from the soil and allowing them to be incorporated into plants.

12.9.1.1 Human alteration of the hydrological cycle

Humans now use more than half of the world's runoff of freshwater. Most of the world's river systems have been altered through diversions and dams. In the United States, only 2% of the rivers run unimpeded, and within a few years, the flow of two-thirds of all the Earth's rivers will be regulated. At present, about 6% of Earth's river runoff is evaporated as a consequence of human impoundment and diversion to irrigation.

Humans also have large effects on local hydrological cycles by changing land cover. Converting forests to parking lots or houses will increase runoff dramatically. Logging of forests reduces transpiration and increases runoff, erosion of soil and leaching of nutrients.

Human alteration of the hydrological cycle can affect climate. Irrigation increases humidity, increasing precipitation and thunderstorm frequency. Land transformation to agriculture or pasture increases temperatures and decreases precipitation. Human drainage or canalization of water in large wetlands, such as the Everglades in Florida, can reduce evaporation, leading to decreases in regional precipitation.

12.9.2 The carbon cycle

Major storage pools of carbon on Earth occur in the atmosphere, oceans, sedimentary rocks and living matter. Despite its importance to global climates and plant life, only a small proportion of Earth's carbon is in the atmosphere. Most is stored as non-gaseous dissolved carbon in the oceans or as carbonate materials in sedimentary rocks (Fig. 12.8).

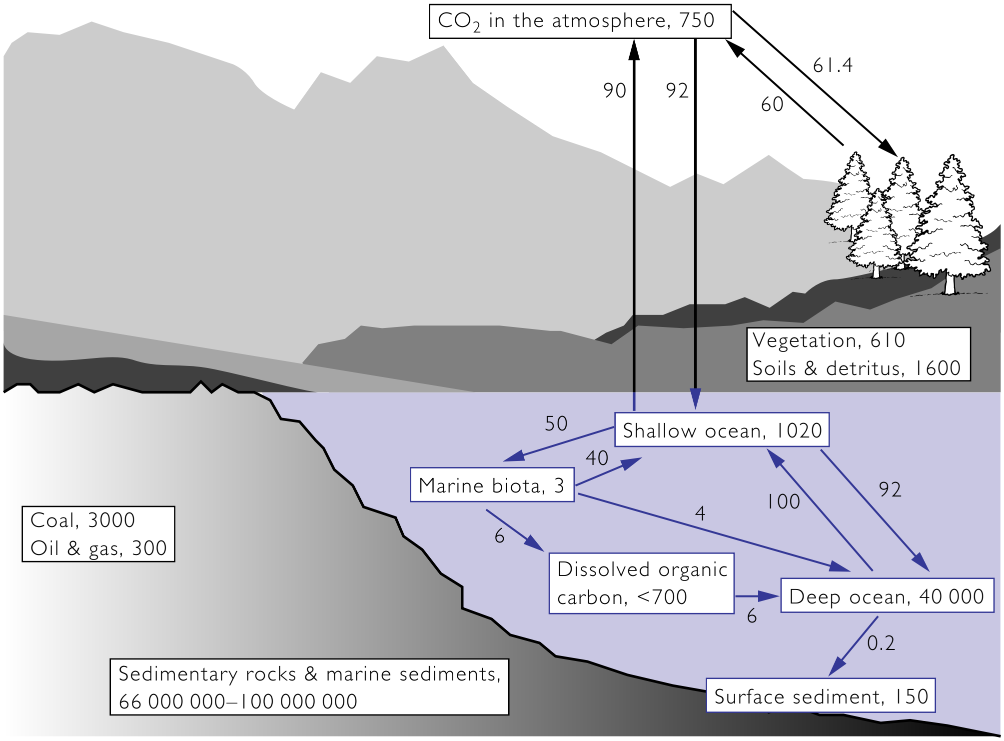


Fig. 12.8 The carbon cycle. The processes of photosynthesis and respiration dominate the major transformations and movements of carbon. Numbers are in billion tonnes of carbon per year. Numbers next to arrows represent yearly fluxes of carbon and numbers in boxes represent storage pools of carbon.

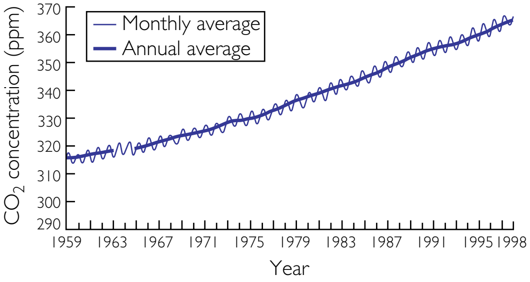


Fig. 12.9 Historic atmospheric carbon dioxide concentration in Mauna Loa, Hawaii. (Courtesy of Scripps Institution of Oceanography, University of California, 1998; with permission of UNEP GRID-Arendal.)

Although marine organisms make up a small part of the overall carbon budget of the Earth, they have a large influence on the distribution of carbon. This is because they convert soluble carbonate ions from seawater into insoluble ocean sediments, by depositing carbon in shells and skeletons that eventually sink to the bottom of the ocean. Biological processes are also important to the carbon cycle on land. Photosynthesis removes carbon from the atmosphere and places it into terrestrial storage. Respiration returns terrestrial carbon to the atmosphere pool. The great forests of Earth, especially in the tropics, are major pools of carbon.

12.9.2.1 Human alteration of the carbon cycle

The increase in carbon dioxide concentration in the atmosphere over the last 130 years represents the best-documented signal of human alteration of the Earth's system. Since measurements began in Hawaii in 1957, carbon dioxide concentrations have risen from 315 to 365 parts per million (ppm) (Fig. 12.9). Records of carbon dioxide concentration from air bubbles trapped in Antarctic and Greenland ice show that until the Industrial Revolution in the 1800s, carbon dioxide concentrations were relatively stable at about 280 ppm for thousands of years. Thus, humans have increased atmospheric carbon dioxide by about 30%, relative to preindustrial times. Humans add carbon dioxide to the atmosphere by burning fossil fuels and converting forests and grassland to agricultural and urban systems.

The carbon cycle includes the fluxes of carbon between the four main reservoirs: fossil carbon, atmosphere, oceans and terrestrial ecosystems. Human activities have altered carbon storage and fluxes between all four of these reservoirs (Fig. 12.10). Fossil fuel combustion and cement production adds approximately 5.5 billion tonnes of carbon dioxide to the atmosphere each year. Land-use changes, primarily deforestation, add another 1.6 billion tonnes, to give a total of 7.1 (± 1.1) billion tonnes of carbon per year added to the Earth's systems through human activities.

Of the carbon released, about 3.2 billion tonnes accumulates in the atmosphere, resulting in the observed increase in carbon dioxide concentration. Oceans are estimated to take up approximately 2.0 billion tonnes per year. Forest sinks and sources are highly variable. Current estimates include a yearly uptake of around 0.5 billion tonnes of carbon through the regrowth of northern temperate forests, an additional 1.0 billion tonnes taken up due to the stimulation of plant growth from increased atmospheric carbon dioxide, and perhaps 0.6 billion tonnes taken up due to a nitrogen fertilization effect (Section 12.9.3.1.).

However, land-use changes are a tremendous source of uncertainty. Urban and agricultural lands are less strong carbon sinks than forests. Changes in land use from 1850 to 1990 are thought to have released 122 (± 40) billion tonnes of carbon into the atmosphere. Future scenarios of land-use changes can result in carbon storage or release ranging from 100 to 300 billion tonnes over the next century. Obviously, with the size of these numbers, there is great variation in projections of future changes in the global carbon cycle.

12.9.3 The nitrogen cycle

Nitrogen ranks fourth, behind oxygen, carbon and hydrogen, among the commonest elements in living systems. It is a necessary component of proteins, nucleic acids, chlorophyll and other common organic compounds. However, despite its presence as the major gas in Earth's atmosphere, nitrogen is often the most limiting nutrient to ocean and terrestrial productivity. This is because the chemical form of nitrogen in the atmosphere, N_2, cannot be used by the vast majority of organisms. N_2 must first be converted into biologically useful forms such as nitrate and ammonia. This process, called **nitrogen fixation**, is performed by only a few species of bacteria and cyanobacteria. Nitrogen fixation also occurs during lightning strikes and volcanic activ-

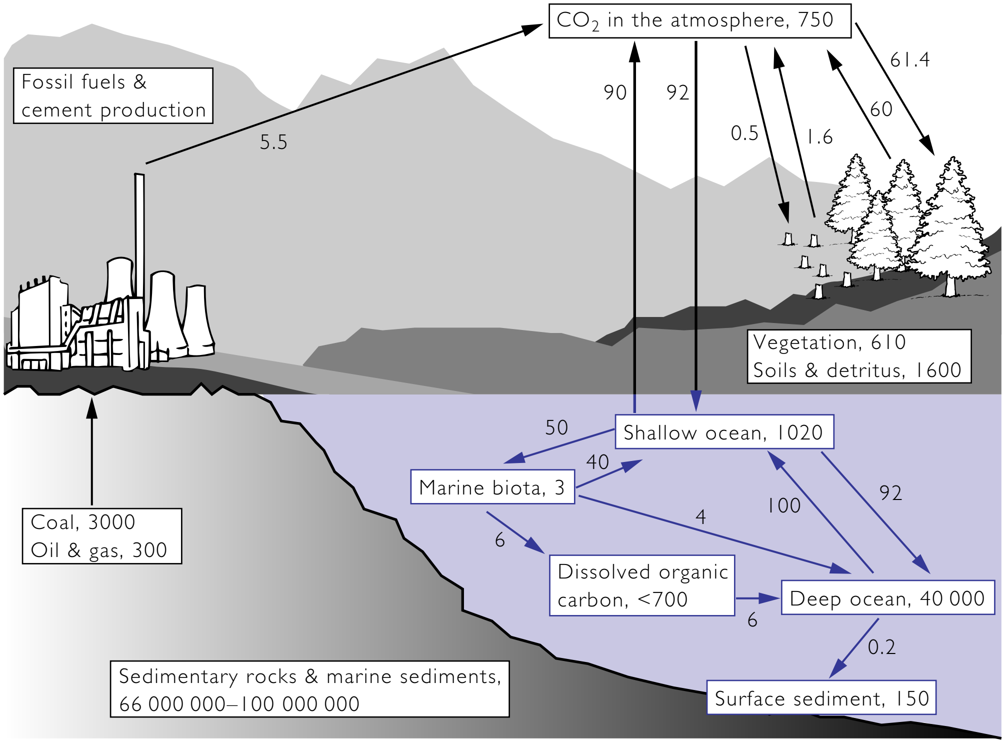


Fig. 12.10 The carbon cycle redrawn to indicate the estimates of human contributions between 1980 and 1989. Numbers are in billion tonnes of carbon per year. Numbers next to arrows represent yearly fluxes of carbon and numbers in boxes represent storage pools of carbon. (Adapted from Schimel 1995.)

ity. Once nitrogen is fixed, it is available for uptake by plants and enters the trophic structure of ecosystems (Fig. 12.11).

The amount of nitrogen being fixed naturally at any one time is small in relation to the pool of previously fixed nitrogen that is in living and dead matter. Most of the previously fixed nitrogen is locked up in soil organic matter, and must be decomposed by microbes before it becomes available again to living organisms. Nitrate and ammonia are soluble in water and are relatively mobile in the soil and in aquatic systems. They are easily leached from soils if they are not taken up by plant roots. Nitrogen, unlike carbon dioxide, is not respired directly back into the atmosphere. It must be converted to inorganic molecules, from amino acids or urea, in several stages.

Micro-organisms play major roles in the nitrogen cycle in addition to nitrogen fixation. They are involved in several chemical transformations. **Ammonification** is the process by which bacteria and fungi convert urea and amino acids to ammonia. Ammonia can be lost to the atmosphere, taken up by plants or converted to other forms of nitrogen. **Nitrification** is the conversion of ammonia to nitrate. This process is performed by bacteria that gain energy from the reaction. Nitrate can be transported in water or taken up by plants. **Denitrification** is the process where bacteria convert nitrate to nitrite, and then to N_2, where it can be lost back to the atmosphere. Movement of nitrogen among different organisms accounts for about 95% of all nitrogen fluxes on Earth.

12.9.3.1 Human alteration of the nitrogen cycle

In 1997, the first publication of a new series on issues in ecology was published by the Ecological Society of America. This paper addressed the human alteration of the global nitrogen cycle (Vitousek *et al.* 1997a). Nitrogen is unique in that there is a huge atmospheric reservoir that must be combined with carbon, hydrogen

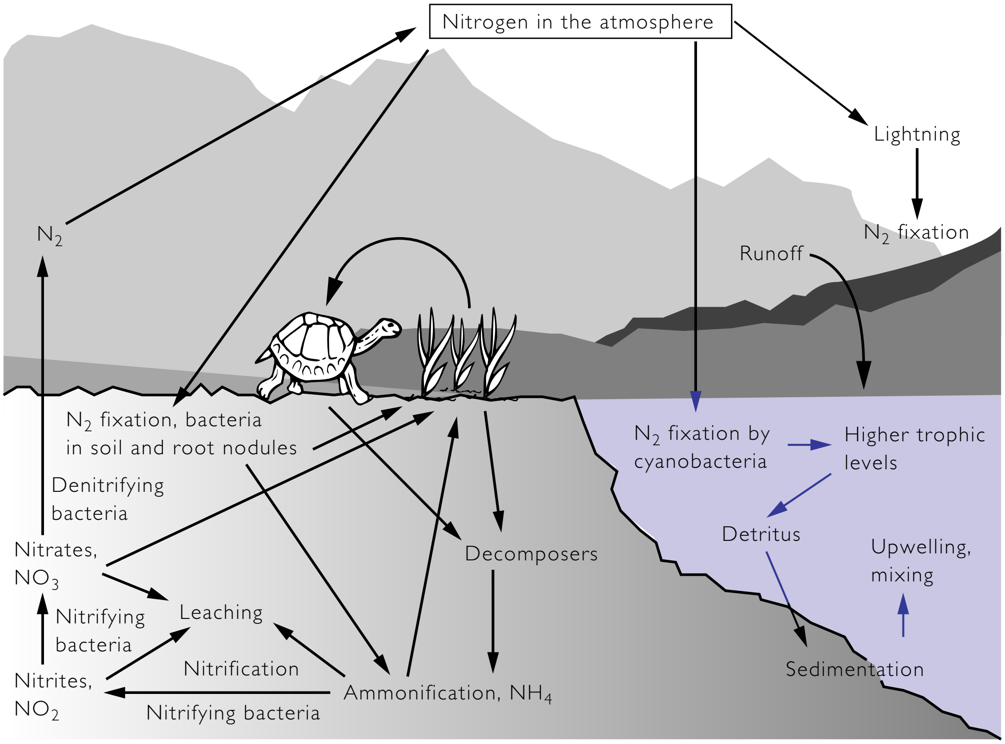


Fig. 12.11 The nitrogen cycle. The arrows in this diagram represent the various pathways and transitions of nitrogen in an ecosystem. Most of the nitrogen cycling occurs through food webs. Transformations between different forms of nitrogen by micro-organisms are essential to this cycle.

or oxygen before it can be used. Before human industrialization, lightning and micro-organisms were the primary mechanisms for nitrogen fixation. The supply of fixed nitrogen is a major factor in the type and diversity of plants in an ecosystem, the population dynamics of grazing animals and their predators, and the primary productivity and nutrient cycles of many ecosystems.

Prior to industrialization, about 90–130 million tonnes of nitrogen was biologically fixed each year on land. Fertilizer manufacture by humans in 1990 was about 80 million tonnes per year. In addition to fertilizers, agricultural land devoted to leguminous crops capable of nitrogen fixation, and the cultivation of rice (which is associated with nitrogen-fixing micro-organisms) has added another 32–53 million tonnes of nitrogen to Earth's ecosystems. The burning of coal, oil and gasoline in automobiles, factories and power plants adds another 20 million tonnes of available nitrogen per year to the atmosphere. Thus, humans have more than doubled the amount of nitrogen input into terrestrial and marine ecosystems.

In addition to increasing the amount of fixed nitrogen available worldwide, humans have also affected the turnover of nitrogen from long-term storage pools. Although estimates of mobilization of nitrogen have a great deal of uncertainty in them, these human activities could release half as much nitrogen again to the Earth's biosphere as is released in fertilizer manufacture, fossil fuel burning and cultivation of legumes. The burning of forests, wood fuels and grasslands emits more than 40 million tonnes of nitrogen per year. The draining of wetlands allows organic material that is decomposing slowly in anoxic conditions to be exposed to oxygen, which greatly increases the rate of decomposition. Estimates of release of nitrogen through this pathway are approximately 10 million tonnes per year. Land clearing for crops mobilizes another 20 million tonnes.

One of the consequences of human activity is the increase in nitrous oxide (N_2O), nitric oxide (NO) and ammonia (NH_3) in the atmosphere (Fig. 12.12). Nitrous oxide is a long-lived **greenhouse gas** that

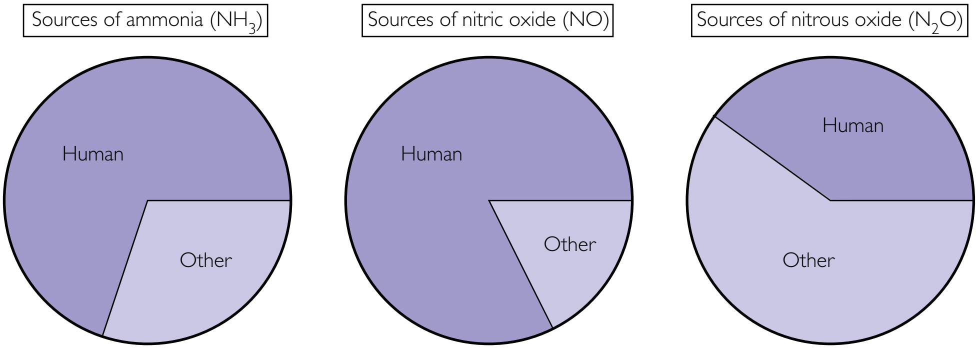


Fig. 12.12 Estimates of the percentage of nitrogen-containing trace gases that are released by human activities. (Data from Vitousek *et al*. 1997a.)

contributes to global climate change. Nitrous oxide absorbs infrared radiation in wavelengths that are not captured by carbon dioxide. Thus, its increase contributes significantly to predictions of global warming. Additionally, as nitrous oxide rises into the stratosphere, it catalyses reactions that destroy ozone, which absorbs ultraviolet radiation. The concentration of nitrous oxide is currently increasing at about 0.2–0.3% per year.

Nitric oxide is shorter lived than nitrous oxide because it is more reactive in the lower atmosphere. Nitric oxide catalyses the formation of photochemical smog, and in the presence of sunlight combines with oxygen and hydrocarbons to form ozone. Ground-level ozone negatively affects human health, as well as the productivity of forests and crops. Nitric oxide can also be transformed into nitric acid in the atmosphere, forming a major part of acid rain.

Human addition of nitrogen to the biosphere may also increase primary productivity and carbon storage in nitrogen-limited ecosystems. At first glance, this may seem to be a desirable outcome of human activities. Increases in carbon uptake and storage in forest, wetland and tundra ecosystems may be a direct consequence of extra sources of nitrogen. However, addition of nitrogen to natural ecosystems eventually leads to limitation by other factors such as phosphorus, calcium or water. This is called **nitrogen saturation**.

Nitrogen saturation leads to increased losses of nitrogen and elements such as calcium and potassium that are essential for long-term soil fertility. For example, as ammonium builds up in soils, more and more nitrate is formed from bacterial transformation. This acidifies the soil, which enhances emissions of nitrous oxide and the leaching of nitrate into streams or groundwater. As nitrate is leached, it carries with it calcium, magnesium and potassium. As calcium is depleted in soils and soil pH drops, aluminium ions are mobilized, reaching toxic concentrations that damage tree roots and kill fish in streams. The more nitrate and ammonium that build up in a soil, the more imbalanced the nutrients become. This may lead to stunted growth and eventual death of plants.

Nitrogen saturation also accelerates losses in species biodiversity, affecting most strongly plants adapted to low nitrogen conditions, and the animals and microbes that are associated with these plants. A long-term experiment where nitrogen was added to grasslands in England showed a marked decrease in species diversity in fertilized plots (Silvertown 1980). This was attributed to increased competitive dominance by a few nitrogen-responsive grass species, and the loss of other species adapted to lower nitrogen conditions. In the Netherlands, where some of the highest rates of nitrogen deposition occur, species-rich heathlands have been converted into grasslands and forests with significantly lower species diversity.

In extreme cases of nitrogen saturation, little nitrogen uptake may occur in soils. This results in dramatically increased nitrogen inputs into groundwater, lakes, ponds, streams, rivers and eventually oceans. Estimates of increases of nitrogen into rivers draining into the North Atlantic Ocean basin range between two and 20 times preindustrial levels. In rivers of the northeastern United States, nitrate concentrations have increased by a factor of between three and 10 since 1900. Increases in nitrate concentration of groundwater in agricultural areas have also been documented. High levels of nitrate in drinking water cause human

Table 12.2 Adverse effects of excess nitrogen on lakes, reservoirs, rivers and coastal oceans. (Adapted from Carpenter *et al.* 1998.)

Increased phytoplankton biomass
Shifts in phytoplankton species to bloom-forming species that may be toxic or inedible
Increases in biomass of gelatinous zooplankton
Increased biomass of benthic and epiphytic algae
Changes in macrophyte species composition and biomass
Death of coral reefs and loss of coral reef communities
Decreases in water transparency
Taste, odour and water treatment problems
Oxygen depletion
Increased deaths of fish
Loss of desirable fish species
Reductions in harvestable fish and shellfish
Decreases in aesthetic value

health problems, especially for infants. Nitrates are converted into nitrites by intestinal microbes. Nitrite in the bloodstream converts haemoglobin into methaemoglobin, which does not carry the levels of oxygen needed by tissues in the body. This can lead to anaemia, brain damage or death.

Increased nitrogen deposition into streams, lakes and rivers can also lead to **eutrophication**, blooms of nuisance and toxic algae, and reduced productivity of fisheries (Table 12.2). Additionally, nitric acid deposition can acidify lakes and streams, killing pH-sensitive plants and animals, thereby reducing productivity and biodiversity. Spring runoff of snowmelt containing high levels of nitric acid can lead to an acid pulse exceeding the pH tolerance of many species and especially affecting young fish.

12.9.4 The phosphorus cycle

Unlike carbon and nitrogen, the phosphorus cycle is a sedimentary cycle. New phosphorus becomes available through the weathering of rock or the uplift and exposure of marine sediments (Fig. 12.13). Phosphorus also has more limited mobility in soil solutions than does nitrate or ammonium. Phosphate dissolves readily in acidic or anoxic water, but with the presence of oxygen and neutral pH, it forms complexes with calcium or iron and becomes immobile. Any phosphorus that

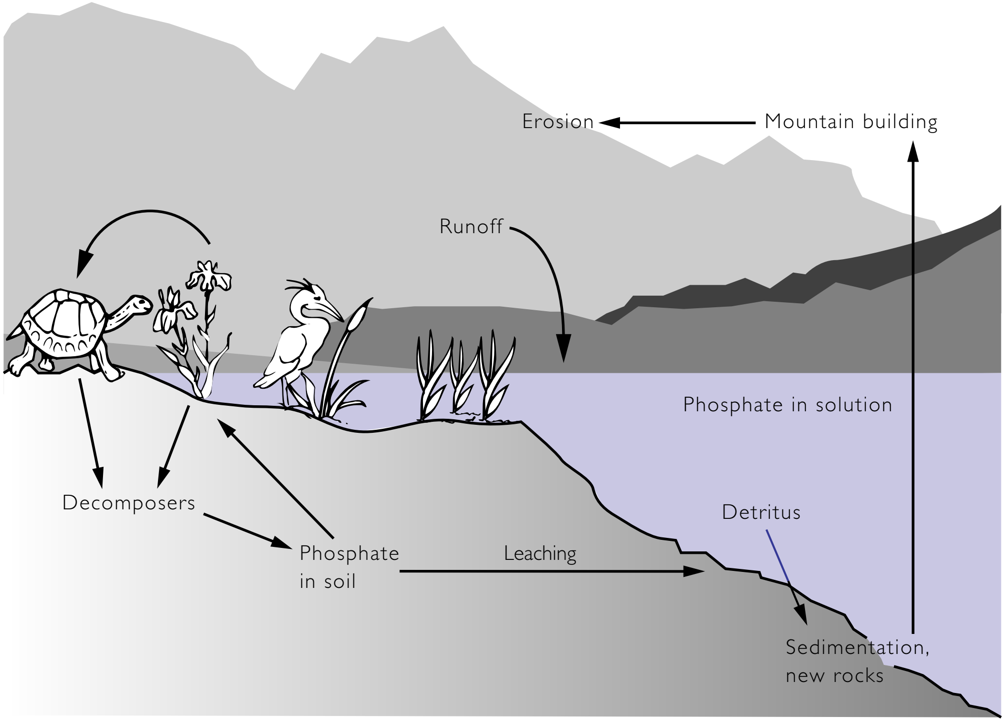


Fig. 12.13 The phosphorus cycle. Most of the cycling of phosphorus occurs locally, due to the absence of an atmospheric component.

becomes available is rapidly taken up by plants. Once incorporated into animals or plants, phosphorus is recycled through decomposition of excretory products and detritus.

12.9.4.1 *Human alteration of the phosphorus cycle*

Humans have had direct effects on the phosphorus cycle through mining phosphate-rich rock for fertilizers, and then applying this fertilizer to agricultural land. Much of the added phosphorus runs off into lakes, rivers and oceans. On a global scale, phosphate mining has more than doubled the supply of phosphorus to coastal seas compared to preindustrial levels. In some urban and agricultural areas, phosphorus availability is 10–100 times greater than preindustrial levels. Additionally, in urban areas, discharge of incompletely treated human waste into streams or rivers can be a significant source of phosphorus.

Phosphorus supply often limits the primary productivity of aquatic systems. For example, a typical freshwater lake may have concentrations of available phosphorus that are 0.0001 times that of living cells. Therefore, increased levels of phosphorus caused by human activities can lead to increased productivity of terrestrial or aquatic systems. It can also result in eutrophication of aquatic and marine systems, with many of the same effects as increased nitrogen supply (Table 12.2).

If productivity is increased, why are phosphorus addition and eutrophication cause for concern? The answer lies in the fact that productivity increases are short-lived, while ecosystem changes and effects on the biodiversity of aquatic systems are long-lasting. Eutrophication brings with it the growth of undesirable algal species, followed by massive die-offs and decomposition. Decomposition uses oxygen, depleting the water column of this necessary gas; most sensitive to oxygen decreases are desirable gamefish and other organisms high on the trophic pyramid.

Chesapeake Bay, located on the Atlantic coast of North America, is one of the largest estuarine systems in the world. However, there are dense human populations around this estuary. The current situation in Chesapeake Bay is the result of excess nutrient loading from sewage discharge, farm land runoff, deforestation, and overharvesting and disease mortality of oysters. Oysters feed by filtering large amounts of water for small food particles. In the past, high populations of oysters filtered so much water that they had a major effect on water quality and clarity. Additions of nitrogen and phosphorus have led to significant eutrophication and changes in water quality in Chesapeake Bay. In certain areas, oxygen concentrations in lower water layers often decline to stressful levels in the summer (Fig. 12.14). This is especially marked if temperature differences between the top and bottom water layers develop, thereby reducing mixing between layers. This allows microbial decomposition of a large phytoplankton biomass in the bottom layers to deplete oxygen.

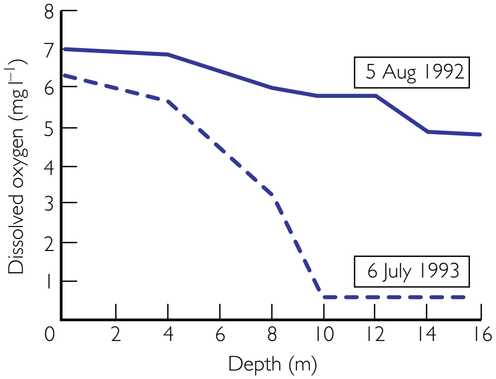


Fig. 12.14 Dissolved oxygen profiles for the Patuxent River, a tributary of Chesapeake Bay, at different times in the summer. (From Breitburg *et al.* 1997.)

Breitburg and co-workers (1997) were interested in how these low oxygen levels might affect aquatic food webs. The food web they examined involved juvenile striped bass, sea nettles (jellyfish), fish larvae and zooplankton (small animals such as copepods that eat phytoplankton) (Fig. 12.15).

Naked goby (*Gobiosoma bosc*) and bay anchovy (*Anchoa mitchilli*) are the two most abundant fish larvae in Chesapeake Bay. They are important prey of juvenile striped bass (*Morone saxatilis*), which is an important commercial and sport fishing species. Sea nettle (*Chrysaora quinquecirrha*) is a jellyfish that is an important predator in the bay. The copepod *Acartia tonsa* is an important component of zooplankton. All species overlap in the salinities and oxygen levels that they are naturally found in. However, species differ in their tolerances and optima for salinity and oxygen.

The effects of low oxygen were different for different organisms. Low oxygen levels had the effect of increasing predation on fish larvae by sea nettles, but decreasing predation on fish larvae by juvenile striped

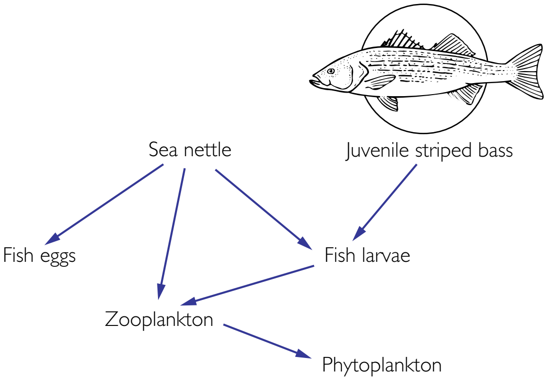


Fig. 12.15 A Chesapeake Bay food web involving the sea nettle (*Chrysaora quinquecirrha*), fish larvae—primarily bay anchovy (*Anchoa mitchilli*) and naked goby (*Gobiosoma bosc*)—and juvenile striped bass (*Morone saxatilis*). (Data from Breitburg *et al.* 1997.)

bass. The increased predation by sea nettles on fish larvae was due primarily to reduced escape behaviour by the larvae. Fish larvae are more sensitive to oxygen depletion than jellyfish. At low oxygen concentrations, they swim slower and cannot escape as well. Juvenile striped bass are even more sensitive to oxygen than fish larvae, thus their ability to catch fish larvae was reduced at lower oxygen.

In contrast to the effect on fish larvae predation, the low oxygen reduced fish egg predation by sea nettles. Fish eggs float passively in water currents. However, because the nettles swam and contracted their bells more slowly, the capture rate for floating or passive objects was decreased.

All organisms in the food web migrated vertically to avoid low oxygen. Fish migrated first and most actively. However, in areas where low oxygen occurs throughout the depth profile, fish cannot avoid low oxygen. Thus, the more widespread the low oxygen levels, the greater the potential for low oxygen to cause major alterations in the food webs of Chesapeake Bay and its tributaries. Because of the differential sensitivity of organisms to oxygen, low oxygen also has the potential to affect the relative abundance of species that are important components of this estuarine ecosystem.

12.10 Human domination of Earth's ecosystems

With the explosive growth of the human population, humans are appropriating a growing percentage of total biosphere production. Current estimates are that humans use over 35–40% of terrestrial primary production for food, fibre, food for livestock and fuels. In addition, global productivity is indirectly modified through the conversion of forests and grasslands to farms, cities or grazing lands.

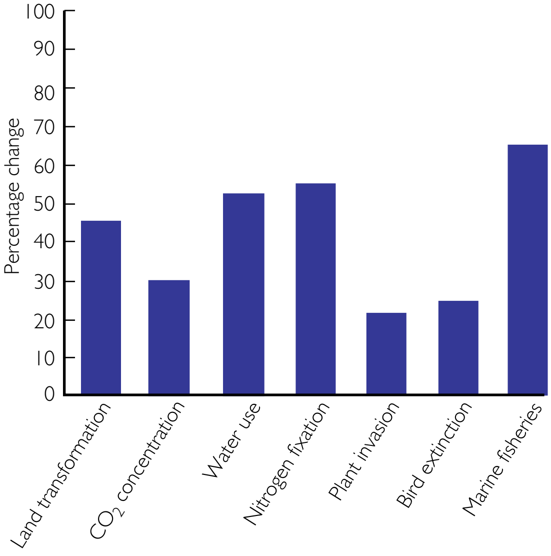


Fig. 12.16 Human-caused changes in the major components of Earth's systems, expressed as a percentage of the total resource. (Data from Vitousek *et al.* 1997b.)

About 8% of Earth's aquatic primary production is used to support human fisheries. However, since fishing is concentrated in coastal areas, about 25–35% of the primary production of these areas is used by humans. In addition, humans use about 26% of global evapotranspiration to grow crops, and about 54% of available freshwater runoff for agriculture, industry and cities. As we have seen in looking at ecosystem engineers, most organisms alter their environment. However, as the human population has grown and technology has developed, the scope and nature of this modification has changed dramatically (Fig. 12.16). Most aspects of the structure and function of Earth's present-day ecosystems cannot be understood without looking at the influence of humans.

The growth of the human population, and use of Earth's resources, is maintained by agriculture, industry, international commerce, and recreational and commercial fishing and hunting (Fig. 12.17). These activities transform land, altering biogeochemical cycles and

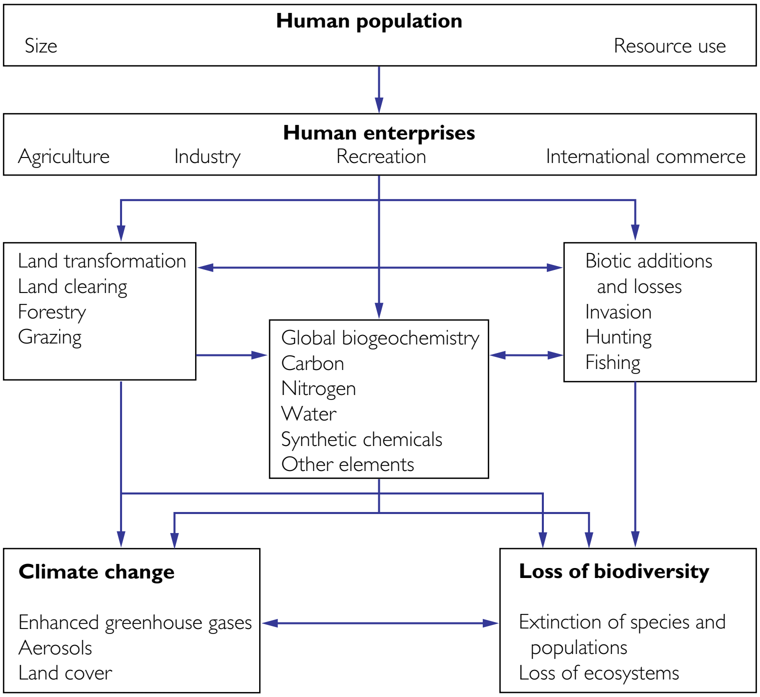


Fig. 12.17 A schematic of the direct and indirect effects of humans on Earth's ecosystems. (Reprinted with permission from Vitousek *et al*. (1997) Human domination of earth's ecosystems. *Science* **277**: 494–499. Copyright 1997, American Association for the Advancement of Science.)

changing biodiversity. Estimates of the fraction of land surface transformed or degraded by humans range from 39% to 50% (Fig. 12.16). Land transformation includes placing 10–15% of the Earth's surface into row-crop agriculture or urban areas, 6–8% into pastureland, and affecting almost all of it by hunting or other activities that involve extracting resources.

Estimates of land transformation are conservative, because much of the land that has not been transformed has been fragmented. **Fragmentation** alters species composition, nutrient fluxes and microclimate in the remaining patches. Land transformation represents one of the major driving forces in the worldwide loss of biodiversity. It can also affect climate at local and regional scales. It contributes about 20% to current human-related carbon dioxide emissions, and more to the increasing concentration of methane and nitrous oxide in the Earth's atmosphere. Finally, land transformation is associated with increased runoff of sediments and nutrients, and with resultant changes in stream, lake, estuarine and coral reef ecology.

Humans also have drastic effects on marine ecosystems. Sixty per cent of the world's population is located within 100 km of ocean coasts. Coastal wetlands have been drained and cleared for urban and agricultural uses. About 50% of the mangrove ecosystems in the world have been altered or destroyed by human activity. Humans use approximately 25% of the productivity in upwelling areas and 35% of the productivity in temperate continental shelves. In 1995, 22% of the world's fisheries were classified as overexploited or depleted, and 44% were at the limit of exploitation (Fig. 12.18).

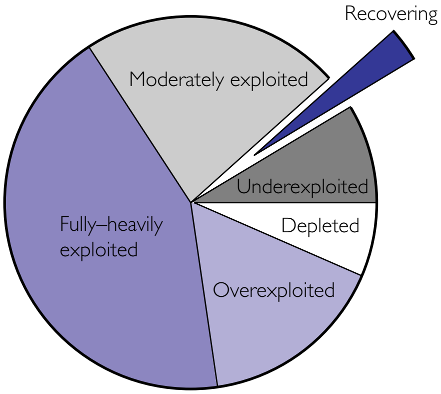


Fig. 12.18 The degree of exploitation of the world's fisheries. (Data from Botsford *et al*. 1997.)

Complicating the overall use of resources in these fisheries is the damage caused by fishing methods. Non-target catches that are discarded average 27 million tonnes annually, about one-third of the total catch. Dredging and trawling damage seafloor habitats and may reduce their long-term productivity and biodiversity.

12.11 Human interactions with ecosystem function

Ecosystems provide many services to humans, including harvestable production, nutrient regeneration, medicines, breakdown and storage of pollutants, crop pollination, pest control and maintenance of clean water supplies. Two of the most dramatic ecological trends of the past century have been losses in biotic diversity and alterations to the structure and function of ecosystems. Ecosystem processes such as productivity, nitrogen mineralization and nitrate leaching respond directly to human activities. These processes also respond to changes in atmospheric composition and climate. Human-induced changes in biodiversity result from habitat conversion, land-use change and the introduction of exotic species.

12.11.1 Human modification of Earth's biological resources

Extinction is a natural process, but the current rate of loss of genetic variability, of populations and of species is far higher than the background rate that existed in the past. Recent calculations suggest that rates of species extinction are 100–1000 what they were before humanity's dominance. Land transformation is the single most important cause of extinction, but hunting and commercial uses have also played important roles. As many as 25% of Earth's bird species have gone extinct as a result of human activity over the last 2000 years, especially on oceanic islands. It is estimated that 11% of the remaining bird species, 18% of the mammals, 5% of the fish and 8% of the plants are currently threatened by extinction.

A disproportionate number of large mammals either have gone extinct or are threatened. These large animals are often ecosystem engineers or keystone species and have large impacts on ecosystem function and structure. Their loss has a domino effect that can affect the survival of other species.

Table 12.3 Types of effects caused by exotic, invasive plant species. (Adapted from Gordon 1998.)

Ecosystem level effects

- Altered geomorphological processes
  - Erosion rate
  - Sedimentation rate
  - Elevation
  - Water channels
- Altered hydrological cycling
  - Water-holding capacity
  - Water-table depth
  - Surface-flow patterns
- Altered biogeochemical cycling
  - Nutrient mineralization rate
  - Nutrient immobilization rate
  - Soil or water chemistry
- Altered disturbance regime
  - Type
  - Frequency
  - Intensity
  - Duration

Community/population level effects

- Altered stand structure
  - New life form
  - Vertical structure
- Altered recruitment of natives
  - Allelopathy
  - Microclimate shift
  - Physical barrier
- Altered resource competition
  - Light absorption
  - Water uptake
  - Occupying growing sites
  - Nutrient uptake

The high rates of species loss do not reflect the fact that even greater losses have occurred in genetic diversity. As ranges decrease and locally adapted populations are lost, genetic variability is reduced in the species as a whole. This reduces the evolutionary potential of the species and its resilience in response to future changes.

Humans are homogenizing the world's biota by transporting species to new habitats at an unprecedented rate. Invading, non-native species are a problem throughout the world, and they have dramatic effects on native ecosystems (Table 12.3). In an analysis of the effects of introduced plant species on Florida ecosystems, Gordon (1998) found that 6 of 31 invasive plant species altered geomorphology, such as increasing rates of sedimentation and erosion (Fig. 12.19). Six species altered the hydrological cycle through processes such as

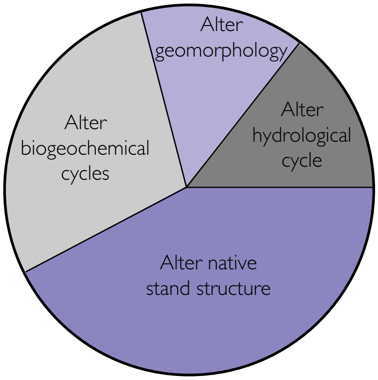


Fig. 12.19 Percentage of introduced species causing ecosystem perturbation of various types in Florida. Data are derived from a study of 31 introduced species. (Data from Gordon 1998.)

altering water-table depth, or surface-flow patterns. Ten to twelve species altered biogeochemical cycles by being nitrogen fixers, altering water chemistry or changing litter accumulation. Up to 18, or 58%, of the exotic species altered native stand structure by adding vine life forms, introducing trees to grasslands, or dominating competition for light in native stands of vegetation.

On many islands, more than 50% of the current plant species are non-native, and in many continental areas over 20% of the flora are non-native. Harbours and estuaries that incur heavy shipping traffic are also prone to introduction of exotic species. Studies in San Francisco Bay have shown that an average of one new species has been established every 36 weeks since 1850. This rate is increasing steadily, with one new species becoming established every 24 weeks since 1970, and one new species established every 12 weeks over the last 10 years. Many of these invasions are irreversible and can cause drastic changes in ecosystem function (Box 12.2). As a case in point, the introduction of exotic grasses into the western United States has altered the fire regime, reduced grazing quality and threatened many native species with extinction. Other introduced species can adversely affect human health and cause economic losses through loss of crops and the need to repair damage caused by exotic species.

12.11.2 Biodiversity and ecosystem function

Species differ in the rates and ways in which they use resources, in their effects on the physical environment and in interactions with other species. Thus, changes in species presence, absence or composition may alter ecosystem processes. For example, the presence of ecosystem engineers such as elephants will affect the proportion of grasses, trees and shrubs in an ecosystem. This, in turn, will affect interception of rainfall, evapotranspiration and regional temperatures and rainfall. Therefore, biotic changes can influence ecosystem processes sufficiently to alter the future state of the world's ecosystems and the services they provide to humans. Ecologists are only now beginning to establish the theoretical, empirical and experimental frameworks to understand and predict how changes in species composition affect ecosystem processes (Fig. 12.20).

There is growing recognition in the ecological community that biodiversity may have important consequences for ecosystem processes. First, the number of species in a community is a substitute measure of the probability of the presence of species with important traits, for example nitrogen-fixing plants. Second,

Box 12.2 Exotic species are a major cause of the loss in biodiversity

It is estimated that the introduction of exotic species is second only to land transformation in causing species extinctions and loss of biodiversity. As an example, the introduction of the brown treesnake (*Boiga irregularis*) into Guam (the largest island of Micronesia) around 1950 led directly or indirectly to the extinction of 12 out of 17 native bird species and 5 out of 12 native reptile species. In addition, the Mariana fruit bat (*Pteropus mariannus* ssp. *mariannus*) has been reduced to one surviving colony on the island. This snake was able to eliminate so many different species because: (i) it was a superior climber, able to access nests and roosting sites; (ii) it was nocturnal, attacking many animals while they slept; and (iii) it was a generalist. As a generalist, it was able to eat many different prey, allowing it to maintain its own population when a particular prey species became rare.

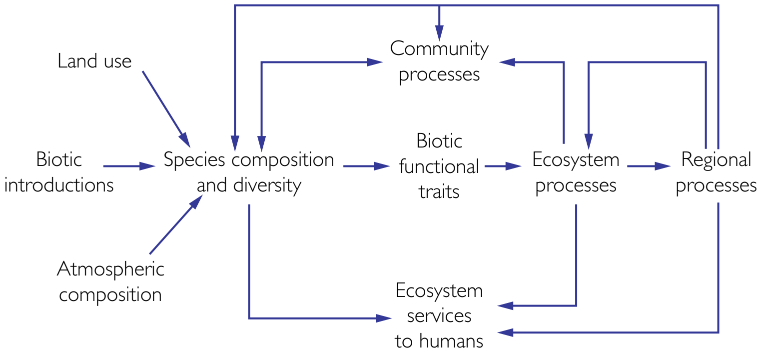


Fig. 12.20 The linkages between species composition, diversity and ecosystem processes such as productivity and nutrient cycling. Regional processes include trace gas fluxes to the atmosphere and nutrient fluxes between terrestrial and aquatic systems. Community processes include competition, mutualism, pathogenicity and predation. Ecosystem services are benefits to humans from ecological processes. (Reprinted with permission from Chapin *et al*. (1997) Biotic control over the functioning of ecosystems. *Science* **277**: 500–504. Copyright 1997, American Association for the Advancement of Science.)

greater diversity allows a greater range of traits to be represented in the ecosystem, increasing the chance for more efficient resource use in variable environments. Third, higher species diversity may increase ecosystem stability by the following:

1 By leading to greater diversity in trophic interactions, alternative pathways for energy flow are provided and energy flow between trophic levels is stabilized.

2 By reducing the susceptibility of the ecosystem to invasion by species with novel traits.

3 By slowing the spread of pathogens through increasing the average distance between susceptible hosts.

There are different hypotheses about the mechanism whereby biodiversity enhances ecosystem function. One hypothesis states that biodiversity is analogous to rivets on an airplane. Several rivets may be lost without detrimental effects. However, eventually the loss of one rivet will lead to catastrophic consequences.

The redundancy hypothesis states that some ecosystem processes can be carried out by a relatively small number of species. Other species are redundant or less necessary for maintaining function. Thus, ecosystems may lose a certain amount of biodiversity without compromising their ability to carry out their functions.

Finally, there is the insurance hypothesis. In this scenario, species replace each other in functions when stress or environmental change occur, so species diversity is especially important when conditions change. Thus, the loss of species may have unforeseen consequences when extreme events such as drought or storms occur.

These disparate views may be reconciled by grouping organisms into **functional groups**, and examining the effects of functional group diversity on ecosystem structure and function. As described in Section 11.3, a functional group is similar to a guild—it is a group of species that serve similar functional roles in an ecosystem. For example, there is the functional group of primary producers, or plants, that form the base of the trophic structure of an ecosystem. This functional group could be subdivided into functional groups of grasses or trees, each of which would access and use resources differently. Differences in the representation of different functional groups can lead to large-scale changes in ecosystems in response to the environment. For example, rising carbon dioxide concentrations can reduce plant transpiration, increasing the level of soil moisture. This may shift the competitive balance in the community from grasses to shrubs, causing replacement of grasslands by shrublands or forests. These changes can in turn feed back into climate change by altering regional temperature and precipitation. An ecosystem may be especially susceptible to the loss of a species if it is the sole member of a functional group.

Species differences within the same functional group can provide stability or increase resilience and resistance to change. This is because a decrease in one species may be compensated for by an increase in another species. In the grasslands of Minnesota, David Tilman found that plots with higher plant diversity maintained higher productivity during drought than plots with lower diversity (Tilman *et al*. 1996). He hypothesized that this was due to the presence of drought-tolerant species in higher diversity plots, which allowed productivity to be maintained.

In Western Australia several species of *Acacia* (a small tree in the pea family that forms mutualisms with bacteria in its roots that fix atmospheric nitrogen) differ in their temperature threshold for germination. Different species will germinate after fires of different intensity. These differences in germination ensure the replacement of soil nitrogen after fire across a broad range of burn conditions.

As timescales increase, an ecosystem will experience a greater range of conditions. This increases the importance of diversity among functionally similar species. Thus, genetic, population and species diversity are important to the long-term maintenance of ecosystem structure and processes.

Despite theoretical expectations, many studies have failed to show a clear relationship between ecosystem function and species diversity. This may be due to the fact that other factors beside the number of species are also important. Those species that modify the availability, capture and use of soil resources often have a dominant influence on ecosystem processes. In other words, the presence or absence of ecosystem engineers can make a large difference in ecosystem function, irrespective of the total number of species present. For example, the introduction of mycorrhizal fungi to mine tailings will greatly enhance phosphorus uptake and plant growth. The introduction of the exotic tree *Tamarix* (salt cedar) to the deserts of the southwestern United States alters water runoff patterns, salinization of reservoirs and recharge of aquifers. This is because the deep-rooted *Tamarix* taps into previously inaccessible deep-water sources, lowering water tables. The introduction of *Eucalyptus* trees into Mediterranean ecosystems has had similar effects. Termites are able to change forest ecosystems to grasslands by bringing clay particles from the subsoil to the surface. This increases water and nutrient retention, allowing shallower rooted grasses to outcompete trees. Due to their open canopy and shallow roots, dominance of grasses changes the fire regime and can cause a general drying and warming of regional climate.

12.12 Investigations into global change and ecosystem function

12.12.1 Tundra plants and climate change

Global circulation models all indicate that global warming in response to increased greenhouse gases will occur first and with greatest intensity at high latitudes. The long-term consequences for tundra ecosystems are projected to include melting of the permafrost, a deepening of the active soil layers, increased release of carbon dioxide and methane from buried frozen organic deposits, reorganization of tundra ecosystems by changing the competitive relationships of existing species, and invasion of the low arctic tundra by subarctic species. The International Tundra Experiment (ITEX) was established in the 1990s to monitor phenology, growth and reproduction of major vascular plant species in tundra ecosystems in response to climate variations and environmental manipulations.

Many different experiments were established, including manipulations of temperature and snow depth. The initial results of these experiments showed that virtually all species responded to temperature increases in some way. However, the responses were highly species-specific, and no general patterns in type or magnitude of response were observed. Some experiments showed that early snowmelt increased the carbon/nitrogen ratios (C : N) in plant tissues. This was an important result, since sustained growth and reproductive responses to global warming will depend on nutrient supply. Increased C : N ratios in litter slow down decomposition and could slow nutrient cycling and plant growth.

12.12.2 Response of stream invertebrates to global warming

Global warming will increase the temperature of running water systems such as streams. Increased temperatures could alter respiratory rates, growth, fecundity, adult size and emergence of stream organisms. A large-scale experiment on an intact system designed to provide information on the potential effects of temperature changes was conducted on a small, first-order stream near Toronto, Ontario (Hogg & Williams 1996). The manipulated stream was 1 m wide by 60 m long by 3.5 cm deep. The stream was divided into two by a metal barrier. Temperatures were intentionally increased by 2°C in spring and summer, and by 3.5°C in the winter in one branch of the stream.

The temperature changes did not cause immediate alterations in species richness or community biomass. However, there were strong effects on some individual species and considerable variation in the effects on different species. There were decreased total animal densities, particularly in fly larvae in the order Diptera. There were also earlier onset of adult insect emergence, increased growth rates, precocious breeding, reduced size at maturity, and altered sex ratios in some species. The scientists conducting the experiment concluded that changes in life history parameters are likely to be more sensitive indicators of shifts in environmental temperature than are changes in species composition, richness, biomass or density. Dispersal of individuals with differing thermal tolerances may be an important mechanism of response to changes in thermal regime. In many ways, these results are similar to manipulations of carbon dioxide and nutrients on plants, where responses are species-specific and often unpredictable.

12.13 Responses to human effects on the biosphere

The recognition of the many and varied effects of humans on the world's ecosystems suggests three possible responses. First, we can work to reduce the rate at which we alter the Earth's systems. This may involve reducing human population growth and increasing the efficiency of resource use. Second, we can accelerate our efforts to understand Earth's ecosystems and how they interact with human-caused global changes. By increasing our understanding of world systems, we may be able to mitigate or manage future changes. Finally, we can increase human involvement in the maintenance of as much natural biodiversity and ecosystem function as possible. Because of the pervasive human influence already present and that which is certain to occur in the future, it is already too late to take a hands-off approach. No matter what combination of these approaches are used, ecological theory and knowledge should drive much of this future involvement.

12.14 Chapter summary

An ecosystem includes all of the organisms as well as all of the abiotic components of a defined area. Ecosystem ecologists examine the flow of energy and matter between organisms and the environment. An early framework for these studies is called the trophic–dynamic concept of ecosystem structure. It involves dividing organisms into different trophic levels, and examining the exchange of energy and matter between these levels. Because of inefficient transfer of energy from one trophic level to another, there is a rapid decline in total energy and biomass with increasing trophic levels. These relationships are often portrayed in trophic pyramids. Decomposer trophic levels are important in the recycling of nutrients within ecosystems. Food webs, detailing the feeding relationships among organisms, have been valuable tools in the study of ecosystem structure and function.

There is evidence to support both bottom-up and top-down control of trophic levels. Aquatic ecosystems often have strong top-down control due to the high efficiency of predation and herbivory. Fewer examples of top-down control are available in terrestrial systems, but there is evidence that this occurs.

Ecosystem engineers are organisms that control resource availability for other organisms through physical changes in the environment. As such, these organisms play major roles in determining the structure of an ecosystem.

Biogeochemical cycles are essential to the flow of nutrients within and between ecosystems. These cycles include hydrological, nitrogen, carbon, phosphorus, calcium, sulphur and any of several other essential nutrients. The growing human population has altered many of these cycles, both on regional and global scales. Alterations in the nitrogen, carbon and hydrological cycles have been especially marked. These have altered global climate and ecosystem structure.

Human population growth has also resulted in a homogenization of the Earth's biota through the introduction of non-native species to new areas throughout the world. These introductions, combined with habitat loss and land transformation, have resulted in a major decrease in worldwide biodiversity. Biodiversity and ecosystem function are linked, but not always in a straightforward way. Various models have been developed to explain this linkage, including an airplane-rivet analogy, the redundancy hypothesis and the insurance hypothesis.

Recommended reading

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