4 Biosphere

When you have read thi7s chapter you will have been introduced to:

- the concepts of biosphere, biomes, and biogeography
- nutrient cycles
- respiration and photosynthesis
- feeding relationships, food chains, and food webs
- pyramids of energy, numbers, and biomass
- ecosystems
- succession and climax
- arrested successions
- colonization
- stable and unstable environments, and reproductive strategies
- simplicity and diversity
- homoeostasis and feedback
- limits of tolerance

32 Biosphere, biomes, biogeography

All the organisms living in a particular area can be described collectively as the 'biota'. The noun implies nothing about the size or type of area: it can be applied to the inhabitants of a vast forest, a small puddle of rain water, or the entire Earth. The region of the Earth occupied by its biota is known as the 'biosphere', sometimes called the 'ecosphere' to emphasize the fact that the biota comprises an interacting system which can be studied at the global level.

Most of the biota occurs at or very close to the surface of land or water, and the biosphere forms an extremely thin layer on the Earth. In the soil, organisms inhabit the upper horizons, where they feed on organic material reaching them from above. They, together with their predators and parasites, constitute the soil biota and their domain extends to no more than a few metres below ground level; most of them are confined to the uppermost few centimetres. When soil samples are being taken in order to study the biota, cores to a depth of 10 cm are considered adequate in some soils. Up to 60 cm in deep, peat soils is considered adequate for microorganisms, whereas 10 cm is usually sufficient for sampling larger animals such as worms (PHILLIPSON, 1971, p. 89).

Above ground, birds and insects fly, newly hatched spiders migrate by 'ballooning' attached to lengths of their own silk, and 'aeroplankton', consisting of plant pollen grains, fungal and bacterial spores, and some single-celled plants, is carried aloft by thermal currents and transported by the wind. The domain of these organisms is effectively limited by the air density below which powered flight becomes impossible, the availability of oxygen for respiration, and temperature. It extends to about 6.5 km, although dormant spores, securely sealed within their casings, can reach the tropopause, at an average height of about 9 km, but sometimes reaching 17 km at the equator (TIVY, 1993, 13–14). Tardigrades, which comprise about 700 species of tiny animals sometimes called 'water bears' or 'moss piglets', have been known to cross the Atlantic, carried on winds that bore them through the lower stratosphere, where they survived in temperatures lower than -100°C (COPLEY, 1999).

Marine life is also concentrated near the surface. It is based on photosynthesizing, single-celled plants, the phytoplankton on which herbivores feed. Plants need light and are consequently confined to the depth of light penetration. In the clearest water, blue-green light can be detected at a depth of almost 1 km, but at least 95 per cent of incident light is absorbed in the uppermost 50 m. There is sufficient light for photosynthesis down to about 150 m in very clear water, but in most sea areas the biologically productive region, called the 'euphotic zone', is much shallower (MARSHALL, 1979, pp. 39–40). At greater depths, organisms rely on organic material descending to them from above, like rain. This sustains life on the ocean floor. In some places, water heated by contact with molten rock below the sea bed and rich in dissolved minerals issues from hydrothermal vents. Depending on their chemical composition the issuing fluids may be black or white; they are known as 'black smokers' and 'white smokers'. A little distance from them, where the temperature is about 40°C, colonies of bacteria able to synthesize nutrients directly from the vent fluid form the bases of richly productive animal communities. Vent communities are unique in their complete isolation from and independence of communities ultimately deriving their energy from sunlight.

Hydrothermal vents are associated with ocean trenches, which are the deepest part of the ocean, and the Marianas Trench is the deepest of all, its floor lying about 11 km below sea level. In addition, it is now known that there are large bacterial populations living up to a few kilometres below the Earth's surface. They are found in deep aquifers and spaces in rocks of a variety of types and in some places the size of the population increases with depth. The fluid extracted from some North Sea oil reservoirs contains up to 16 kg of bacteria a day (PARKES, 1999). The depth at which these populations are found may not exceed that of the Marianas Trench, however. At its greatest, then, the biosphere extends from about 11 km below sea level to the lower stratosphere at a maximum of about 20 km above sea level. Nowhere is it more than about 31 km deep, a figure that can be compared with the mean radius of the Earth, which is 6371 km. If you pictured the Earth as a large orange, diameter 6.4 cm, the biosphere would fill the pits in the skin and cover its surface to a maximum depth of less than 0.3 mm and in most places to no more than half of that.

Although the biosphere is confined to so thin a layer, the biota contained within it is diverse and its character varies markedly from one region to another. Wolves and conifer forests are typical of northern Canada and Eurasia, tall, dense, broad-leaved evergreen forests of the equatorial regions, grasslands of the interiors of continents, and deserts of the continental subtropics. The consistency of composition of large areas covered by such biotic types allows them to be grouped. If only the vegetation is considered, the groups are 'formation types', the largest unit recognized in a hierarchy of types of plant community and usually identified by the predominant kinds of plant. If the animals are included, the groups are known as 'biomes'. Biomes are defined by all the species within them and the relationships between those species and their environment.

Such a definition describes a type of community, but says little about the detail of its composition. A hot desert, for example, will support plants and animals of a certain type, but the actual species may be local: the Australian, Sahara, and North American deserts support different species of organisms adapted to very similar conditions.

This suggests that biomes are, in fact, climatic regions and that the concept refers mainly to the environment. This is broadly true, and Figure 4.1 shows how major biomes are related to temperature and precipitation. The similarity of type, but with different constituent species, arises through convergent evolution. Natural selection favours those species best adapted to the conditions under which they live, and some climatic regimes impose constraints to which only a limited number of biological adaptations seem possible. Species thriving under such regimes resemble one another, though they are not closely related. Just as biomes appear to be climatically defined, climatic regimes appear to be definable biologically (see section 21).

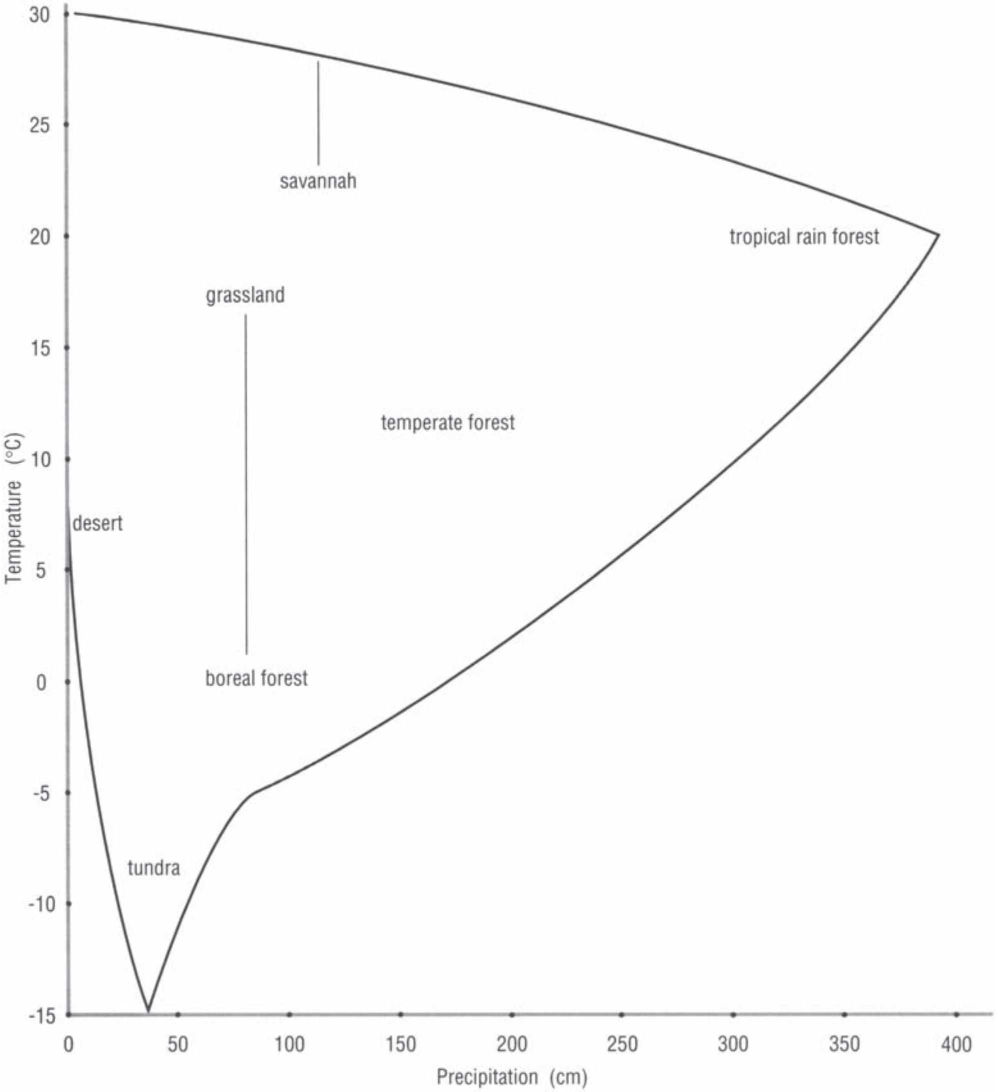

Figure 4.1 ***Biomes and climate***

Difficulties with so direct a linkage between biomes and climates begin to appear at the boundaries between biomes. These are never sharp, biomes being separated by transition zones (called 'ecotones') containing species from both adjacent biomes, and some ecotones are broad: that between tundra and coniferous forest ('taiga') is up to 160 km wide (TIVY, 1993, p. 96). It is also possible that the northern edge of the taiga may still be advancing northward following the end of the last glaciation. Further south, some biomes may have resulted from human activities. Repeated forest burning, to drive game or clear land for cultivation, favours the growth of grass, allowing populations of grazing herbivores to increase, leading to the destruction of tree seedlings by nibbling or trampling and the permanent conversion of forest to grassland. Savannah grasslands, prairie, and steppe are all believed to have resulted from such intervention. Not only does this weaken the link between biome and climate, it blurs the natural borders between biomes. If over-grazing exacerbates the spread of deserts during prolonged drought, for example, where should the purely climatic border be located?

With these limitations in mind, the world can be divided into biomes. Between the high-latitude tree line and the deep snow of the polar regions, the tundra comprises lichens, mosses, sedges, flowering herbs, and dwarf shrubs and trees, the animal population swelling by migration during the brief summer. Along its low-latitude borders, the tundra gives way to taiga or boreal forest, comprising mainly coniferous trees and animals associated with them. At still lower latitude, these merge into mixed coniferous and broad-leaved temperate forest. Continental interiors support temperate grassland, such as the prairie of North America, pampas of South America, veld of South Africa, and steppe of Eurasia, or the tropical savannah, which is partly wooded in places. Mediterranean climates support chaparral, a type of grassland with drought-resistant scrub. Deserts occur in the subtropics and humid equatorial regions support tropical rain forest. Biomes closely resembling those of high latitudes also occur on mountains in low latitudes. Climb a high mountain at the equator, and you will move from rain forest to temperate forest and eventually to a type of vegetation similar to tundra before entering the permanently snow-covered heights.

Although they are not called biomes, the oceans can also be divided horizontally into zones, each of which supports a typical biota. There is some migration between zones. Benthic organisms are those which inhabit the sea floor, but pelagic species move vertically between the surface and the floor. These are the minority of animals, however, benthic species accounting for about 98 per cent of the total (MARSHALL, 1979, p. 40). Some pelagic organisms have little or no power of independent movement and drift with tide and current near the surface. These are known as 'plankton', a grouping that includes bacteria, single-celled plants (phytoplankton), and small animals (zooplankton).

Below the surface, marine zones are defined by depth. As Figure 4.2 shows schematically, ocean depth is determined largely by distance from continental coasts. Beyond the shore lies the continental shelf, sloping at a gradient between about 1:500 and 1:1000 for a distance of several hundred kilometres. At a depth of about 200 m the gradient steepens, to an average of about 1:700 but up to 1:4 in places, down the continental slope to a depth of about 2000 m. The continental rise, where sediment that has slid down the shelf and slope accumulates, slopes at 1:100 to 1:700 and continues to the deep ocean floor. The neritic zone corresponds to the level overlying the continental shelf, the bathyal zone to the region above the slope, and the abyssal zone continues

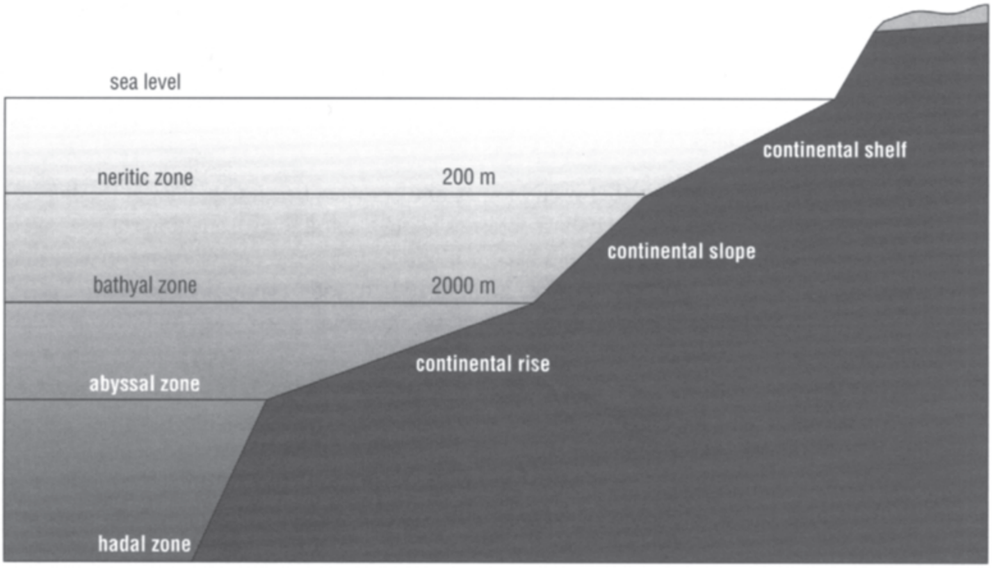

Figure 4.2 ***Marine zones and continental margin (not to scale)***

down the rise to the floor. The deepest part of the ocean, in trenches below the general level of the floor, is called the hadal zone.

Close examination of the composition of biomes quickly reveals that although the biome concept is useful as a kind of shorthand to describe a type of environment, species vary widely from one example of a particular biome to another. Temperate forests comprise different trees in different continents, for example, and Old World monkeys are taxonomically distinct from New World monkeys. Biogeography, the study of the geographic distribution of species, is the discipline which addresses such differences.

Biogeographers have divided the world into regions according to the flora and fauna more or less peculiar to them and generally separated by geographic barriers to migration. The number of regions varies from one authority to another, but at least six faunal areas are generally recognized. In the northern hemisphere, the Nearctic covers North America and Greenland, the Palaearctic Eurasia as far south as the Himalayas, North Africa, and part of Arabia. In the southern hemisphere the Neotropical region covers Central and South America, the Ethiopian the remainder of Africa, Arabia, and Madagascar, the Oriental the Indian subcontinent and southern and south-eastern Asia excluding New Guinea and Sulawesi, and the Australasian Sulawesi, New Guinea, Australia, and New Zealand. In addition, some biogeographers recognize an Oceanian region, covering the Pacific islands, and an Antarctic region. (TIVY, 1993, p. 58).

Floral divisions follow similar boundaries, but the Nearctic and Palaearctic are merged and given the name Boreal, and the Ethiopian and Oriental together form the Palaeotropical. Holarctica is a name formerly used to describe the whole of the northern hemisphere, all of which was once joined in the supercontinent of Laurasia.

When these vast areas are studied in more detail, a hierarchy develops, allowing increasingly local designation. Regions can be divided into ‘domains’ and domains into ‘sectors’ and ‘subsectors’.

At local level, however, further complications emerge. Some plant species are described as ‘native’ to distinguish them from ‘exotics’, which are plants introduced by humans. Botanists use this distinction frequently, but what is exotic today may have been native in the past, perhaps during a previous interglacial, and some exotics have been present for a very long time and are fully naturalized, meaning that they are able to grow and reproduce without human assistance. In areas that were once glaciated, most plants arrived as immigrants when the climate warmed and land was exposed by the glacial retreat. Other species may become extinct in part of their range, these days depressingly often.

Plant and animal distribution is constantly changing. It cannot be studied in isolation from the climatic and tectonic history of the Earth and its study is directly relevant to current concerns over the loss in biodiversity (see section 50).

33 Major biomes

Several biome classifications are used, but most agree the world can be divided into about 10. These are usually listed as: polar regions and tundra; temperate forest; tropical rain forest; tropical seasonal and monsoon forest; tropical grassland; temperate grassland; deserts; mountains; wetlands; and oceans.

As their name indicates, the polar regions occupy approximately the area in latitudes higher than 60.5° N and S. These latitudes mark the Arctic and Antarctic Circles. They are defined as the latitudinal limit at which the Sun fails to rise above the horizon on at least one day in each year and fails to sink below the horizon on at least one day.

Ice sheets cover a large area at each Pole. Sea covers most of the Arctic. Some of the sea is frozen throughout the year. The ice sheet proper—ice lying permanently on land—is confined to Greenland. Antarctica is a large continent divided into two parts by the Transantarctic Mountains. There are two Antarctic ice sheets, the East and West, lying to either side of the mountain range. The East Antarctic ice sheet covers about twice the area of the West Antarctic sheet. The West Antarctic ice sheet extends over the sea surface as ice shelves. There are several ice shelves, the largest being the Ronne shelf in the Weddell Sea and the Ross shelf in the Ross Sea.

Polar climates are cold and away from the coasts they are extremely dry. These are also the most extremely seasonal climates.

No plants can grow where the ground is permanently covered by ice and snow. Animals cross the ice and feed in the water. Both Arctic and Antarctic waters are very productive.

Beyond the edge of the permanent ice the ground supports tundra vegetation. There is no tundra vegetation on the continent of Antarctica, because all of the mainland is at too high a latitude. Small areas occur on the Falkland (Malvinas) and other islands. Tundra covers a much larger area of North America and Eurasia. The plants include grasses, sedges, and flowering herbs. Woody plants occur only as low shrubs in places sheltered from the desiccating winds.

Protecting Antarctica

Antarctica is unique in being the only continent with no native human inhabitants, although it has a population of scientists and support workers, some of whom remain through the winter. At one time seven countries claimed territorial rights in Antarctica. These were Argentina, Australia, Chile, France, New Zealand, Norway, and the United Kingdom. In addition, the Soviet Union, United States, Belgium, Germany, Poland, Sweden, Japan, and South Africa engaged in Antarctic exploration, but claimed no territorial rights.

Recognizing the great value of the continent, on December 1, 1959. Argentina, Australia, Belgium, Chile, France, Japan, New Zealand, Norway, South Africa, the Soviet Union, the United Kingdom, and the United States signed the Antarctic Treaty *(www.acda.gov/treaties/arctic1.htm)*. This made the entire continent a demilitarized zone that would be preserved for scientific research. Without commenting on any territorial claims, it forbade signatory nations from establishing military bases on the continent, or conducting manoeuvres, testing weapons, or disposing of radioactive waste. The Treaty binds its members in perpetuity, but allows for a review of its provisions every 30 years. The initial signatories were later joined by Brazil, China, Germany, Finland, India, Italy, Republic of Korea, Peru, Poland, Spain, Sweden, and Uruguay.

On October 4, 1991, a protocol to the Treaty was signed. This banned oil exploration for 50 years and included measures to protect the natural environment.

Temperate forests occur mainly in the Northern Hemisphere. They are bordered to the north by the tundra and extend southward to the Tropic of Cancer (23.5° N). Much smaller areas occur south of the Tropic of Capricorn (23.5° S) in a narrow strip along the western coast of South America, in the south and west of South Africa, in the south of Australia, and in both islands of New Zealand.

In the north the forests are dominated by coniferous species, especially spruce, pine, fir, larch, and hemlock, in places mixed with birch. In Canada and Alaska this is known as the boreal forest. In Russia it is called the taiga.

Along its southern borders broad-leaved deciduous trees become increasingly common in the coniferous forest, producing mixed forest. This gives way to predominantly broad-leaved deciduous forest across most of Europe north of the Alps and on the eastern half of North America as far south as the Gulf of Mexico. Around the Mediterranean and in parts of California, South Africa, and Australia the forests consist of evergreen trees, some broad-leaved and some coniferous, that are adapted to a climate with a pronounced summer dry season.

Tropical rain forest is found in low-lying areas along a belt to either side of the equator. The temperature is consistently warm. In Libreville, Gabon, for example, the mean monthly daytime temperature varies between 28°C and 31°C. Rainfall is heavy, but often variable and with a distinct dry season. Libreville has fairly dry weather from early May to the end of August. In the Amazon Basin, too, the rainfall is less in the summer months than in winter.

Broad-leaved evergreen trees dominate the vegetation. Many grow to a great height and their crowns form a completely closed canopy. Smaller trees and shrubs grow beneath the dominants, producing several horizontal layers. Each layer supports its own populations of epiphytes (plants that grow on the surface of other plants, but without obtaining nutrients from them) and animals. Together with the large number of species contributing to the community, the three-dimensional structure gives tropical rain forest an unparalleled ecological richness.

Monsoon climates are strongly seasonal, with a long dry season in winter and a short wet season in summer. Forests adapted to this type of climate, found mainly in southern Asia, consist of broad-leaved deciduous trees that shed their leaves during the dry season. Monsoon forest contains fewer tree species than tropical rain forest.

On tropical mountainsides, and especially on the eastern slopes of the Andes and southern slopes of the Himalayas, the character of the tropical forest changes with increasing elevation, as the temperature decreases with height (by an average 6.5°C per kilometre). On the lowest slopes the forest becomes more open. There are gaps in the canopy and the trees, although of the same species as those below, have thicker trunks and smaller leaves. There are more ferns, mosses, and other plants growing on the tree bark. This is known as mountain, or montane forest.

Higher still, moist air forced to rise up the mountainside is chilled and its water vapour condenses to form mist. This produces cloud forest. The ground is wet and often boggy and mosses are common. The trees are small, often stunted, and have tough, leathery leaves.

Above the cloud forest the trees become smaller and more scattered. Ferns and mosses are abundant and the forest has a strange, ethereal look. It is known as elfin woodland and its upper boundary is the tree line, beyond which the temperature is too low for trees to survive.

Saving the tropical forests

Tropical forests are being cleared at a rate of about 2 per cent of the area every 10 years in Asia and about half of that in South America. Montane and monsoon forests are being lost more rapidly than lowland forests, which often lie on very wet, boggy or swampy ground.

They are cleared mainly to provide land for farming. The demand for timber contributes to this because although young trees will grow naturally to restore areas of cleared forest, they are not always given an opportunity to do so. Farmers occupy the cleared land.

Attempts to arrest the loss of tropical forest are based on establishing plantations to supply timber and on finding alternative livelihoods for local people so they no longer need to farm. Throughout the tropics, large areas of plantation forest are being established and the total area of plantation is increasing rapidly. Plantations supply timber more profitably than the natural forest, and adjacent land is used for farming by modern methods that produce higher yields. Tourism brings in a steadily increasing income.

The natural forest is then seen as a resource for research, tourism, and for the harvesting of certain products that cannot be grown on farms.

Grasses thrive in climates that are too dry to support forests and temperate grasslands are found in the interior of continents, far from the nearest coast, where the climate is of the continental type. Winters are cold, summers hot, and precipitation is sparse. These grasslands are known as prairie in North America, steppe in Eurasia, pampas in South America, and veld in South Africa.

They cover an immense area. In Eurasia grassland is the natural vegetation over the area approximately bounded by latitudes 40° N and 50° N and longitudes 20° E and 90° E. The steppes extend from Hungary to Mongolia. In North America the prairie extends from the southern half of the Canadian prairie provinces of Manitoba, Saskatchewan, and Alberta to Texas.

Land that will grow grass will often grow cereal crops, which are also grasses. Consequently most of the prairie and much of the steppe has been cleared for farming.

Tropical grasslands are found in South America, over much of Africa between the Sahara and Kalahari Deserts, on the western side of India, and surrounding the deserts of Australia. The climate is warm and strongly seasonal, with pronounced dry and rainy seasons. Mean temperature ranges between about 18°C in winter and 32°C in summer. Winter is the dry season.

In addition to grasses, which are the dominant vegetation, tropical grasslands also include small trees that are adapted to the dry season. Acacias are typical. The extensive pasture supports large herds of grazing mammals, together with the predators that hunt them.

Wetlands occur throughout the world, but they are localized. They are found along most coasts and in river deltas and estuaries. Outside the tropics coastal wetlands form salt marshes, comprising plants that tolerate submergence by salt water at each high tide followed by exposure to the air at low tide. In the tropics they form mangrove swamps, usually with just a few species of mangrove trees.

Inland, wetlands occur as bogs and around freshwater lakes and where large rivers flow across very level ground. The Everglades, Florida, are a freshwater wetland, as is the extensive marshland area around the mouths of the Tigris and Euphrates Rivers, in southern Iraq. Wetlands support a wide variety of wildlife.

People like to live near sea coasts and beside rivers. River flood plains are very fertile, because of the silt deposited on them with each flooding. Consequently, coastal and riverside wetlands are under constant threat of development for housing or farming. Draining them is not usually difficult, although it may be expensive.

In 1971, an international conference at Ramsar, Iran, led to the Ramsar Convention *(www.ramsar.org/index.html)* on Wetlands. By 1999, the governments of 116 countries had signed the Convention. This commits them to designating and then protecting wetlands of international importance, especially as waterfowl habitat, within their own borders. Altogether, 1006 Ramsar sites have been designated, covering a total area of 71.8 million hectares.

Oceans are counted as a single biome because, although they occur in every part of the world, their waters are joined and many of the species living in them migrate over long distances. Together, the oceans cover 70.8 per cent of the surface of the Earth, a surface area of 361 million km^2, to an average depth of 3.7 km. They hold about 1370 million km^3 of water. Phytoplankton, comprising minute, mainly single-celled, plants supply food for marine animals. These include members of the zooplankton, which include the larvae of many larger species, as well as fish, marine mammals, and sea birds (see section 4.32).

Deserts form wherever the potential rate of evaporation over a year exceeds the amount of precipitation. The rate of evaporation varies according to temperature, so the minimum precipitation needed to prevent an area from becoming desert varies with the mean temperature. There is an absolute lower limit, however, of about 250 mm of rain a year, below which desert will develop in any climate.

In a belt stretching across the edges of both tropics desert climates are produced by subsiding air at the edges of the Hadley cells (see section 2.15). This air is warm and extremely dry. It produces high surface pressure, with air flowing outward from it and preventing moister air from entering the region. The Sahara, Arabian, and Thar Deserts are caused by this climatic regime in the Northern Hemisphere and the Kalahari and Gibson Deserts in the Southern.

Deserts also occur in the deep heart of large continents. The Turkestan, Takla Makan, and Gobi Deserts are of this type. Air loses moisture where it is forced to rise as it crosses a mountain range. This can produce a desert on the lee side. The deserts of the southwestern United States are formed in this way, as is the Atacama Desert in South America.

Air also subsides over both Poles, producing the polar deserts. These are covered thickly with ice and snow, but only because such precipitation as does fall is unable to melt or evaporate. In fact, the precipitation is low and the interior of Antarctica is the driest of all deserts, with an average annual precipitation of about 25 mm.

Despite their aridity, many species have adapted to survive in deserts. There are succulent plants, such as the cacti in America and certain euphorbias in Africa, that store water in their leaves and stems. Other plants survive most of the time as seeds, germinating and completing their life cycles in a matter of a few weeks, or even days, whenever rain falls, which very occasionally it does. These plants sustain desert animals and there are many other animal species that venture into deserts without being resident there.

Desertification

Lands bordering deserts have an arid climate. Droughts are common and from time to time prolonged droughts occur. During a drought most small plants disappear. Trees and shrubs may appear as though dead, and may be dead. The land closely resembles the desert nearby. This type of change has been observed in recent years in parts of Ethiopia and in the region known as the Sahel, along the southern border of the Sahara. Eventually, though, the drought ends. When the rains return the vegetation quickly recovers. Despite appearances, drought of this kind does not indicate the permanent expansion of the desert that is implied by the term ‘desertification’.

Desertification can occur, however. If marginal land adjacent to a desert is cropped too intensively the fertility of the soil may become exhausted. Crop yields will decline and when drought strikes the vegetation may be unable to recover. Similarly, grazing the land with too many livestock will destroy the vegetation. In both cases plant roots that bind soil particles together are lost. Wind can then lift the dry soil, blowing it away, sometimes to bury any plants or crops that have managed to survive nearby. Tree roots bind soil particles and the trees themselves provide some shelter from the wind. Trees are often cut down for use as fuel or for building materials.

Poor irrigation can sterilize land by rendering it saline (see section 3.25). Plants die and farmers abandon their fields.

Nearly one-quarter of the land area of the Earth is estimated to be at risk from soil degradation leading to desertification. Remedies are based on better land management. Water can be used more efficiently for irrigation. Crop varieties can be genetically modified to grow in saline soils. Trees can be grown to shelter crops.

Mountain habitats change with increasing elevation, due to the fall in temperature with height. This averages 6.5°C per kilometre and determines the elevation at which the temperature remains below freezing throughout the year. This varies with latitude. In the high Arctic and in Antarctica the summer freezing level is at sea level. In temperate latitudes, where summer sea-level temperatures are typically about 22°C, it is at about 3400 m above sea level and in the tropics, where the sea-level temperature is about 30°C snow will lie permanently above 4600 m.

Temperature determines the type of vegetation. In the tropics, rain forest gives way to a transitional type of forest at about 1000 m. Starting at about 2000 m there is montane forest, extending to about 3000 m, where it gives way to elfin woodland. At about 4000 m there is grassland, in some places forming alpine meadows. This extends to the permanent snow line. Mountains are exposed to strong winds and heavy precipitation, but there are many sheltered places. Consequently, the climate varies over quite short distances. These variations are reflected in the type of plants.

Although all mountains support similar types of habitats, the composition of the plant and animal communities varies. The alpine plants of the Andes belong to entirely different species from those of the Himalayas, for example. Regardless of their elevation, plants growing in low latitudes receive more intense sunlight than those in high latitudes. Consequently, species that thrive in a particular temperature in the tropics may fail at the same temperature in northern Europe. Tropical mountains may support a type of tundra, but one that contains many more species than the tundra of the far north.

Outside the conventional biomes, there are organisms known as extremophiles that inhabit environments much too hot, cold, acid, alkaline, or saline for other species. Acidophiles thrive where the pH is below 5.0 and alkaliphiles where the pH is higher than 9.0. Halophiles inhabit very saline environments. Hyperthermophiles live in temperatures of about 105°C. They can tolerate temperatures as high as 113°C and some species fail to multiply at temperatures below 90°C. Thermophiles prefer cooler temperatures, of about 60°C, and psychrophiles prefer temperatures below -15°C. All extremophiles are single-celled and are classified in the domain Archaea.

34 Nutrient cycles

Plants synthesize carbohydrates directly from gaseous carbon dioxide and water, and use mineral compounds dissolved in soil water to synthesize the other substances they need to construct their own tissues. Animals consume the plants, carnivores consume herbivores, and the metabolic wastes and dead tissue from plants and animals provide food for another range of organisms, which break down complex organic molecules into simpler compounds that dissolve in water to be taken up once more by plant roots.

All the nutrient elements on which life depends are involved in cycles during which they may pass through the soil, water, air, and rock, as well as through living organisms. These biogeochemical cycles operate on a global scale; 'nutrient' cycles are those biogeochemical cycles involving elements necessary for life. Agriculture, manufacturing industry, and transport also move chemical elements between land, air, and water, nowadays in amounts equal to a significant proportion of those moving through the natural cycles. Of all the phosphorus carried by rivers to the sea, for example, human activities contribute an estimated two-thirds (BEGON *ET AL.*, 1990, p. 705), and the carbon emitted by the combustion of fossil fuels is about 5.1 per cent to 7.5 per cent of the amount released through the respiration of the world's biota (BEGON *ET AL.*, 1990, p. 708).

Cycling represents the movement of elements between reservoirs. Rocks, the oceans, the atmosphere, and the biota are reservoirs. The routes by which molecules move among them vary in length. A molecule released from the bedrock by weathering processes that produce soil may be absorbed by a plant root. It has now moved from one reservoir, the rock, to another, the biota. When the plant dies, that molecule will be returned to the soil as part of a much larger organic molecule. Decomposition will break the large molecule into smaller ones and the nutrient molecule may be taken up by the root of another plant. This is a very short cycle; if the plants involved are annuals it may take only a matter of months to complete. Should the molecule be released into the atmosphere rather than almost immediately being taken up by a plant, the cycle will take longer; the molecule will remain airborne for days or weeks until rain water washes it to the ground. If the molecule enters the ground water and moves from there to the sea, its cycle will be longer still.

Molecules may also enter reservoirs in which they remain for many millions of years. Consider, for example, the carbon that once resided in plants and, some 300 million years ago, became part of the organic material that was converted to coal, where it remains to this day. Calcium reaching sea water may find its way into the shells of marine organisms and from there enter sediments that eventually become limestone, where it remains until geologic processes expose it to the air once more and weathering releases it.

Reservoirs also vary in size. Far more nitrogen is in the air than elsewhere in its cycle. The atmosphere is also the principal reservoir for carbon, whereas the hydrogen that plants need for photosynthesis is derived from water, for which the oceans are the biggest reservoir. Rocks are the principal reservoir for many nutrient elements.

Living cells consist predominantly of carbon, hydrogen, and oxygen. Together with nitrogen (N) and phosphorus (P), these account for more than 1 per cent of their total dry weight. In addition to these, the biota as a whole require calcium (Ca), chlorine (Cl), copper (Cu), iron (Fe), magnesium (Mg), potassium (K), sodium (Na), sulphur (S), together with very small traces of aluminium (Al), boron

(B), bromine (Br), chromium (Cr), cobalt (Co), fluorine (F), gallium (Ga), iodine (I), manganese (Mn), molybdenum (Mo), selenium (Se), silicon (Si), strontium (Sr), tin (Sn), titanium (Ti), vanadium (V), and zinc (Zn). To give an idea of the proportions in which these nutrients are used, a mature holm oak *(Quercus ilex)* forest was analyzed. The proportion of the above-ground dry weight accounted for by each mineral is shown in Table 4.1 (DAJOZ, 1975, p. 278). These figures refer only to a particular example and would be different for other plant communities.

Table 4.1 ***Minerals in an oak forest as a proportion of the total***

Element	*% of total*
Ca	68
N	13
K	11
P	4
Mg	3
Na	0.6
Mn	0.3
Fe	0.3
Zn	0.1
Cu	0.09

Nitrogen, a constituent of proteins, moves through a fairly complex cycle, illustrated in Figure 4.3. Gaseous nitrogen (N_2) is the main ingredient of our atmosphere, but it is chemically unreactive and plants cannot use it directly. Lightning provides the energy to oxidize some, which then dissolves in rain droplets to form nitric acid (HNO_3), but 96–97 per cent of soil nitrogen is 'fixed' biologically. Soil bacteria, of the genus *Rhizobium,* live in nodules attached to the roots of legumes, the plant family of peas, beans, lupins, clovers, and their relatives. Other genera, including *Azotobacter* and *Clostridium,* live freely in the soil. They are able to use gaseous nitrogen directly, as are some aquatic cyanobacteria such as *Anabaena*. These organisms convert nitrogen into ammonia (NH_3).

Some of the nitrate (NO_3^-) and ammonia is absorbed by plant roots and some leaches from the soil to enter ground and surface water, where it nourishes aquatic plants. Plants are eaten by animals, which utilize their nitrogen in the form of the amino acids from which they synthesize proteins.

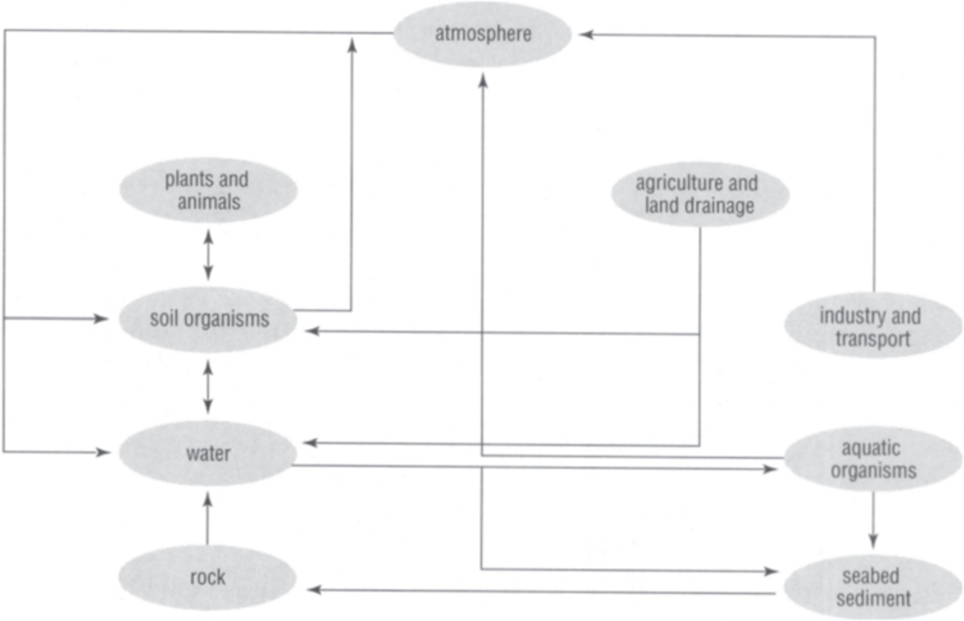

Figure 4.3 ***The nitrogen cycle***

Organic wastes return to the soil and water, where other bacteria convert organic nitrogen into ammonia or ammonium (NH_4^+) compounds. Yet more bacteria, including *Nitrosomonas* and *Nitrobacter,* convert these into nitrites (NO_2^-) and then into nitrates (NO_3^-), which can be taken up again by plants.

In the oceans, some nitrogen forms part of the organic material that accumulates as sediment and this may eventually be transformed into sedimentary rock. Weathering reactions can then release the nitrogen into water, to re-enter the cycle.

Ammonia is volatile, and whenever it is released a certain amount evaporates. This takes it back to the atmospheric stage in the cycle, but not for long, because it soon dissolves in rain droplets and returns to the surface.

It is denitrifying bacteria which complete the cycle. Reversing the nitrifying process, various species convert nitrates to nitrites, nitrites to ammonia, and nitrates to gaseous nitrogen or nitrogen oxides.

Humans enter the cycle through the manufacture of nitrogen fertilizers, an industrial process that fixes gaseous nitrogen into a soluble compound. More than 50×10^6 tonnes yr^{-1} of nitrogen fertilizer is now being produced (BEGON *ET AL.*, 1990, p. 706), compared with the 54×10^6 t yr^{-1} fixed biologically (KUPCHELLA AND HYLAND, 1986, p. 55). High-compression internal combustion engines and high-temperature industrial furnaces and incinerators also cause the oxidation of nitrogen and its emission in exhaust gases. Such emissions cause pollution, with consequences that are fairly well understood, but the consequences of doubling the rate of the nitrogen cycle are unknown.

Carbon also resides in the atmosphere, as carbon dioxide, and passes through a similar cycle, illustrated in Figure 4.4. In this case, however, green plants can use the gas directly, the process of photosynthesis incorporating it in carbohydrates. These are consumed by animals and the decomposition of organic wastes involves the oxidation of their carbon, releasing it once more as

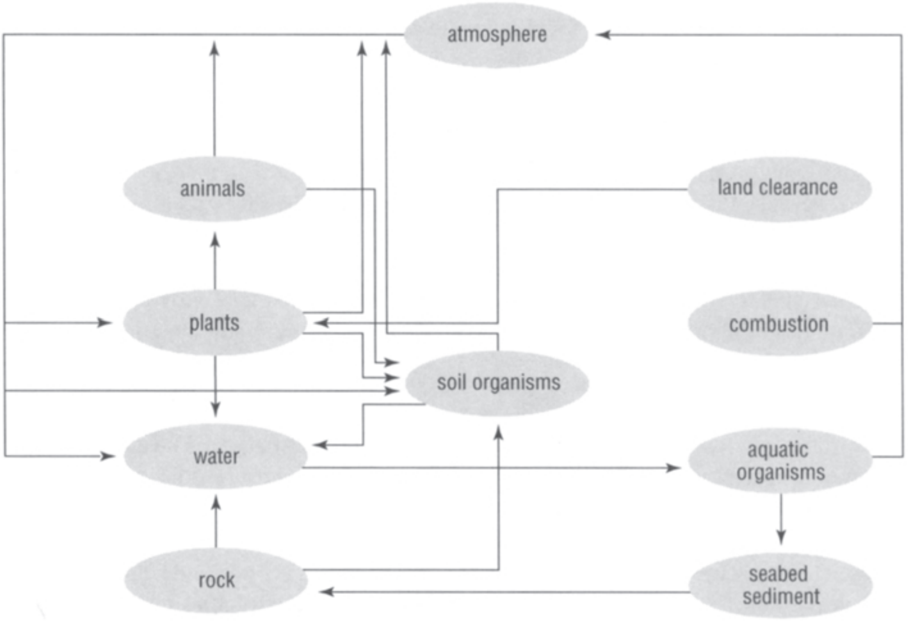

Figure 4.4 ***The carbon cycle***

carbon dioxide. This release occurs through respiration, and all aerobic organisms, including all plants and animals, oxidize carbon in this way and excrete carbon dioxide.

Atmospheric carbon dioxide also enters water directly, dissolving to form carbonic acid (H_2CO_3). This dissociates into hydrogen (H^+) and bicarbonate (HCO_3^-) ions, then into more hydrogen and carbonate (CO_3^{2-}) ions. Carbonate ions combine with positively charged ions, such as calcium (Ca^{2+}), forming salts, some of which are insoluble, such as calcium carbonate ($CaCO_3$). In the oceans the formation of calcium carbonate is exploited by animals and some single-celled plants, but whatever the route by which it forms, calcium carbonate tends to accumulate in sediments in shallow water (below about 4 km, at a level called the carbonate compensation depth, the low temperature and high carbon dioxide saturation of sea water cause calcium carbonate to dissolve). Carbonate sediments may be converted into sedimentary rock, effectively removing carbon from the cycle until such time as the rock is exposed to weathering.

'Stored' carbon is returned to the cycle by human activities. The burning of fossil fuels is the best known and most important, many climatologists believing that an increase in the atmospheric concentration of carbon dioxide may perturb climates (see section 13). It is not the only human intervention, however. The kilning (heating) of limestone converts calcium carbonate to calcium oxide, or 'quicklime' (CaO), with the release of carbon dioxide; the subsequent addition of water produces calcium hydroxide ($Ca(OH)_2$), or 'slaked lime'. Calcium oxide is used mainly in the chemical process industries, and both products are used in construction, for example to make mortar, although this recombines the hydroxide to form calcium carbonate. Calcium hydroxide is also used in flue-gas desulphurization processes to remove sulphur dioxide from the gases produced by burning fossil fuel containing sulphur compounds, mainly in power stations. The exhaust gas is passed through an aqueous suspension of calcium hydroxide and the sulphur reacts to form insoluble calcium sulphate, which is precipitated. The technique removes sulphur dioxide, but at the cost of releasing carbon dioxide when the limestone is kilned to convert the carbonate to oxide.

Sedimentary rock may not be returned to the surface at all. Some is subducted at destructive plate margins, where one crustal plate is sinking beneath another. This returns the rock to the Earth's mantle. Nitrogen, carbon, and the other elements of which the rock is composed then form part of the interior of the Earth, returning to the surface, after an indeterminately long time, in volcanic eruptions.

All the nutrient elements are engaged in broadly similar cycles, but the atmosphere is not the only principal reservoir. Phosphorus is derived from rocks and released by weathering. Plants absorb it mainly as orthophosphate (the ions $H_2PO_4^-$, HPO_4^{2-}, and PO_4^{3-}). Some become incorporated in the bones of vertebrates, where it may remain for many years, but eventually the phosphorus is precipitated with ocean sediment and is converted once more into rock. Each year some 13×10^6 tonnes of phosphorus is removed from ocean water by sedimentation (BEGON *ET AL.*, 1990, p. 702).

Sulphur, also an important ingredient of proteins and protein-carbohydrate complexes, is derived from both lithospheric (rock) and atmospheric reservoirs of comparable size. Volcanoes release a fairly small amount of sulphur. Several species of marine phytoplankton excrete dimethyl sulphide (DMS), possibly as a by-product of metabolic processes for osmotic regulation. Much of the DMS breaks down in the water, but some enters the air, where it is oxidized in several steps to sulphur dioxide and then to sulphate aerosol. This contributes about 44×10^6 t S yr^{-1}, and sulphate-reduc-ing bacteria release gases, principally hydrogen sulphide (H_2S). Rock weathering also releases sulphur compounds. The amounts of sulphur reaching surface fresh waters from the atmosphere and the weathering of rocks are approximately equal.

Coal contains an average of 1–5 per cent S and oil 2–3 per cent (BEGON *ET AL.*, 1990, p. 707). When the fuel is burned the sulphur is released as sulphur dioxide unless measures are taken to remove it from exhaust gases. At present, the amount entering the air from fossil-fuel combustion is comparable to that entering the air by natural processes, but with the difference that combustion emissions are concentrated in industrial regions of the world.

Human intervention in the biogeochemical cycles is now occurring on a very large scale. This increases the amounts of nutrients available to plants. In the 1960s, for example, rainfall over most of Britain was delivering more than 12 kg S ha^{-1} annually and sulphur deficiency in farm crops was uncommon (COOKE, 1972, p. 75). Increasing the atmospheric concentration of carbon dioxide increases the rate of growth in many plants and the addition of nitrogen and phosphorus also stimulates growth. This is not necessarily welcome; the addition of phosphorus to lakes and slow-moving rivers can cause eutrophication (see section 23).

At the same time, such emissions and discharges can cause damage to wildlife and, in some cases, to human health. The fertilizing benefit does not justify the pollution cost. Both are indiscriminate and there are more efficient ways of supplying fertilizer to plants which need them.

35 Respiration and photosynthesis

Photosynthesis and respiration are the complementary sides of the process by which we, together with all aerobic organisms, obtain energy. That energy comes, of course, from the Sun. Photosynthesis is the series of chemical reactions in which light energy is used to synthesize carbohydrate; respiration is the series of reactions by which carbohydrate is broken down and oxidized to release energy as cells require it.

Respiration is not the same thing as breathing, although the words are often used synonymously. It is the series of chemical reactions by which cells derive energy from the metabolization of nutrients. Breathing is the mechanical pumping of air to bring it into contact with gill or lung membranes across which gases are exchanged: the process by which oxygen enters the body for the purpose of respiration and carbon dioxide, the by-product of respiration, leaves it and is exhaled.

It seems likely that breathing evolved in early fishes from movements originally linked to obtaining food (YOUNG, 1981, p. 102). In invertebrates, oxygen enters the body passively, by diffusing through openings in the body surface. Whether such animals can be said to breathe is ques-tionable, but they certainly respire, as do all single-celled organisms and plants.

Historically, photosynthesis evolved before aerobic respiration. During the early evolution of life, the atmosphere contained little or no free oxygen, and organisms derived energy from other exothermic (energy-releasing) reactions. Some bacteria, descendants of the original anaerobes, continue to do so. Denitrifying bacteria obtain energy by reducing nitrate to nitrite or to gaseous nitrogen; others reduce sulphate or carbonate, releasing sulphide or methane as by-products. Hydrogen sulphide (H_2S) is produced by the bacterial reduction of calcium sulphate, and methane by the reduction of organic compounds.

Yeasts, which we use in brewing and bread-making, obtain their energy by breaking down glucose, as do aerobic organisms, but the breakdown does not proceed so far and the by-products are ethanol (alcohol) and carbon dioxide (which makes bread rise). The anaerobic reaction is $C_6H_{12}O_6 \rightarrow 2C_2H_5OH + 2CO_2$, the aerobic one $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$. Energy can be obtained by oxidizing alcohol; it can be (and is) used as a fuel. Because it does not proceed all the way, to the complete breakdown of glucose into carbon dioxide and water, anaerobic respiration, or fermentation, is less efficient than aerobic respiration.

Significantly, both these types of respiration involve detaching carbon from an organic molecule and oxidizing it to carbon dioxide. They form part of the carbon cycle, and other varieties of anaerobic respiration play an essential role in other biogeochemical cycles (see section 33). Indeed, were it not for them, nitrogen and sulphur would long ago have accumulated as stable compounds from which the elements could not be released and life on the planet might have come to an end.

Some bacteria can live either aerobically or anaerobically, depending on the environment in which they find themselves. Others are obligate anaerobes. Oxygen kills them and consequently they are found only in environments from which gaseous oxygen is rigorously excluded. Hydrogen sulphide, for example, is produced below the surface of waterlogged mud and, as its common name of 'marsh gas' suggests, methane is produced in stagnant water. Methane is also produced by bacteria that inhabit the airless digestive tracts of ruminant mammals and termites. The bacteria produce enzymes that break down cellulose and thus enable their hosts to digest plant material, a task which requires the tough cell walls to be broken and the cell contents released. In return, the bacteria enjoy an environment sheltered from the air, and abundant food. They live in the rumen (the first chamber of the ruminant stomach) in vast numbers: there are 10^{10}–10^{11} of them in every millilitre of rumen contents, as well as 10^5–10^6 protozoa, some of which feed on the bacteria.

Methane absorbs long-wave radiation and nowadays there is concern about its contribution to the greenhouse effect (see section 13), but this arises from an increase in its atmospheric concentration due to human activities, especially the great expansion in cattle and sheep farming and leaks from natural-gas pipelines (natural gas is principally methane). Methane-producing bacteria also inhabit the flooded fields in which rice is grown, and the expansion in rice production is associated with an increase in methane production. Whether steps should be taken to reduce emissions from these sources is a matter for debate, and we are now increasing greatly the amount of nutrients engaged in the global cycles, but the fact remains that the contribution of the anaerobes is crucial. For this reason it may be wise to protect certain of their habitats, such as estuarine mudflats and marshes.

Anaerobic environments are now relatively uncommon, but during the early stages of evolution there was no free oxygen on Earth. All environments were anaerobic and all organisms were adapted to them. This remained the condition of the Earth for a very long time. Living organisms are believed to have been present on Earth nearly 4 billion years ago. By about 3 billion years ago some of them, perhaps resembling present-day algae and cyanobacteria, were exploiting sunlight as a source of energy: they had evolved a method of photosynthesis. This uses carbon dioxide and water as raw materials for the synthesis of carbohydrate and releases oxygen as a by-product.

Oxygen is highly reactive. As it entered the environment in gaseous form, so it combined with substances around it. At that time, the environment was in a reduced state and little by little it became oxidized. Atmospheric methane was oxidized to carbon dioxide and water, carbon monoxide to carbon dioxide, and exposed iron rusted to form the banded iron formations (BIF) that are now among the most important sources of iron ore, in places hundreds of metres thick, extending over vast areas, and containing 40–60 per cent iron. Some sedimentary rocks, especially sandstones, acquired a coat of this haematite rust and became what are now known as the 'red beds'. This gradual oxidation of the environment began some 3.2×10^9 years ago, BIF were completed about 2.2×10^9 years ago, and the red beds formed between about 2.2×10^9 and 6×10^8 years ago (KUPCHELLA AND HYLAND, 1986, pp. 109–110).

Then, with nothing left to oxidize, oxygen began to accumulate in the air and dissolve in water. For organisms living at the time it was extremely poisonous, because what could oxidize minerals could equally well oxidize organic compounds, disrupting cell metabolism. To this day, much of the biochemistry in our bodies is dedicated to rendering surplus oxygen harmless. Should the mechanism falter, free oxygen can cause cancer and is believed to be involved in the processes of ageing (HARMAN, 1992). Most of the single-celled organisms alive while free oxygen was accumulating must have been killed by it in what was the most serious pollution incident the world has ever experienced (JOSEPH, 1990, pp. 99–103). Survivors from that global poisoning retreated to the airless muds where they have lived ever since, some migrating many millions of years later to the equally airless digestive tracts of animals.

Respiration in those days was anaerobic and, in the absence of aerobic respiration to utilize the oxygen released by photosynthesis, the oxygen continued to accumulate. By about 600 million years ago, at the beginning of the Cambrian Period, oxygen accounted for about 0.2 per cent of the atmosphere and it did not reach 2 per cent until 200 million years after that, at the commencement of the Silurian Period. Then the concentration increased steadily to its present 21 per cent, where it has remained fairly constant for the last 400 million years, although there have been excursions. There is evidence that in the late Palaeozoic Era, about 350 million years ago, the oxygen concentration rose, possibly to as much as 35 per cent, then decreased to 15 per cent in the space of 120 million years (GRAHAM *ET AL.*, 1995). This fluctuation may have been due to biological events, but no one knows.

Photosynthesis, the source of the free oxygen, can be described simply: $CO_2 + H_2O \rightarrow CH_2O + O_2\uparrow$, the energy for the reaction being supplied by light and captured by chlorophyll, the coloured compound contained in chloroplasts, cell organelles that are believed to be descended from free-living organisms. In fact, there are four groups of chlorophylls; those in land plants are known as chlorophylls *a* and *b,* those in marine algae *c* and *d*. Chlorophyll absorbs light, especially from the blue and red parts of the spectrum, and for each photon absorbed an electron is emitted. Water tends to dissociate spontaneously into hydrogen (H^+) and hydroxyl (OH^-) ions. Within the cell, some electrons from the chlorophyll combine with hydrogen ions, which move to a hydrogen acceptor (nicotinamide adenine dinucleotide phosphate, or NADP); the chlorophyll replaces its electron with one taken from a hydroxyl, and hydroxyls combine into water molecules with a surplus of oxygen ($4(OH) \rightarrow 2H_2O + O_2\uparrow$). This is the source of the released oxygen. Other excited (energized) electrons emitted by chlorophyll are passed along a chain of donors and acceptors in the course of which they supply the energy to attach phosphate groups to adenosine diphosphate (ADP), converting it to adenosine triphosphate (ATP), the substance that transports energy, releasing it (by losing a phosphate) where energy is required; the process is known as photophosphorylation.

With its attached hydrogen, the NADP engages in a series of reactions, powered by the ATP, in which carbon dioxide is reduced and carbohydrates are synthesized. Because the first stage, directly involving chlorophyll, requires light, it is known as the ‘light stage’ of photosynthesis. The reduction of carbon dioxide and synthesis of carbohydrate is known as the ‘dark stage’. The reactions are summarized, in very simple form, in Figure 4.5. They are described more fully in biology textbooks.

When the first organisms evolved a means of using free oxygen to oxidize carbohydrate they gained a major advantage. Respiration exploits exothermic reactions to produce ATP, the universal biological source of portable energy. A single anaerobic respiratory reaction produces 2 ATP molecules; an aerobic reaction produces 38. Inevitably, once aerobic respiration appeared the organisms equipped to use it prospered. This is why the world today is dominated by aerobes and, because of the energy available to them, probably why some were able to evolve to a much larger size than would be possible for an anaerobe.

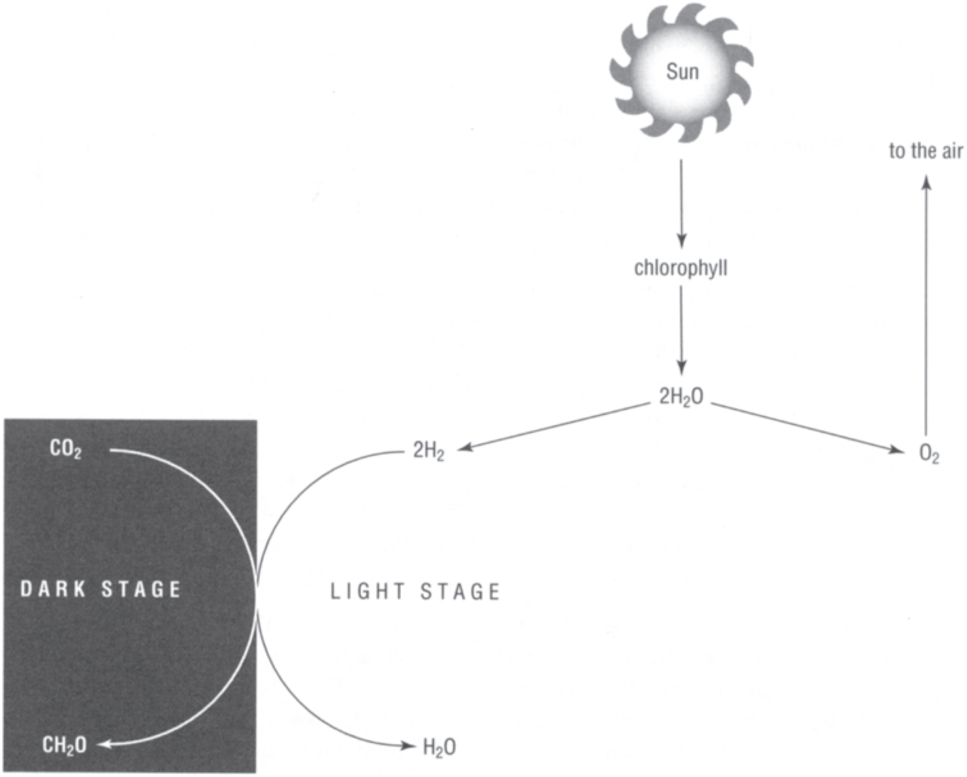

Figure 4.5 ***Photosynthesis***

Photosynthesis consumes carbon dioxide and releases oxygen, respiration consumes oxygen and releases carbon dioxide. Essentially, this is the carbon cycle and it balances: the amount of carbon dioxide absorbed by photosynthesis equals the amount released by respiration (including respiration by plants). Energy derived from the burning of fresh plant material ('biomass fuels') does not affect the cycle, because precisely the same amount of carbon dioxide is released by combustion as was absorbed by photosynthesis during the growth of the plants.

There is a final twist to the story, and it concerns photorespiration. This is a version of respiration associated with the light stage of photosynthesis, but one that generates no ATP. It amounts to a waste of carbon dioxide by the plant. There is a group of plants, however, which do not photorespire, at least not to any significant extent. They are known as C_4 plants, because the first step of their photosynthesis yields a four-carbon compound (oxaloacetic acid); the other, C_3, plants produce a three-carbon compound (phosphoglyceric acid). C_4 plants grow faster than C_3 plants, because they synthesize more glucose for each unit of leaf area, they can photosynthesize at higher light intensities than C_3 plants and, because of the efficiency with which they use carbon dioxide, they can grow at lower carbon dioxide concentrations than C_3 plants.

C_4 plants occur naturally in low latitudes. Most are grasses and they are economically important. The group includes maize, sugar cane, and sorghum. Should the atmospheric concentration of carbon dioxide continue to increase, it is uncertain how C_4 plants might respond. C_3 plants, which include wheat, rice, sugar beet, and all trees, would benefit (provided other nutrients were available to them) but possibly at the expense of C_4 plants where the two groups grow in the same area.

Photosynthesis and respiration are the two processes on which all life is based, at least on our planet. They provide the mechanisms by which energy is captured and utilized.

36 Trophic relationships

Rabbits eat grass and foxes eat rabbits. The grass, rabbits, and foxes comprise a 'food chain', and at first glance the relationship appears simple. True, many food chains are longer, but not much longer. The grass → rabbits → foxes chain has three links, or levels, and some chains may have four or, more rarely, five. A tree leaf, for example, may be eaten by a caterpillar, the caterpillar by an insect-eating bird, and the insect-eating bird by a bird of prey. This chain, of leaf → caterpillar → bird (1) → bird (2), has four levels. To add a fifth level it would be necessary to find an animal that feeds on birds of prey. This would be difficult, perhaps impossible, and fifth levels are uncommon, because few carnivores specialize in hunting other carnivores.

It is not too difficult to see why this is so. Rabbits must eat a considerable quantity of grass, which is a not especially nutritious food, even for an animal such as a rabbit with a digestive system adapted to deal with it. The rabbit provides the fox with a substantial meal, but it is only one meal and the fox needs to eat every day. Thus the fox thrives only if there is a population of rabbits to keep it supplied, and the rabbit thrives only if there is a substantial area of grass on which it may graze. Take these together, omit the rabbit, and it is clear that the fox subsists on the produce of a considerable area of grass. Try to add a fifth level and the area of grass must be increased in proportion, to supply sufficient grass to feed a large enough rabbit population to sustain enough foxes to feed whatever monster it is that has taken to eating foxes.

This relationship can be measured and described in several different ways, which are explained in the next chapter. It can also be demonstrated in terms of the land area required to support an individual of a particular species, although this varies according to the size of the individual and the richness of the habitat. Rabbits do not travel far, most grazing within an area of no more than about 60×10^3 m^2 and many in a much smaller area. Rabbits released experimentally 600 m from the place where they had been captured found their way back to their burrows, but rabbits released 1 km from their burrows failed to do so (THOMSON AND WORDEN, 1956, pp. 104–105). Foxes seek food in ranges varying, in mid-Wales, from 2.5 to 15 km^2, females having smaller ranges than males (CORBET AND SOUTHERN, 1977, p. 317). Clearly, the bigger the animal the more space it needs. A European wildcat *(Felis silvestris)* has a range of 600×10^3 to 700×10^3 m^2, a tiger 65–650 km^2. Today we are concerned for the survival of tigers and similar large predators, but they are at risk precisely because they are large predators. Exclusively carnivorous mammals of their size occupy such extensive ranges that they were never common, and any fragmentation of their habitat that breaks up the ranges into smaller 'islands' with barriers the animals cannot cross threatens them with starvation, even if the total area of suitable habitat is little reduced.

The wolves of Isle Royale

Populations are usually regulated by the food supply available to them. In the grass → rabbits → foxes food chain, the number of foxes in an area is ultimately determined by the amount of grass available to the rabbits. While this is usually the case, there are exceptions.

Isle Royale, in Lake Superior, U.S.A., is a national park in which moose *(Alces alces)* feed on balsam fir *(Abies balsamea)* and grey wolves *(Canis lupus)* feed on moose. In winters when there is more snow than usual, moose cannot move so quickly and wolves hunt in larger packs. The wolves kill more moose than they do in years when there is less snow and they hunt in smaller packs. Because of this, winters with heavy snow lead to a reduction in moose numbers. This leads to a reduction in browsing and is followed by an increase in the growth of balsam fir.

Changes in the weather cause changes in the hunting behaviour of wolves, with an effect that cascades through the populations of moose and balsam fir (POST *ET AL.*, 1999).

Feeding relationships, based on grouping species according to their diets, are known as ‘trophic’, from the Greek *trophe,* meaning ‘nourishment’. They can be generalized. At the base of every food chain there are ‘autotrophs’, organisms that can synthesize organic molecules from inorganic ones. Autotrophs may be ‘photoautotrophs’, using photosynthesis (see section 34) to combine carbon and hydrogen into carbohydrate, or ‘chemoautotrophs’, which derive energy from the oxidation of other compounds, but also synthesize organic molecules. Autotrophs are primary producers. Green plants are photoautotrophs and are by far the commonest primary producers in both terrestrial and aquatic food chains.

All other organisms, which cannot synthesize organic compounds from inorganic precursors, are ‘heterotrophs’ (‘other nourishment’). All animals, fungi, and some bacteria are heterotrophs. They are described as consumers, because their food comprises organic material obtained by consuming other organisms, and they form a hierarchy. Herbivores, which feed exclusively on plant material, that is, on the primary producers, are primary consumers. Secondary consumers feed on primary consumers and are, therefore, carnivores. Carnivores which feed on other carnivores are tertiary consumers. Any food chain can thus be represented as: primary producer ? primary consumer ? secondary consumer ? tertiary consumer.

The food chain concept is extremely useful, but only up to a point. It has been used, for example, to trace the fate of certain chemically stable compounds that are consumed by organisms low in a food chain and then concentrated at higher levels. DDT is the best-known example. In the 1950s, large amounts of DDT were used in Illinois to control the beetle *(Scolytus scolytus)* that spreads the fungus *(Ceratocystis ulmi)* which causes Dutch elm disease. The insecticide was ingested by earthworms, presumably from eating dead leaves coated with it. They were not harmed by it, but in spring American robins *(Turdus migratorius)* feed mainly on earthworms. The DDT they ingested with each earthworm accumulated, eventually to a lethal dose. Earthworms were found to have a sublethal concentration of 33–164 mg DDT kg^{-1} (milligrams per kilogram of body weight) in their bodies, and autopsies revealed that robins had an average of 60–70 mg DDT kg^{-1} in their brains. This story was recounted by Rachel Carson in *Silent Spring* (CARSON, 1962, pp. 102–105), but although the effect was very serious, it was also local. Many birds died, but in the United States generally, the overall population of robins actually increased during the period of most intensive spraying (MELLANBY, 1992, pp. 62–63).

Such stories gave rise to the popular and widely accepted view that stable compounds, such as DDT, can accumulate along food chains in a simple fashion. Each consumer stores the dose acquired from each of the organisms it eats and eventually an organism high on the food chain receives a lethal dose. In fact it is far from simple. The substance may be excreted or converted metabolically into harmless compounds, and even when it is stored in the body the amount may peak before it reaches a lethal concentration. In humans, for example, DDT continues to accumulate in the body for many years, but eventually reaches a peak, far below the concentration that could be harmful, after which it is excreted at approximately the same rate as it is being absorbed (MELLANBY, 1992, p. 67).

This suggests that the food-chain concept should be used cautiously, but it is not its principal limitation. In the real world, few organisms are restricted to a single food item. Foxes do eat rabbits, but rabbits are not all that they eat, and rabbits graze plants other than grass. Figure 4.6 illustrates a very simplified trophic structure for a temperate-climate pond. In this diagram, organisms are arranged in five trophic levels, with plants, the primary producers, at level 1 and birds, quaternary consumers, at level 5. Birds, however, do not feed exclusively on the fish that comprise level 4; they also feed on all the organisms at level 3 and on several of those at level 2. The only general rule to be derived from the diagram is that organisms never feed on those at a trophic level higher than their own, and, although generally true, this is more a logical consequence of the way trophic levels are defined than a reflection of what you might observe were you to study pond life. Dragonfly nymphs, for example, capture and eat fish larvae and sometimes small fish. Most animals, in fact, eat a fairly wide variety of food, depending on what is available, and diets often change from season to season. Over the course of the year, the blackbird *(Turdus merula)* has a typically varied diet, summarized in Table 4.2 (HILLSTEAD, 1945, p. 72).

Table 4.2 ***Items making up the diet of the blackbird* Turdus merula**

Item	*% of total*
Animal	
Insects (pest species)	22
Insects (beneficial)	3.5
Insects (other)	5.5
Earthworms	4
Snails and slugs	2.5
Miscellaneous	1.5
Vegetable	
Fruit (cultivated)	25
Fruit and seeds (wild)	24.5
Wheat	2.5
Roots	2.5
Miscellaneous	6

When linked, food chains become ‘food webs’, and even when reduced to their barest essentials these are usually very complex. Figure 4.7 illustrates a food web typical of European heathland (GIMINGHAM, 1975, pp. 55–59). This is also arranged into trophic levels, of which in this case there are four, but as with the pond food web, animals at higher levels feed on organisms from more than one lower level. Wildcats, for example, hunt mice and voles, which are primary consumers (vegetarians) at level 2, but will also eat shrews, which feed on insects and spiders and are consequently secondary consumers at level 3. Frogs, lizards, and meadow pipits also straddle trophic levels by feeding on both herbivorous (level 2) and carnivorous (level 3) insects, and they themselves are preyed upon by carnivores at higher levels.

Except in environments with few species, food-web diagrams must necessarily group species together; to list them all would make the diagrams so intricate as to render them incompre-hensible. Some ‘insects’ feed on leaves, others on shoots, or sap. All are primary consumers, but their feeding preferences have different effects on plants, and although sheep are the only large herbivorous mammals listed, heathlands also support deer and cattle, which feed on different parts of the vegetation. Nor do most food-web diagrams include organisms that feed mainly or exclusively on dead plant material—the decomposers which complete the nutrient cycle.

Illustrations of food webs provide more information than do food-chain diagrams, but their principal value lies in their ability to identify the ecological niche (see section 37) each group occupies. Relationships in almost all natural environments are extremely complex. By expressing them, in effect, as niches, food-web diagrams are useful summaries of that complexity.

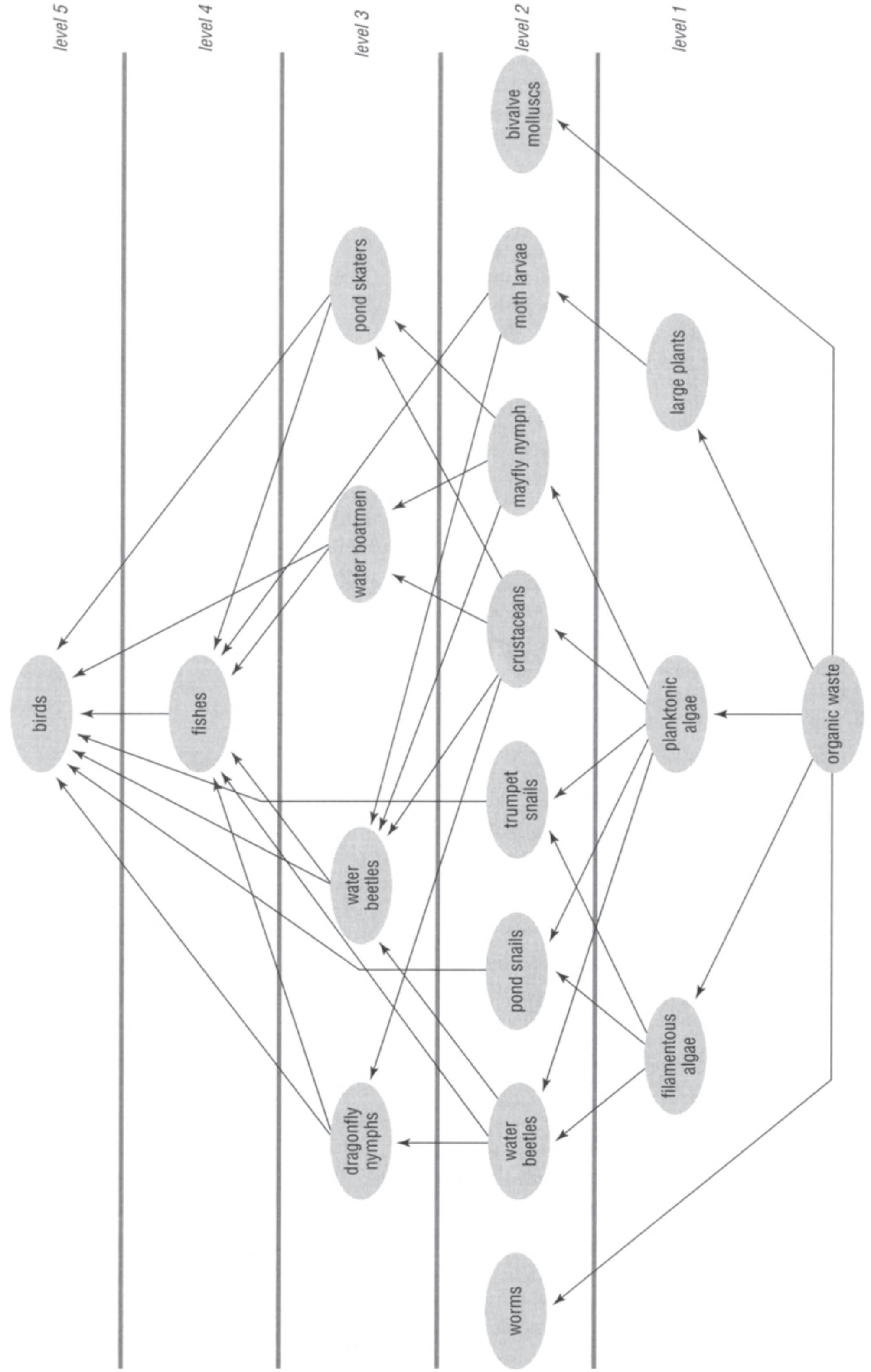

Figure 4.6 ***Simplified food web in a pond***

After Dowdeswell, W.H. 1984. **Ecology: Principles and practice.** ***Heinemann Educational Books, Oxford***

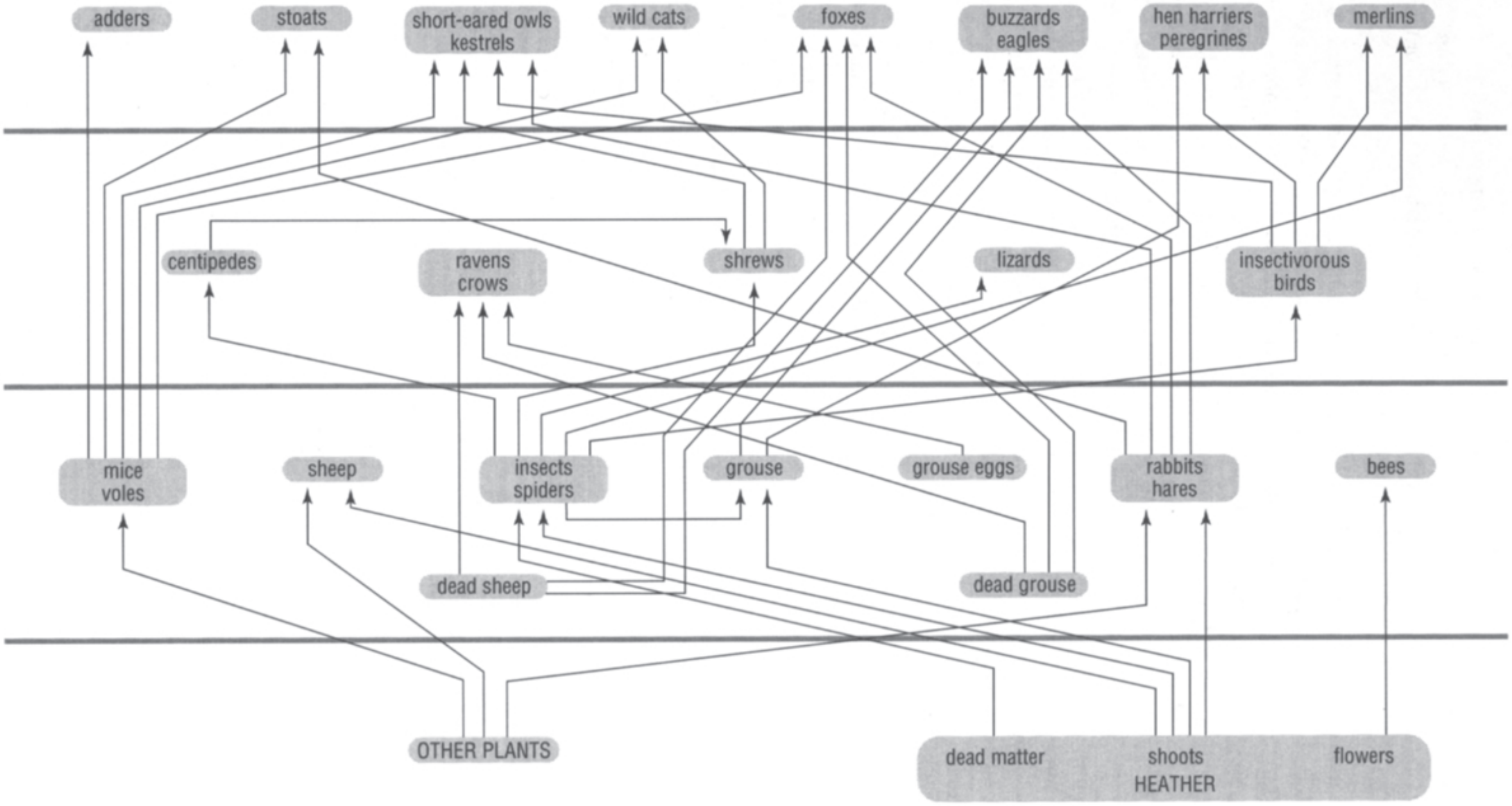

Figure 4.7 ***Simplified heathland food web***
After Gimingham, C.H. 1975. An Introduction to Heathland Ecology. *Oliver and Boyd, Edinburgh*

37 Energy, numbers, biomass

Many plants are required to sustain a herbivorous animal and many herbivores are required to sustain a carnivore. Anything that affects the size of a population at one level must have repercussions at higher levels, but these are not always straightforward, such is the complexity of the food webs of which food chains are only a part.

In the simple grass ? rabbits ? foxes chain, a reduction in the rabbit population might be expected to result in an increase in the amount of grass (fewer consumers) and a decrease in the fox population (fewer prey). Some years ago, this happened in Britain, when large numbers of rabbits died from myxomatosis. Predator populations fell. In some places, stoat numbers were reduced to one-third of their pre-myxomatosis levels, rabbits being the principal prey of stoats (POLLARD *ET AL.*, 1974, p. 139). No longer nibbled, grasses also grew taller; and that was where the complications began. Being taller, they cast more shade on the ground, which suppressed the growth of many small herbs, including wild thyme *(Thymus drucei),* which until then grew in a few places in Devon and Cornwall. When they first hatch, larvae of the large blue butterfly *(Maculinea arion)* feed on wild thyme and are camouflaged to resemble its flowers. After their third moult, the caterpillars leave the thyme and enter into a symbiotic relationship with ants, living in ant nests until they pupate. As the grasses grew and the thyme disappeared from the sward, adult butterflies were unable to lay their eggs in appropriate places, and on 12 September 1979 the large blue butterfly was formally pronounced extinct in Britain, its last colony, in Devon, having died out (ALLABY, 1981, pp. 142–143). A reduction in the population of primary consumers led to an increase in the producer population, but in this case it also caused the decline of another primary consumer.

Recognizing the need to quantify the organisms at each trophic level, in his book *Animal Ecology,* published in 1927, the British ecologist Charles Elton (1900–91) proposed a method for showing graphically the relationships between levels. If the producer organisms are represented by a rectangle of a size proportional to their number, and similar rectangles are drawn one above another to represent the numbers present through the hierarchy of consumer organisms, the result is a stepped pyramid. Consumer organisms ingest organic matter and convert it into a different kind of organic matter: rabbits convert grass into ‘rabbit stuff’ and foxes convert ‘rabbit stuff into ‘fox stuff’. Consumers, therefore, are also producers from the point of view of those at higher trophic levels, and are sometimes described as secondary or tertiary producers (but not primary producers, of course).

Figure 4.8 shows such a pyramid for four trophic levels comprising the typical population living on temperate grassland. In this form it is known as a ‘pyramid of numbers’ and it illustrates the way numbers at each level are usually about one-tenth of those at the level below.

In the example chosen, however, the relationship does not hold at the highest level, of tertiary consumers: 10000 secondary consumers provide sustenance for no more than 10 tertiary consumers, not the 1000 that might be expected. This arises from the organisms themselves. At levels 2 and 3 these are insects, and at level 4 they are insectivorous birds and mammals, which are very much larger than insects. If animals, or plants for that matter, at one level are of markedly different size from those at another, their relationship will not be revealed very clearly merely by counting them. Many more herbaceous plants than large trees are needed to support a herbivore population, and a given number of plants can support many more rabbits than cattle.

Numbers can be misleading, but it should be possible to relate organisms of different sizes by an equation along the lines of: x herbs=1 tree, or x rabbits=1 cow. This leads to the concept of ‘biomass’ or ‘standing crop’, which is simply the total mass of organisms, usually expressed as

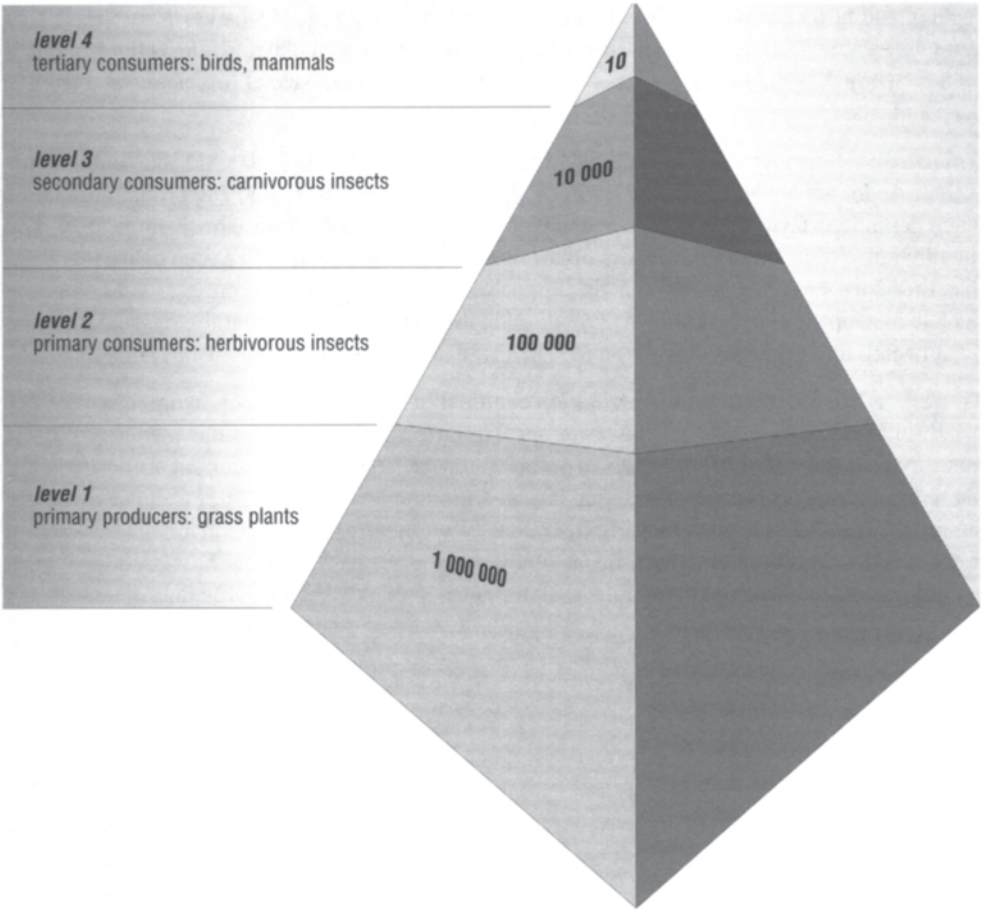

Figure 4.8 ***Pyramid of numbers per 1000 m^2 of temperate grassland***

their dry weight, because the amount of water held in tissues varies widely from one species to another. In principle, it is obtained by collecting, drying, and weighing, although in the real world this is rather more easily said than done. Removing the entire root system of a plant can be difficult, some small and very specialized primary consumers are liable to be missed, and some plant parts are temporary, such as leaves that die back before flowering (BREWER, 1988, p. 318).

Nevertheless, biomass has been estimated for various biomes and for the world as a whole. In tropical rain forest, for example, the mean biomass is 45 kg m^{-2} of ground surface, in temperate deciduous forest it is 30 kg m^{-2}, and in tundra it is 0.6 kg m^{-2}. The global biomass, counting both land and marine organisms, is 1841×10^9 t (BEGON *ET AL.*, 1990, p. 652).

Biomass can be estimated for each trophic level and drawn as a stack of rectangles, in the same way as numbers. This produces a second type of pyramid, called a pyramid of biomass. Usually, this slopes less steeply than the pyramid of numbers.

Although the pyramid of biomass is more useful than the pyramid of numbers, unfortunately it does not quite resolve the difficulty. In particular, it takes no account of metabolic rate, which is the rate at which an organism converts food into energy for its own use. This is related to body size, activity, and temperature. We metabolize faster when we are active than we do when resting, and faster in cold weather than in warm weather, but in cold weather plants and many animals become dormant and their metabolism slows. Since metabolic rate affects the amount of food consumed, estimates of biomass can vary with the average size of organisms at a trophic level and with the temperature.

A more serious disadvantage emerges where population sizes are subject to wide fluctuation. This is the case for aquatic environments, where phytoplankton (small plants) can proliferate rapidly when conditions favour them, then decline just as rapidly. Zooplankton (small animals) feed on the phytoplankton and their numbers follow those of the plants, but with a time delay. It is possible, therefore, to take a sample shortly after a decline in phytoplankton numbers but before the decline in zooplankton, and draw a pyramid of biomass that suggests that the consumers heavily outweigh the producers; the pyramid is inverted and this is clearly an absurd situation.

There is a third way to express trophic relationships, however, which avoids most of the disadvantages and is the one ecologists prefer. This is expressed as a pyramid of energy. What is measured is not the number or weight of organisms at each level, but the amount of energy, entering as sunlight and becoming food, that passes from one level to the next. Producers ‘capture’ sunlight for photosynthesis. The carbohydrate they synthesize provides food for consumers, but it can also be considered as the transfer of energy and measured as the heat produced when organic matter burns. Figure 4.9 shows trophic relationships in terms of the flow of energy and

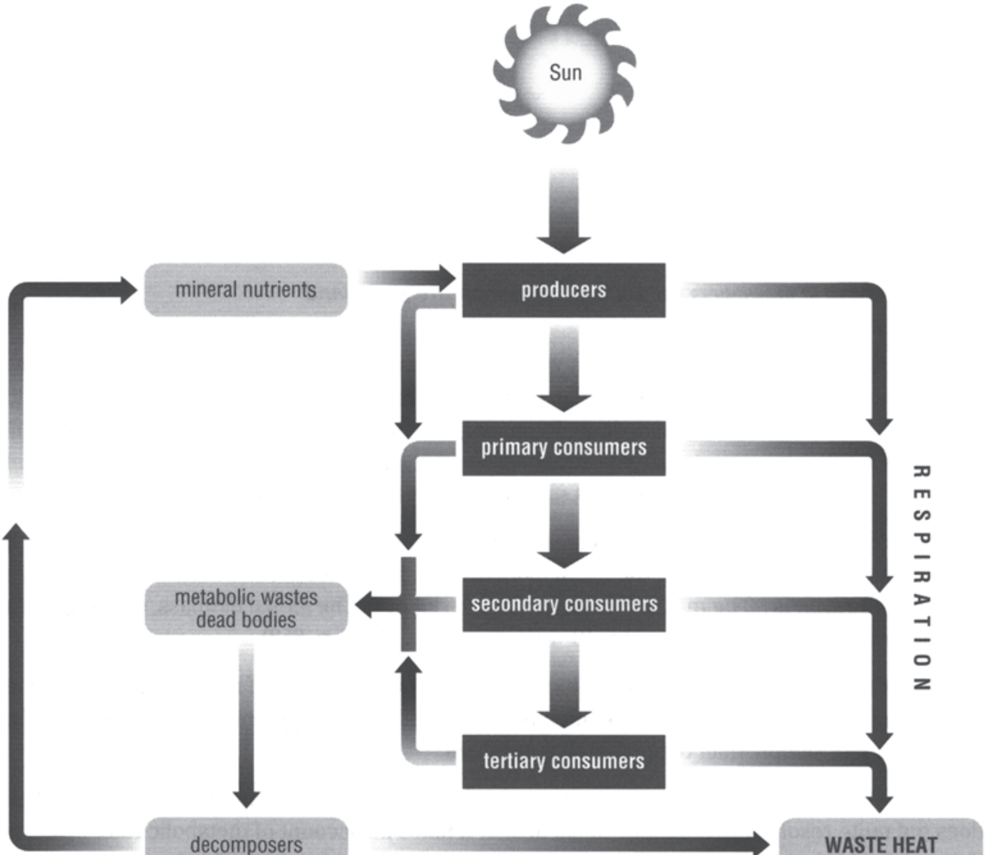

Figure 4.9 ***Flow of energy and nutrients***

mineral nutrients. In doing so it explains why numbers and biomass decrease so sharply at higher trophic levels as to produce pyramids. All organisms, including plants, use most of the energy they receive in respiration. Carbohydrates are oxidized to drive the ADP-ATP mechanisms that provide cells with the energy to maintain themselves, and whenever energy is changed from one form to another a proportion is lost as low-grade heat. Unless biomass is increasing, as when a newly planted forest is still growing, for example, eventually all the original solar energy is transformed into waste heat. Biomass then remains constant. In a mature forest, it has been calculated that total photosynthesis delivers 188 MJ m^{-2} yr^{-1} (MJ=megajoule), plant respiration uses 134 MJ m^{-2} yr^{-1} and respiration by all heterotrophs uses 54 MJ m^{-2} yr^{-1}; all incoming energy is used in respiration and ends as waste heat (BREWER, 1988, p. 319).

Of course, the forest may still be growing, or declining, and it may be useful to know this. The technique for estimating overall increase or decrease begins by measuring or calculating the total amount of sunlight used in photosynthesis by plants within a defined area. This produces a figure for gross production *(G)*. The amount of energy used in respiration *(R)* is then calculated. What remains is the net production *(N)*. It remains distributed among the plants present in the area and indicates an increase in their growth or numbers, its value being calculated as $N=G-R$. If N is positive, growth is occurring, if negative the plant community is in decline.

Unfortunately, the results can be misleading, because the calculation takes no account of the herbivores feeding on the plants. In fact, N also equals $T+C+D$, where T is the increase in plant biomass, C the amount consumed by herbivores, and D the amount lost through the death of plants and the shedding of dead parts, such as leaves and old branches. In the case of agricultural or forestry crops, an ability to calculate T accurately is of obvious value.

Techniques have been developed for acquiring the data needed to make these calculations. Instruments can measure the amount of sunlight to which the plants are exposed over a year. The amount of that energy used by different plant tissues is calculated from measurements of the amount of heat energy they yield when burned. The stomach contents of animals can be measured, as can amounts of dead material reaching the ground surface.

Production and consumption are being measured in terms of energy, and the results of those measurements describe how energy flows from producers to the hierarchy of consumers. Displayed graphically, it forms the third and most useful of the ecological pyramids: a pyramid of energy.

In some well-studied cases energy flow has been measured in great detail, and, in addition to providing information about the plant and animal community as a whole, such studies can also throw light on the efficiency with which energy is used at each trophic level. In particular, they can determine how efficiently herbivores are consuming plant material and how this changes over time, perhaps from season to season. This is of considerable interest to those seeking to grow a commercial plant crop.

'Ecological energetics', the branch of ecology that deals with the flow of energy, represents a boundary zone in which life scientists and physicists meet, but as ecologists. Its existence and great importance in ecological studies demonstrates the interdisciplinary character of all the environmental sciences.

38 Ecosystems

It is all very well to measure the flow of energy through the trophic levels of a community of organisms, but limits must be set to the boundaries of that community. It must be defined in such a way as to distinguish it from other adjacent communities. Such a boundary will imply nothing about the size of the community; it may be as small as the untended corner of a field or as large as a forest. What matters is that in some way it is noticeably different from the communities adjoining it. An area of woodland, for example, may be limited by the boundaries of the cultivated fields surrounding it, a pool by its banks, a marsh by the adjoining drier land where the water table is lower.

There are several ways of approaching the task. In Europe it was undertaken primarily by botanists, who devised ways of classifying plant communities and, from this, a discipline called 'phytosociology', or the sociology of plants. A leading figure in this development was a Swiss botanist, Josias Braun-Blanquet (1884–1980). He began his career in Zürich and in 1930 became the first director of the Station Internationale de Géobotanique Mediterranéenne et Alpine, at Montpellier. The scientists who worked with him from about 1913 became known as the Zürich-Montpellier (or ZM) School and their ideas are still influential.

In their system, sometimes known as 'Sigmatism', from an acronym of the name of the Montpellier Station (BOWLER, 1992, p. 526), plant associations were classified in ways similar to the taxonomy used to classify species. It begins with the concept of the 'minimal area', the smallest area in which a particular plant association can develop fully. For oak woodland this is about 200 m^2, for acid grassland about 9 m^2, and minimal areas have been calculated for every type of vegetation. A stand of plants can be examined only if it covers at least the minimal area for its type. The stand is then sampled within a marked area or quadrat, known as a relevé or Aufnahme, which is usually half the area of the stand and must be larger than the minimal area. All the plants within the relevé are recorded with estimates of the area each covers and the way they grow: solitarily, as clumps, small or large patches, or large colonies. This is their 'sociability'. Relevés are then grouped into classes, called phytocoena, which can be compared.

A somewhat similar scheme was developed at about the same time as the ZM School at Uppsala, Sweden, by ecologists led by J.Rutger Sernander (1866–1944) and later by Gustaf Einar Du Rietz (1895–1967). The Uppsala School called their basic plant unit a 'sociation' and sociations with the same dominant species could be merged, as 'consociations' (MOORE, 1982, pp. 59–62).

During the early years of this century, the foremost British ecologist was Sir Arthur George Tansley (1871–1955), who became a prominent conservationist. Tansley also held that the key to understanding natural communities lay in studying plant associations, but he placed great emphasis on the relationships among plants and between plants and animals, what he called 'biotic factors'. He described his scheme in *Practical Plant Ecology,* published in 1923. He called the basic vegetation unit a biome. An updated and revised version of this book was published in 1946, with the title *Introduction to Plant Ecology*. In it he introduced to a popular readership a word he had coined in 1935, in an article in the journal *Ecology,* which had been absent from the earlier edition. It is a word that has become familiar to us all. 'A wider conception still is to include with the biome all the physical and chemical factors of the biome's environment or habitat—those factors which we have considered under the headings of climate and soil—as parts of one physical *system,* which we may call an *ecosystem,* because it is based on the οικος or home of a particular biome' (TANSLEY, 1946, p. 207).

In the United States *(www.bio.swt.edu/simpson/ecology/ecointro.html),* meanwhile, ecologists were strongly influenced by a Danish botanist, Eugenius Warming (1841–1924). Warming recognized what he called plant 'communities' that were influenced in their development by other organisms, such as parasites. He maintained that a plant has certain physical capabilities which determine where it can grow. Many eminent ecologists adopted the Warming approach, but eventually one group broke away from it. Frederic E.Clements (1874–1926) was one of a team of botanists who embarked on a study of the ecology of the prairie, a task that was considered urgent, because the natural grassland of North America was everywhere threatened by agricultural expansion. The European method, which relied on the skill of an observer to characterize vegetation types, was useless on the prairie. Clements and his colleagues devised a more rigorous method. They marked off measured areas, called ‘quadrats’, of varying sizes but usually one metre square, and recorded every plant growing within them by species and by number in each species. A number of quadrats sited randomly over a large area allowed the distribution of species to be determined fairly accurately and provided raw data for statistical treatment.

Clements also cleared selected quadrats of all vegetation, then monitored the way species recolonized them. This led him to his theory of succession leading to a climax (see section 38).

The British and American approaches to ecological studies strongly influenced one another. Today they have almost merged, and the ecological methods based on the ecosystem concept that are taught in Britain and North America are very similar. It is important to remember, however, that the tradition of the ZM and Uppsala Schools remains strong elsewhere in Europe, and with the introduction of the National Vegetation Classification (NVC) British ecologists have also embraced the phytosociological approach.

An ecosystem, then, comprises all the organisms living within a definable area and ecosystem studies take account of relationships among them and of the physical and chemical factors affecting them. Figure 4.10 illustrates, very simply, the way an ecosystem may be structured. Its energy is supplied by the Sun and transmitted from one trophic level to another (see section 36). Its

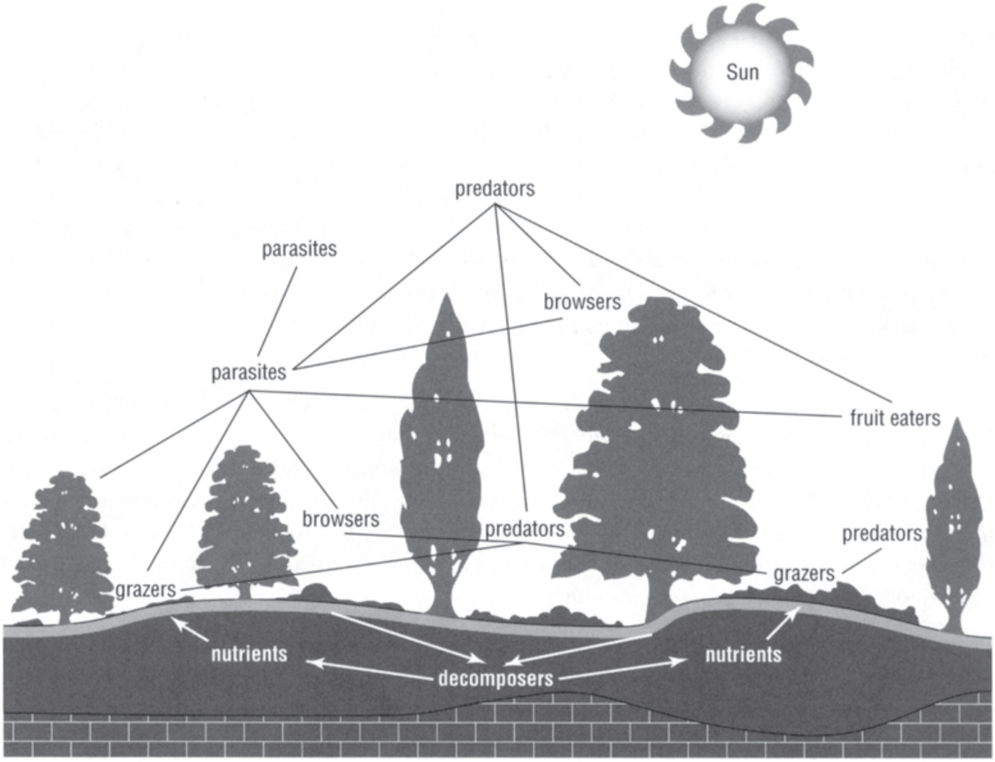

Figure 4.10 ***Ecosystem***

chemical nutrients are supplied from the underlying bedrock by means of weathering, to which the soil biota contributes. Green plants, here trees, shrubs, and herbs, are the primary producers. Producers compete with one another for light, water, and nutrients. The herbs are grazed, the leaves of trees and shrubs browsed, and some animals feed on fruits. Fruit-eaters, grazers, and browsers compete with one another for food and for other resources such as nesting sites. All the primary consumers (herbivores and fruit-eaters) are subject to predation, and there are also carnivores, such as birds of prey, that will take small predators; they are tertiary consumers. All the plants and animals are hosts to parasites and these have parasites of their own (known as 'hyperparasites' or, if they kill their hosts, 'parasitoids'). All these are also subject to predation. Metabolic wastes and dead organic material provide food for decomposers, which form another trophic hierarchy (which can be represented by inverted pyramids otherwise similar to the other ecological pyramids).

The illustration allows for parasitism, but makes no mention of mutualistic relationships, which are often important. These occur when two different species live in close association with one another to the benefit of both; if one benefits but not the other, the relationship is known as 'commensalism'. The term 'symbiosis', by which people often mean what ecologists call 'mutualism', is now used to describe all close relationships between organisms of different species; it includes commensalism, mutualism, and parasitism.

As the illustration suggests, ecosystems exist in three dimensions, although one of those dimensions may be small. Animals that live on the surface of water, known collectively as 'pleuston', and the bacteria, microscopic plankton (called 'nanoplankton'), and minute animals that live in the uppermost few centimetres of the sea (called the 'neuston') inhabit an ecosystem as wide as the ocean itself, but only a few centimetres deep (MARSHALL, 1979, pp. 42–43).

Other ecosystems have to be considered in all three dimensions, the most obvious being forests of all types. These are dominated by mature trees, most of them so spaced that their foliage overlaps to form a canopy. Below them there are young trees and shrubs, the young trees unable to grow taller for want of light for photosynthesis. When mature trees die and fall a gap appears in the canopy, sunlight penetrates more strongly to lower levels, and a young tree completes its growth to replace the dead tree; the canopy closes once more. Lower still there are tall herbs and below them small herbs and such plants as mosses. Figure 4.11 shows the arrangement schematically, with the several forest strata labelled. Each of the layers supports its own population of specialized consumers, with their predators and parasites, and so although the forest comprises a total ecosystem, the layers can also be regarded as smaller ecosystems within it.

Ecosystems are alive, of course, but they are also like supermarkets, vast stores of resources offering space, shelter, food, and drink to those who visit them. As in supermarkets, some of those resources are alive; some, such as water, are not. Unlike supermarkets, they require that most of the goods they display be consumed on the premises, although limited exceptions are permitted. Birds, for example, may gather food in one ecosystem but roost in another. In return for this licence, they distribute seeds and so assist in the spread of plants. Flying insects have the same liberty and pollinate flowers in return.

There is another difference. Resources are not advertised as such, but rather presented as raw materials from which customers may make what they will, as though supermarkets displayed not vegetables, but seeds and soil; not butter, but grass and cows. A member of a species entering an ecosystem afresh must explore, seeking the resources it needs. If it finds them it may settle and establish itself, utilizing a space or food source for which no other species has found any use. It makes a home for itself, finds the food it prefers, and is said to have created a 'niche'.

Figure 4.11 ***Forest stratification***

Niches do not exist until organisms fill and thus define them, but once a niche is defined it can be vacated. Then another member of the same species, or of a different species, may enter to occupy it. The concept is of function: the niche describes the occupied habitat, what its occupant does, how it feeds, when and for how long it is active, and when and for how long it is present and absent.

Ecosystems must be definable, but their borders are not always sharp. Except where cultivation or other human activities produce sharp boundaries, they more commonly shade into one another. Forests, for example, do not simply stop at their edges. The trees become more widely scattered, different species thrive, often of smaller trees and shrubs, and the forest seems to merge into the different ecosystem adjoining it. Such border regions are called 'ecotones' and are often richer in species than the ecosystems to either side. They support many of the species from both adjacent ecosystems as well as species peculiar to themselves.

Studies of ecosystems reveal how species interact, and they allow an important generalization. No matter how different two ecosystems may appear, as systems they function in very much the same way. This means that ecologists can use the same approach to unravel the complexities of rain forests, grasslands, deserts, or any other type of community, including the artificial ones produced by humans. Agricultural ecosystems are of great interest and even private gardens in towns prove rewarding subjects.

In recent years there has been much popular concern over the supposed fragility of ecosystems. Here it is impossible to generalize; each case is different. It is characteristic of all systems that they maintain themselves in a fairly constant state and ecosystems are no different in this regard, reacting to perturbations in ways that restore their integrity. Not all ecosystems are equally robust, however, and for any ecosystem there is a degree of disturbance that exceeds its tolerable limits, after which it cannot recover.

Fears of damaging ecosystems are based on the sound conservationist principle that we should aim to minimize the disruption we cause, but there is a risk that this principle may be confused with the old idea of a 'balance of nature'. This supposes a perfect order of nature that will seek to maintain itself and that we should not change. It is a romantic, not to say idyllic, notion, but deeply misleading because it supposes a static condition. Ecosystems are dynamic, and although some may endure, apparently unchanged, for periods that are long in comparison with the human lifespan, they must and do change eventually. Species come and go, climates change, plant and animal communities adapt to altered circumstances, and when examined in fine detail such adaptation and consequent change can be seen to be taking place constantly. The 'balance of nature' is a myth. Our planet is dynamic, and so are the arrangements by which its inhabitants live together.

39 Succession and climax

When buildings are demolished and the land cleared, after a short time plants appear. Before long they blanket the site, their flowers cheering the desolate landscape, their seeds blowing in the wind. One of the most poignant features of war is the speed with which wild flowers colonize the ruins of bombed and shelled cities. In Britain, the symbol by which we remember the war dead is the common field poppy, the flower that coloured the battlefields of northern Europe.

These plants are opportunists. Their seeds are everywhere and those of some can remain in the soil, dormant but viable, for a very long time. Unable to survive in competition with most other plants, when the land is bare they germinate, grow rapidly, flower, and produce seed before more aggressive species arrive and they lose their advantage. Many have brightly coloured flowers to attract pollinating insects. They are annuals.

Farmers and gardeners regard them as weeds, but ecologists recognize them as members of a pioneer community, the first colonizers to arrive on newly exposed ground. They are tolerant of strong, direct sunlight, they can grow in a soil that contains few nutrients and is too acid or alkaline for most plant species, and neither drought nor temporary waterlogging can destroy them.

Soon, other plants begin to appear, their seeds borne on the wind or dropped by birds, and the composition of the plant community changes. Some of the primary colonizers vanish from the scene. The new plants include biennials and perennials, in which the vegetative parts do not die at the end of a growing season, although the stems and leaves may disappear. Many perennials spread vegetatively as well as producing seed. The annuals produce their seed, but in the following year it is unable to germinate, because all its previous sites are now occupied.

Woody plants, which grow more slowly than herbs, also establish themselves. They grow taller than the herbs and shade them, so the community changes yet again as it becomes dominated by shrubs. Among the woody plants there are trees, which grow even more slowly. Eventually, however, they shade out some of the shrubs. The early arrivals tolerate exposure to full sunlight but, as the taller ones shade the ground, conditions develop that are suitable for shade-loving plants.

Leave the bare ground undisturbed and little by little it will be transformed. In most parts of lowland Britain it is likely to develop into woodland. The sequence of distinct vegetation types is called a 'successional series' or 'sere', each type within the series being a 'seral stage', and the process is known as 'succession'. Figure 4.12 illustrates five seral stages in the succession from open ground to mature woodland. It starts with annual herbs, only partly covering the ground,

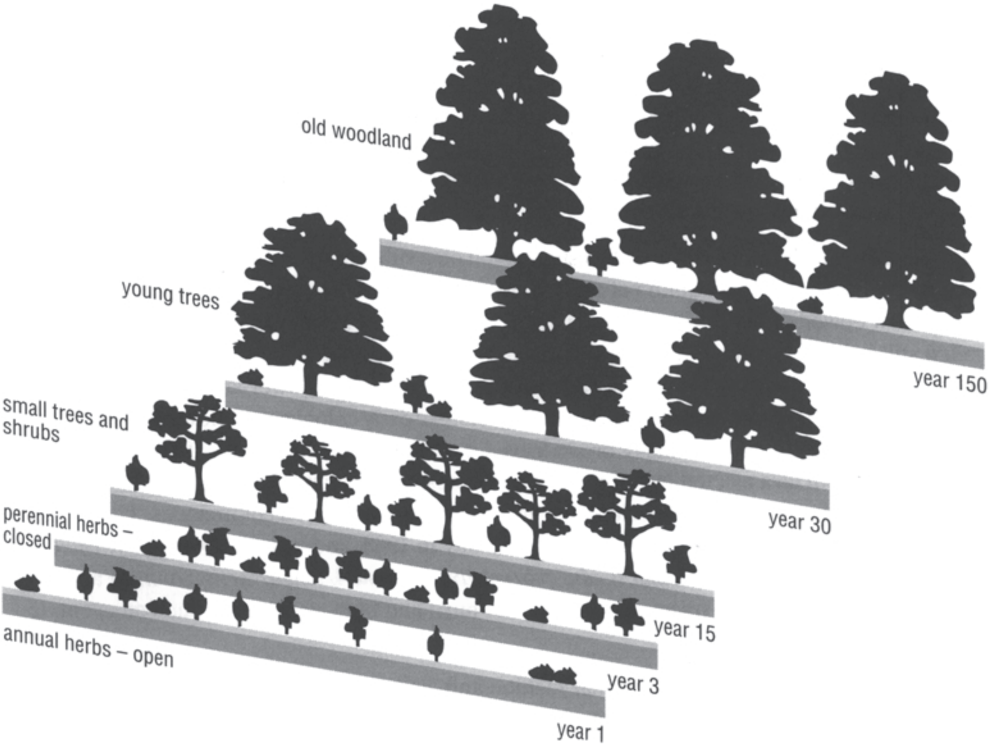

Figure 4.12 ***Succession to broad-leaved woodland***

some of which remains bare. These are succeeded by perennials, which establish a complete ground cover, and are followed in turn by small trees and shrubs, young woodland trees and, finally, the mature woodland. The full succession takes about 150 years from the arrival of the first annuals to maturity.

It is not only bare soil that will be colonized in this way. Any open surface may provide a site for a succession provided it offers some physical stability. A newly exposed sand bar will be colonized, as will a lava flow once it has cooled, and a succession does not need to occur on a large area. When a forest tree falls, exposing an area of ground to full sunlight, a 'microsere' ensues as woodland herbs flourish and the dead tree decomposes, the site eventually returning to its original, woodland, condition. This fact even has forensic applications. A study of the organisms present in a decaying corpse provides information about the time elapsed since death, because decomposition is effected by a series of fungi, flies, beetles, and bacteria that appear in a known order, a 'carrion microsere' (BEGON *ET AL.*, 1990, p. 383).

A succession that begins on very dry land, such as bare sand or rock, is called a 'xerosere' (from the Greek *xeros,* meaning 'dry'). It can be seen on stabilized sand dunes or in abandoned quarries. If a succession begins in water it is known as a 'hydrosere'.

Aquatic environments sometimes border waterlogged ground with dry ground beyond and in such places it is possible to see all the seral stages in a hydrosere at the same time. Sediment on the lake bottom provides anchorage for plants such as water lilies. Close to the shore, sedges grow in partly decomposed organic matter, sedge peat, undercut by a wedge of lake water. The sedge peat adjoins a band of sphagnum peat lying above rock. Sphagnum peat develops beneath mosses of the *Sphagnum* genus, plants which can absorb and hold large amounts of water. In hollows, *Sphagnum* mosses sometimes form raised bogs supporting a variety of herbs and woody plants that rely on rain for their supply of water and mineral nutrients. Such bogs and peat, lying well above the water table and isolated from it, are known as 'ombrogenous'. Still further from the lake edge, a deep layer of woody peat supports coniferous trees. Birch trees grow on part of the woody peat that is overlain by a humus-rich soil layer. The humus also extends further from the water to where it overlies a typically dry-land soil profile supporting larger trees. This succession is illustrated in Figure 4.13.

Land clearance by humans will initiate a succession on a subsequently undisturbed site, but most successions are set in train quite naturally. During the Pleistocene, the repetition of glacial and interglacial episodes led to vegetation successions, some of which can be traced through the pollen still held in the soil. Following the most recent retreat of the ice sheets, regions that had been covered by them were recolonized by plants migrating from lower latitudes. Arctic-alpine species, such as *Dryas octopetala* (mountain avens), were early colonizers, followed by birch trees, pines and other conifers, and finally broad-leaved deciduous trees (GODWIN, 1975, pp. 451–483). Islands built from lava ejected by submarine volcanoes can appear quite suddenly, and once the surface has cooled, colonizing species start arriving and a succession commences. The island of Surtsey, to the south of Iceland, emerged in this way in 1963, and in June 1995 a tiny, 1-hectare island called Late Iki *(www.volcano.si.edu/gvp/volcano/region04/tonga/metis/var.htm)* appeared near Tonga, in the Pacific. Volcanoes on land can burn and bury vegetation. Such an event, too, is followed by a plant succession.

Seral stages appear to occur in a regular fashion and lead to a plant community, with its associated animals, that remains unchanged until some event disturbs it. This final stage is called a 'climax'. According to Frederic E.Clements, the American grassland ecologist who first proposed the concept in the early years of this century, the climax is the natural vegetation of a region, the type of vegetation that will develop if large enough areas are left free from outside interference. This being so, any vegetation type that differs from the climax must be regarded as immature. The climax, in Clements's view, acquired the status of a single, mature organism. Within it, individual plants develop according to the conditions under which they grow, a successful species being one that can adapt to a variety of different conditions by assuming different forms. This

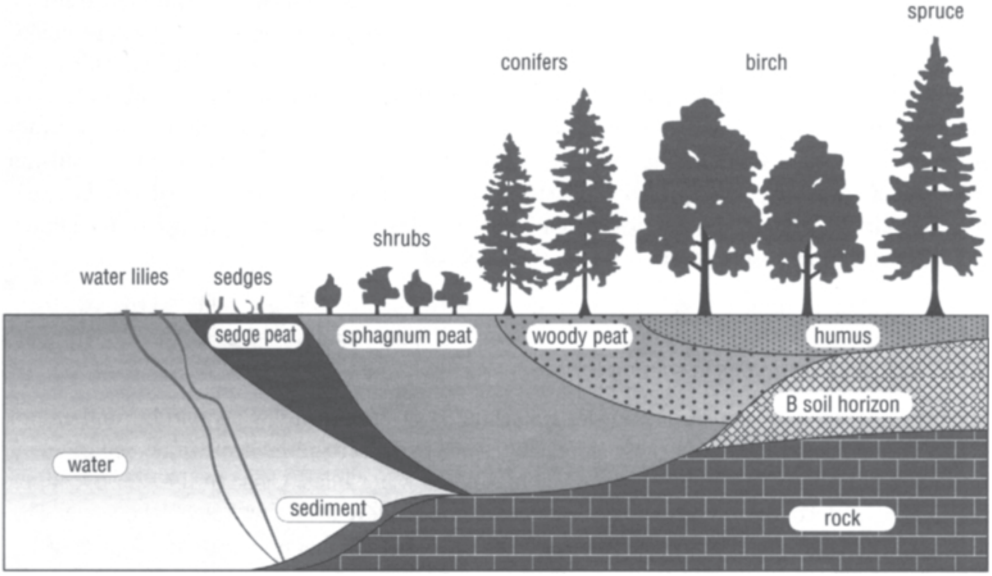

Figure 4.13 ***Succession from a lake, through bog, to forest***

holistic view contradicted the Darwinian explanation of evolution by natural selection, but it became very influential and has left an enduring popular impression of the climax as an almost mystical superorganism.

Doubts were soon cast on this interpretation, most notably by another American ecologist, Henry Allan Gleason (1882–1973). He argued that all plants grow wherever they can; if similar plant communities occur in different places it is because conditions in those places are similar (BOWLER, 1992, pp. 521–525). In 1927, Gleason wrote that detailed studies showed very complex successional relationships among plant communities within a region and he rejected entirely the idea that seral stages proceed in a systematic fashion (BREWER, 1988, p. 381).

In fact, seral stages can be explained in Darwinian terms. Species arrive haphazardly, and those tolerant of the conditions survive. In surviving, however, they may alter those conditions in ways that favour other species more strongly than themselves. This is natural selection acting on variation between and within species, and it can produce unexpected but well-documented surprises. When conifer forests are cleared, their regeneration may be delayed for a long time if alder invades, because nitrogen-fixing bacteria live in alder roots, allowing the species to thrive in nitrogen-poor soil. Other plants actively inhibit the establishment of species that would otherwise replace them in the succession (BREWER, 1988, pp. 386–387).

For all their over-simplification and mystical overtones, the concepts of succession and climax remain useful. It is true that any exposed surface will be colonized by plants and that the annual pioneers will usually be replaced by perennials, arriving later. It is also true that the ensuing succession will reach a stage that endures. It is not true, however, that the seral stages can be predicted accurately. Once a succession begins, chance plays too great a part and small variations in conditions from one part of a site to another have too large an effect for its progress to pursue a regular, repeatable course. Clear an oak woodland, for example, and it may regenerate as oak woodland, but then again it may not. What follows may be a ‘secondary succession’ (where the primary succession was the one leading to oak woodland) involving communities of different composition and leading to a quite different climax. Some ecologists call the resulting climax a ‘plagioclimax’; others restrict this term to the climax resulting from a succession interrupted by human activity and use ‘biotic climax’ for the result of a secondary succession in which humans played no part. Nor is it true that the apparently final stage, the climax, is permanent. It remains dynamic and capable of change, although its rate of change is very much slower than that observed in preceding stages.

With these qualifications, it is possible to use the concepts. When derelict land is restored, for example, the first plants to be sown are pioneers, the opportunist colonizers that can survive the initially harsh conditions. They are followed by others, and an understanding of successions and an idea of the climax most suitable to the intended use of the land provides guidance for subsequent plantings to those responsible for managing the site. Many people maintain that forests should be replanted on land from which original primary forest was cleared by farmers many centuries ago. There are plans in Britain to develop large forests in several parts of the country, mainly for amenity use. This cannot be achieved simply by planting attractive trees. The operation begins with the planting of pioneer species, short-lived but tolerant of wind and full light, that will provide shelter for the longer-lived, but more slow-growing, desired species. In other words, a succession must be initiated and supervised, albeit an abbreviated one.

‘Succession’ and ‘climax’ are concepts that should be used with care. In their simplified, popular versions they are misleading. Properly understood, however, more as metaphors than as detailed accounts of processes observable in the real world, they provide valuable guidance to those planning new uses for land and for conservationists seeking to enhance the environmental quality of degraded sites.

40 Arrested successions

If ever you are fortunate enough to visit California, you may have a chance to visit the Sierra Nevada, where you will see in its native habitat one of the most famous trees in the world. Its botanical name is *Sequoiadendron giganteum* and its common names include the Sierra Redwood, Big Tree, Giant Sequoia, Mammoth Tree, and Wellingtonia. It is famous, of course, for the superlatives that describe it, and some individual trees have been given their own names. The General Sherman Tree, for example, is said to be the most massive tree in the world, weighing about 2000 tonnes, and is believed to be more than 3000 years old. It is in the Sequoia National Park. Although S. *giganteum* is not the tallest tree species in the world, it can grow to an impressive 100 m (the tallest is another native of the Californian coastal belt, the Coast Redwood, *Sequoia sempervirens,* which can grow to 120 m).

For those of us who may never visit California, smaller specimens of *S. giganteum* are grown in many gardens and arboretums. There is a fine avenue of them at the Younger Botanic Garden, near Oban in Scotland.

Should you encounter one of these trees, examine its bark. This is so spongy you can punch it quite hard without hurting your hand. The bark protects the trunk of the tree against fire. It burns only slowly and the air entrapped in its loose fibres provides thermal insulation. Not only can the tree survive fires, the heat of a fire is needed to cause its seeds to germinate. Fire clears the ground of dry litter and smaller plants, and before these can recover, *S. giganteum* seedlings will have established themselves.

Sierra Redwoods are not the only trees to rely on fire to maintain their dominance in the plant community. Longleaf or pitch pine *(Pinus palustris)* is fully adapted to environments where fire occurs naturally every 3–10 years. At first its seedlings grow very slowly, producing a dense clump of long needles on a short stem with the growing tip of the tree hidden at their centre. The needles protect the tip against fire, and while it remains small the tree develops a large root system. Its roots established, the seedling grows rapidly and its growing tip is carried upward, beyond the reach of low-level fires. Then the tree develops a thick, fireproof bark. Its cones will not open to shed their seeds unless they are heated strongly, but once released they germinate rapidly; such cones are described as 'serotinous'. This adaptation to fire allows longleaf pines to form large stands along the coastal plain of the south-eastern United States (KENDEIGH, 1974, p. 113). Longleaf pines do not grow in splendid isolation, of course. Other plants share the habitat with them and some of these are similarly adapted to fire. Wire grass *(Aristida stricta),* in particular, flowers profusely following a fire in spring, which is when natural fires are most common, but not after winter fires, although fires at any season encourage its growth (BREWER, 1988, p. 69).

Forest fires may occur at the surface, at ground level, or among the tree crowns. Surface fires clear away accumulated litter and destroy smaller plants, but although they are hot, with temperatures reaching more than 100°C, conditions remain cool just a few centimetres below ground. Ground fires smoulder below ground, advancing very slowly, destroying roots and consuming litter, but rarely producing flames. They can cause great damage to ecosystems such as temperate heaths and even bogs, which are not adapted to them. Crown fires are commonest in pine forests, where trees retain dead needles for some time before shedding them. They can advance rapidly. Generally, trees will be killed by fire if the actively growing tissue all around the inside of the stem (the cambium) is heated to more than about 64°C. Thick or spongy bark protects the tree by insulating the cambium. Some tree species survive crown fires, which kill their tops, by sprouting new stems from the base (BREWER, 1988, pp. 66–69). Where there is a pronounced dry season, if many of the trees in a coniferous forest have multiple stems it is often an indication, of past fire (in British broad-leaved forest, multiple stems are more likely to indicate past coppicing).

Consider the effect of recurring fires on the seral stages by which plant communities approach a stable climax. As Figure 4.14 shows, the number of species increases as the community develops, but the fire repeatedly destroys this growing diversity. In effect, the fire returns the community to a much earlier seral stage, after which the succession resumes. Should the fires end or be prevented, as in the right-hand curve in the figure, the number of species continues to increase until it reaches a maximum. After that, some species are eliminated by competition, according to the competitive exclusion principle derived mathematically by A.J.Lotka and V.Volterra and first demonstrated experimentally in 1934 by the Russian biologist Georgyi Frantsevich Gause, 1910–86 (and sometimes known as Gause's principle). The principle states that two or more species requiring identical resources cannot coexist in an environment where one or more of those resources are limited, because one species will prove more successful than the others, monopolize the scarce resource (s), and its competitors will fail and disappear. Consequently, the usual pattern for diversity during seral stages shows a slight fall prior to the stable climax, as shown in the figure.

For as long as fires continue to interrupt the succession, however, the final climax cannot be attained. The succession is arrested and then repeated. Such a succession, controlled by abiotic factors, in this case fire, is known as an allogenic succession (one controlled by biological organisms, where those of one seral stage produce conditions favourable to those of the succeeding stage, is known as an autogenic succession) (BEGON *ET AL.*, 1990, pp. 630–633).

Arrested successions clearly complicate the concept of an ecological climax. F.E.Clements, who first proposed climax communities argued for what is now known as the 'monoclimax hypothesis', according to which large regions support a single type of climax community determined by climate. If the succession is repeatedly disturbed, for example by fire, he would maintain that the climax which would be attained were it not for disturbance is the true climax. Most ecologists consider this unsatisfactory, because it fails to describe the situation they observe in the field.

A possible alternative introduces the concept of the 'polyclimax', in which a region supports a number of different climaxes, each identified according to the factor controlling it, of which climate is but one. A particular soil may produce an 'edaphic' climax, for example, and repeated fire produces a fire climax (or pyroclimax).

Attempts to escape the difficulties inherent in the monoclimax hypothesis lead to further complications, not to mention a rapid proliferation of terms. Is a forest mainly composed of mature trees a climax community? It may seem so, but trees grow slowly compared to a human lifespan and within the forest some species may be increasing in number at the expense of others. Is a fire climax really a climax, or merely an arrested succession on its way to a climax it never reaches? Add to these sources of confusion the fact that few supposed climaxes remain for long in a true equilibrium and it is hardly surprising that many modern ecologists prefer to avoid using the climax concept at all (BREWER, 1988, pp. 400–401).

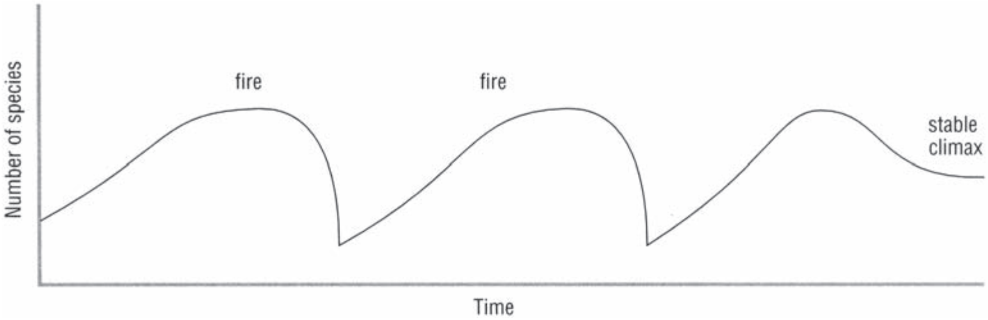

Figure 4.14 ***The effect of fire on species diversity***

Fire provides an obvious example of an abiotic factor disturbing successions, but by no means is it the only one. Very fierce sea storms, of the kind that occur only occasionally at intervals of some years, generate winds and waves that can cause similar disturbance in coastal environments. Hurricanes in tropical regions and even storm-force winds (103–120 km h^{-1}), which rarely occur inland in temperate regions, but are capable of uprooting trees when they do, will arrest a succession. Nor can climate be regarded as constant. Glacial and interglacial episodes cause profound ecological change and if the word ‘climax’ is held to imply permanence, then such major climatic changes, and some less dramatic ones, appear to qualify as disturbances.

Human activities also cause disturbance, of course, when natural vegetation is cleared and the land put to economic use. Farmers exploit the natural process by removing all plants from their fields, then introducing crop plants to take the place of the primary colonizers that would otherwise soon appear, their crops taking opportunistic advantage of the absence of competition for light, water, and nutrients to achieve rapid growth.

Fire in Yellowstone

In 1988 fire swept out of control through Yellowstone National Park in the United States. In all, some 400000 ha was burned, amounting to 45 per cent of the total park area (of 890000 ha) and about 8000 ha was said to have been virtually destroyed. Despite all efforts to extinguish them, the fires ended only with the first substantial falls of snow in the autumn.

Yellowstone is naturally prone to fire and its species are adapted to it. Fire removes surface litter and old, woody plants, leaving ash on the surface and stimulating fresh growth. Official policy over the years had aimed to curb natural fires, most of which had been extinguished successfully. The policy arose in part from public concern about the effect of fire on wildlife, which it was presumed to harm, an impression strongly conveyed by the Disney movie *Bambi*. The result of the policy was that surface litter accumulated until, when eventually it did ignite, the fire proved unquenchable. In fact, controlled burning at intervals of a few years is ecologically beneficial. By the spring of 1989 plants were recovering and a secondary succession had begun, and as the park recovered its biological diversity increased.

Since 1992 a management scheme has been adopted that divides the park into three zones. In the first, comprising about 10 large areas, fires will be suppressed. In the second, covering most of the park, fire will be allowed to burn but will be controlled. In the third, a 2.4 km strip just inside the park boundary, fires will be permitted but under even more strictly controlled conditions. Even in zone 1, fires will be started if too much dry, flammable material accumulates.

It can also happen that humans, other species, and abiotic factors combine to produce an arrested succession. Suppose, for example, that an area of temperate forest is cleared. Humans may have felled the trees or fired them. Unless the forest is fire-adapted and already at a fire climax, the removal of shade will cause grasses and herbs to germinate and flourish. Ordinarily, after a time tree seeds will start to germinate, seedlings will appear and grow and eventually the forest will return. The first two diagrams in Figure 4.15 illustrate this. It may be, however, that the humans cleared the forest precisely in order to encourage the growth of grass to feed their livestock. Grass growth is encouraged by grazing, because the blades grow from ground level and are unharmed, but as they graze the herbivores also destroy tree seedlings. This delays the regeneration of forest, but does not halt it altogether and after a few years scrub vegetation begins to shade out the grass. At this point, the humans remove their animals, wait for dry weather, and fire the pasture, destroying both grass and scrub, but encouraging the grass by once more returning the succession to an earlier stage. Repeated firings and intensive grazing gradually eliminate most of the woody plants by destroying them each time seeds lying dormant in the soil germinate and before the new plants produce seed. In this way forest can be converted into grassland, as is shown in the third illustration in the figure. In North America, prairie vegetation can be maintained only by setting fire to it every 1–3 years (BREWER, 1988, p. 75) to rid it of the shrubs and seedlings that would otherwise come to dominate it as it developed towards forest. African pastoral-ists also maintain their savannah pastures by periodic burning. It may well be that at least some of the great grassland biomes were formed by this type of human intervention, although natural fires occur readily enough in such regions and sweep rapidly across the plains.

It is attractive to think of biological communities increasing in diversity as they proceed through seral stages to a climax. Undoubtedly this does occur, but successions are often arrested

Figure 4.15 ***Effect of grazing on succession***

naturally or by human activities. Most of the landscapes we see around us, from town gardens and parks to the farmed and forested countryside, are artefacts, made by humans, and the biological communities they support are those of successions arrested at some stage short of their climax. Too great a concentration on the concept of the climax may obscure the importance and considerable biological value of such arrested successions.

41 Colonization

When buildings are demolished, exposing an area of bare ground, in most of Europe the first plant to arrive is often the rosebay willowherb *(Chamaenerion angustifolium)*. Indeed, the speed with which it appears after a major fire has earned it its other common name of 'fireweed'. It is a tall, colourful plant that quickly forms large stands and its prominence tends to hide the smaller plants growing with it. Groundsel *(Senecio vulgaris)* and coltsfoot *(Tussilago farfara),* for example, are other early arrivals. Why do these plants appear first so predictably and other common wild plants only later?

If a species is to establish itself in a new habitat, it must be able to reach the site. The first species to arrive will be those that had only a short distance to travel and no formidable barrier to cross, such as a wide expanse of sea or a mountain range. To ease its journey, a plant should produce light seeds that are distributed by the wind and, to increase their chance of finding suitable conditions in which to germinate, it should produce them in great abundance. Having reached a suitable location, they must germinate rapidly. This means that many of the seedlings and young plants will die in the overcrowded conditions that occur when so many seeds germinate, so mortality is very high.

The early colonizers have all of these characteristics. They are annuals, which appear quickly only to disappear when their season ends, although there are also perennials which produce an overabundance of seeds and tolerate high mortality. In all these species, seed production far exceeds the quantity necessary to ensure establishment on available sites, but what may appear to be over-production of seeds probably serves a useful purpose. Natural variation in the genetic composition of individuals (genotypes) means there are countless small physical differences in the plants that begin to grow (known as phenotypic variation). These differences ensure that on any vacant site a proportion of individual plants will possess the characteristics that allow them to thrive, whereas those lacking the necessary features will die, but the survivors will be sufficiently numerous to form a viable colony, passing on to their progeny characters that are appropriate to the local environmental conditions (GRIME, 1979, p. 118).

Once arrived, the would-be colonizers must be able to survive. Small, light, wind-blown seeds contain little sustenance for the young plant. Unless light, water, and nutrients are present and available from the moment the seed germinates, the plant will die. This means that initial colonization is often patchy. Within a bare-ground site, some places will be wetter than others, more or less shaded, or offer a more or less balanced suite of mineral nutrients. Figure 4.16 shows, diagrammatically, how this can produce a dense clump of a species, where mortality of potential colonizers is low, surrounded by a thinner stand where conditions are less favourable, within a larger area which the species finds inhospitable and from which it is absent.

On open ground, the most critical environmental factor is usually light intensity. Photosynthesis is the process by which green plants obtain energy and its rate is directly proportional to the intensity of light: the brighter the light, the faster plants can synthesize carbohydrate. Plants use much of their captured energy for respiration and there is a point, called the compensation point,

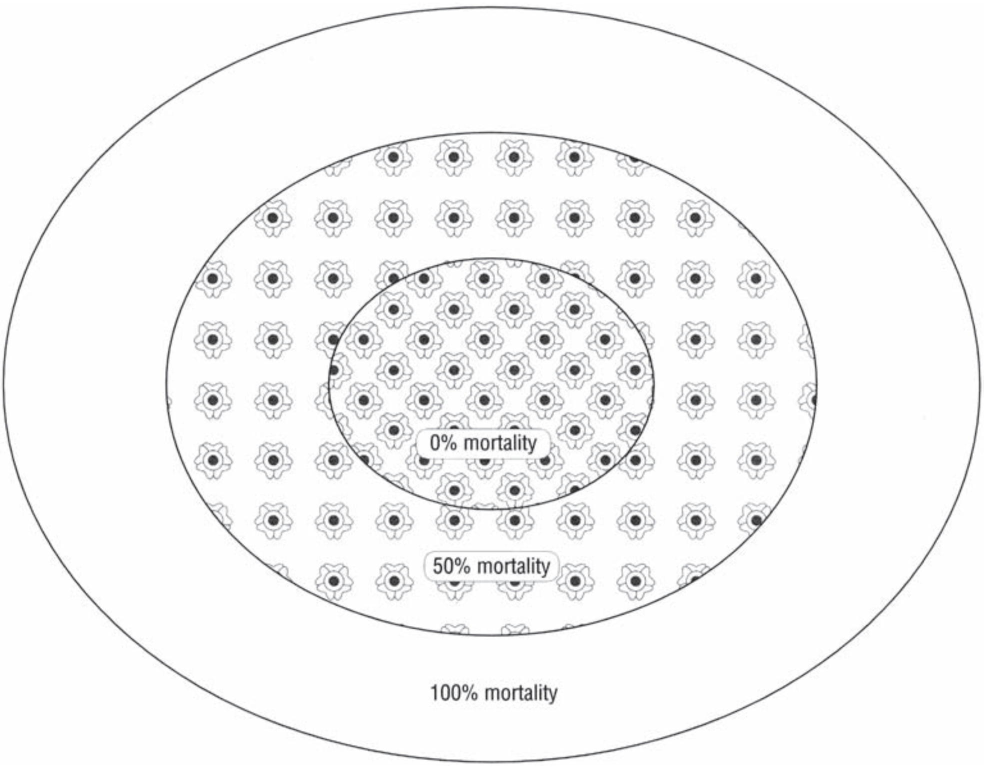

Figure 4.16 ***Establishment of colonizers In an area of habitat***

at which the amount of energy being captured (or carbon dioxide absorbed, which is the same thing) by photosynthesis is equal to the amount being used for (or carbon dioxide emitted as a by-product of) respiration. At the compensation point, a plant can survive but not grow; below the compensation point energy output exceeds input and it will fail; but above the compensation point there is a surplus of energy available for growth and reproduction.

It might seem, therefore, that most plants should prosper on open ground, where they are exposed to full sunlight, but it is not so simple. The compensation point varies widely from one species to another. Shade-loving plants can grow well under much lower light intensities than sun-loving plants, because their compensation point is lower. If the light is too intense, however, photosynthesis is inhibited by other chemical reactions in cells, which destroy chlorophyll and inactivate other substances. This adverse effect of high light intensity is called solarization, and susceptibility to it also varies according to species.

The ideal colonizer of bare ground, therefore, will be a sun-loving plant. Should seeds of a sun plant be blown on to shaded ground they may germinate, but the plants will not form a true colony. Rosebay willowherb can be found in woodland, growing in shade, but although it can grow, the dim lighting provides insufficient energy for it to flower. At the end of the growing season the plants die without having reproduced; if they reappear in the following season it is because fresh seed has entered the site from outside (DOWDESWELL, 1984, p. 7).

Ground may be bare not because of disaster or demolition, but for reasons of its chemistry: it may be poisonous to most plants. Even poisoned land may be colonized, however, because the strategy that allows colonizers to adapt rapidly to the conditions they find embraces tolerance for at least some toxic substances. This phenomenon has been most widely observed on heaps of mine waste contaminated with high levels of copper. An early colonizer is bent grass *(Agrostis tenuis)*. It is generally intolerant of copper, but among the countless seeds blown on to the heaps a few give rise to tolerant individuals and it is these that reproduce, eventually to produce a tolerant population that in time is joined by other tolerant species (BEGON *ET AL.*, 1990, pp. 74–75).

At one time, the manufacture of sodium carbonate (washing soda), a very important industrial chemical, caused severe air pollution and left behind an extremely alkaline waste, with a pH of nearly 14, which was simply dumped, especially in Lancashire, England. In some places this material covered several hectares to a depth of several metres. Amid the alkaline material were small patches of very acidic soil, where ash from boilers was dumped on top of the soda waste and the two wastes did not mix. Rain, slightly acid because of the dissolved carbon dioxide it contained, and acid air pollutants such as sulphur dioxide reduced the extreme alkalinity at the surface, although 70 years later at depths of more than 55 cm the pH was still more than 12.0. Yet the alkaline waste sites were colonized by lime-loving plants and now support a diverse community, including most notably a wide variety of orchids, and the acid sites have also been colonized, though by fewer species (MELLANBY, 1992a, pp. 64–66).

Much has been learned about colonization from studies comparing the natural populations of islands with those of the mainland from which they originated. In 1963, the ecologists Robert H.MacArthur and Edward O.Wilson proposed that the number of species present on an island is determined by a balance struck between immigration and extinction. At first, we may assume that a newly formed island is bare. Species begin to arrive, so the immigration rate is high. The extinction rate is low, because so far there are few species to become extinct. As time passes, the immigration rate will fall, because an increasing proportion of incoming individuals belong to species already present. Simultaneously, the extinction rate will increase as a result of intensifying competition for resources, predation, and parasitism (BREWER, 1988, pp. 302–306). Figure 4.17 describes the situation as a graph in which the straight-line curve for decreasing immigration intersects that for increasing extinction, the point of intersection indicating the number of species.

Islands vary, of course. Some are larger than others, some further away from the mainland, and these factors affect colonization and the eventual number of species. Immigration to a remote

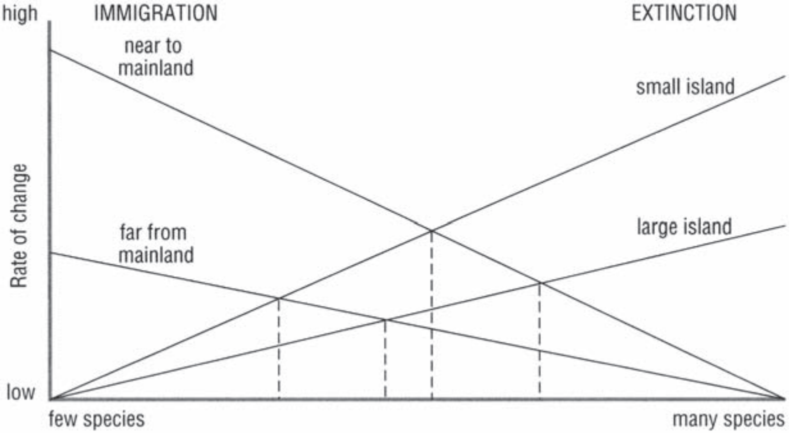

Figure 4.17 ***Island colonization as a ratio of immigration to extinction***
After Brewer, Richard. 1988. **The Science of Ecology.** ***Saunders College Publishing, Fort Worth, TX***

island will begin at a lower rate than that to a nearby island, because migrants must travel further and more will perish on the way. The rate of immigration decreases and the rate of extinction increases regardless of the starting value, and so the intersection point, or final number of species, is likely to be lower on a remote island than on one nearer the continental coast. The size of the island also affects the diversity of its established population. Size does not affect the rate of immigration, but small size does increase the rate of extinction, because a small island offers fewer resources than a large one. As common sense would suggest, a large island finally supports a more diverse population than a small one.

The composition of an island population will change constantly as immigrants continue to arrive, albeit at a reduced rate, and residents become extinct. It has been confirmed many times by observation that once equilibrium has been reached, the number of species on an island remains fairly constant regardless of when or how often it is sampled, although the species themselves change.

MacArthur and Wilson supported their theory experimentally, by counting all the arthropods on four small (about 15 m across) islands on the Florida Keys, then employing a professional exterminator to kill all of them by fumigating the islands with methyl bromide, after which they monitored their recolonization. Wilson has pointed out that an island of 1000 km^2 supports, on average, about 50 species of land birds, whereas an island of 10000 km^2 supports about 100 species (WILSON, 1992, pp. 208–214). This is known as the area effect and it is described mathematically by the species-area equation: $S=CA^z$, where S is the number of species, A the area, C a constant, and z a parameter related to the types of organisms (such as grasses, arthropods, reptiles, mammals, birds, etc.) and distance from source areas. It is only fair to mention, however, that the species-area concept has been criticized as an over-simplification, and critics have pointed out that the equation utilizes the constant C and a value, z, that are somewhat arbitrary.

Understanding how colonization proceeds is of great environmental importance, because areas of habitat isolated amid much larger areas of land managed for forestry, agriculture, industry, or urban development are ecologically somewhat similar to islands. Consider, for example, town parks surrounded on all sides by streets and houses. As we seek to restore land damaged by past human activities we need to know what kinds of species to expect the habitat to support and the approximate order in which we may anticipate their arrival. Armed with a knowledge of the processes involved we will be in a better position to predict the resources each arriving group of species will require and ensure they are available. In this way we will be more likely to redress past despoliation effectively. We may also be better placed to prevent future despoliation, because the detailed information about the species composition of different types of community at each stage in their development will make it easier to estimate the consequences of interference. Finally, we may more accurately identify areas, such as islands, that may be especially vulnerable to ecological disturbance.

42 Stability, instability, and reproductive strategies

Every so often, according to popular legend, vast armies of lemmings gather together and then stampede into the sea in a spectacular mass suicide (HUCK, 1995). Curious though it may seem, the popular legend is true. Mass migrations of Norway lemmings *(Lemmus lemmus)* occur every 3 or 4 years, although the huge mass migrations are much less common. Should the migrants meet a barrier, the migration is halted temporarily until the lemmings seem to panic, perhaps because they are so crowded, and rush the obstruction. They swim well, so rivers present no serious obstacle to them, and if they reach the coast, which sometimes they do, they simply set out to swim across the sea as though it were a river, drowning in the attempt. During their flight, the ordinarily pugnacious lemmings become even more than usually aggressive to one another, and if they cross vegetated land they will devastate it, eating everything.

Thousands of miles from Scandinavia, desert and migratory locusts (*Schistocerca gregaria* and *Locusta migratoria*) *(www.fao.org/WAICENT/FAOINFO/AGRICULT/AGP/AGPP/Locusts/index.htm)* behave in a very similar way. Flightless, immature insects, called 'hoppers', change colour, then begin to move together across the landscape. As they march they also mature and when their wings are developed they take to the air, drifting with the wind in swarms that can exceed 250 km^2 in area (BARON, 1972, pp. 1–2 and 39–52). We think of locust plagues as phenomena confined to Africa and low-latitude Asia, but in the past they have also affected southern Europe and North America; the last serious outbreak in the United States and Canada occurred in 1938 (HUTCHINS, 1966, pp. 86–89).

Norway lemmings and locusts live in environments rendered unstable by climatic extremes, differing from the other inhabitants of such regions only in the spectacular migrations that bring them to our attention. Other species increase in population size and then suffer a collapse in their numbers. When snowy owls *(Nyctea scandiaca)* are seen in Scotland, and occasionally as far south as France and central Europe, it is a sign that populations of the small rodents and hares which form their usual diet have collapsed. Such irruptions of snowy owls from the Arctic occur at intervals of 4 years or so.

Environments are unstable if the living conditions they afford vary widely and unpredictably. Conditions in many parts of the world vary according to season. Winters may be very cold, one season dry, another wet, and temperature and the availability of water will influence plant growth and therefore the amount of food for animals. Being seasonal, however, such changes are predictable, and plants and animals can and do adapt to them. Seasonal climates do not confer instability on environments. In deserts and in the Arctic, on the other hand, there are sequences of favourable and unfavourable years. Food may be abundant for a time and then disappear when temperatures remain depressed during the growing season or when no rain falls for several successive years. These environments are inherently unstable, but organisms adapt to them nevertheless. As always, their adaptations ensure the continuance of the species.

During the good times, species reproduce prolifically, taking full advantage of the abundance of resources, and mortality is relatively low. Numbers increase steadily. Individuals are consequently crowded more closely together, but this does not halt population growth. It is halted by an environmental change wholly unconnected with the reproductive behaviour of species. The usual effect of the environmental change is to reduce the food supply drastically, but it may be the water supply that fails or the temperature may exceed tolerable limits. Most individuals die, but prior to the collapse they were so numerous that natural variation makes it highly probable that just a few among them will survive the period of environmental deterioration to become the parents of the first generation to be produced when conditions improve.

Lemmings, for example, become so numerous that either they quite literally eat themselves out of house and home, or they pollute what food remains, thus rendering it unpalatable, or, more interestingly perhaps, their intensive grazing induces increased production of defensive chemicals by plants, again rendering them inedible (BREWER, 1988, p. 193). At this point the lemmings begin to die in large numbers or, in the case of the Norway lemming, commence their migration. Many lemming migrants also die, of course, but a few find new sources of food and found a new population. In Figure 4.18, the situation is described by curve 2, showing a gentle rate of increase in population, starting from an already high level, followed by a sudden rapid decrease.

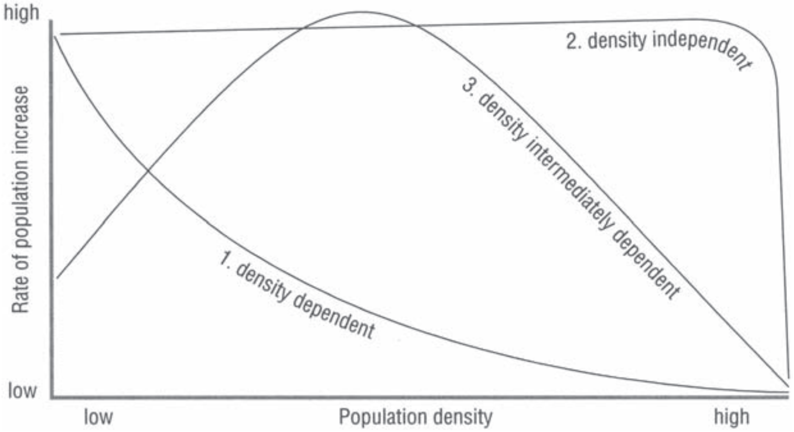

Figure 4.18 ***Population growth and density***

Population size is always regulated. Were it not, numbers could increase indefinitely, which is absurd. The question, therefore, centres on the mechanisms by which they are regulated. Lemming populations are regulated primarily by factors external to the animals themselves and independent of the density of the population. The obvious alternative to density-independent regulation is regulation by density-dependent factors, with effects illustrated by the first curve in Figure 4.18. As numbers increase, the pressure on the food supply may increase, causing an increase in mortality, especially among young animals, leading to reduced reproduction. At the same time, crowding may facilitate the transmission of disease, and large numbers of individuals within a confined area may attract more predators. Beyond a certain point, as the population density increases the rate of population growth decreases.

Density-dependent factors affect all species and are usually associated with stable environments. They may also act in conjunction with density-independent factors in unstable environments, however. At high densities lemmings may alter their behaviour in ways that make them more quarrelsome and less inclined to mate (BREWER, 1988, p. 193). Locust migrations appear to be triggered by sexually immature females under crowded conditions: when reared in isolation the insects exhibit their *solitaria* (non-migratory) markings and behaviour; when reared in large numbers they are of the *gregaria* (migratory) type (JOHNSON, 1963). Migration and reduced reproduction are most likely to occur immediately prior to the exhaustion of resources, but in an unstable environment the resources themselves are unreliable. Were they not exploited while they are abundant, leading to population densities high enough to trigger behavioural and physiological responses, they would shortly disappear anyway. The immediate responses may be density-dependent, but the underlying regulation is density-independent.

Rapid and violent fluctuations in the population of one species have consequences for other species. These are most notable among Arctic animals, such as snowy owls, lynxes, and foxes, the secondary consumers which feed on such primary consumers as lemmings, hares, and voles. Predator populations fluctuate, with a time lag, in response to changes in prey populations and also in response to changes in the populations of competing predators. In Canada, for example, populations of snowshoe hares (*Lepus americanus,* also known as the varying hare and snowshoe rabbit), lynxes, and red foxes fluctuate over a roughly 11-year cycle; that of the Arctic fox varies over 3 years, its population increasing when prey is abundant but rival predators are less numerous (DOWDESWELL, 1984, p. 31).

Curve 3 in Figure 4.18 illustrates a third way in which population size may respond to the environment. In stable environments, colonial species are stimulated to breed by the proximity of other members of their own species and do so until they are so crowded as to occupy all the available nest sites. This intermediately dependent regulation of population is most clearly seen in sea birds that nest in large colonies.

Species inhabiting unstable environments are opportunists. They must seize resources while they are there and to achieve this they must be able to reproduce rapidly. Producing large numbers of progeny, they can afford only the minimum investment in each. In plants, small seeds containing little nutrient are released in huge numbers. Among animals, large numbers of eggs are laid and abandoned to their fate or, if they are mammals, large litters are produced several times a year. Survival rates for the progeny are low, but the resource is overwhelmed and competitors excluded by sheer weight of numbers. As a reproductive strategy it is highly successful and is known as r-selection ('selection' because it results not from some deliberate scheme devised by the organisms or their ancestors, but by natural selection, which favours it). It is a typical adaptation to unstable environments, shared by primary colonizers of newly cleared sites.

In stable environments, a different reproductive strategy, called *K*-selection, is more successful. Species adopting it produce few young. Offspring develop slowly, often with considerable parental care, and many of them survive. Plants falling into this category produce few seeds, but with large nutrient stores. Animals tend their young. This strategy allows a species to maximize the efficiency with which it exploits reliable resources. Humans are a *K*-selection species. Parents produce very few young, care for them during a long period of development, and most young survive. We know from this that our species is adapted to stable environments.

These reproductive strategies produce different patterns of population growth when species first arrive in a new habitat or when additional resources become available. Opportunistic, *r*-selection species reproduce rapidly, so their numbers increase dramatically. On a graph, this results in a J-shaped curve and that is what it is called, although its resemblance to the letter J may be less than precise. Figure 4.19 shows a J-shaped growth curve and, as the figure indicates, growth is limited when the number of individuals exceeds the carrying capacity of the environment. During the growth phase the rate of increase is so rapid that the failure of resources when the carrying capacity is exceeded produces a dramatic decline in numbers: an 'overshoot-and-collapse'. *K*-selection species may also increase in number rapidly at first, and if they are judged by data for population change alone it can be difficult to distinguish them from *r*-selection species during the

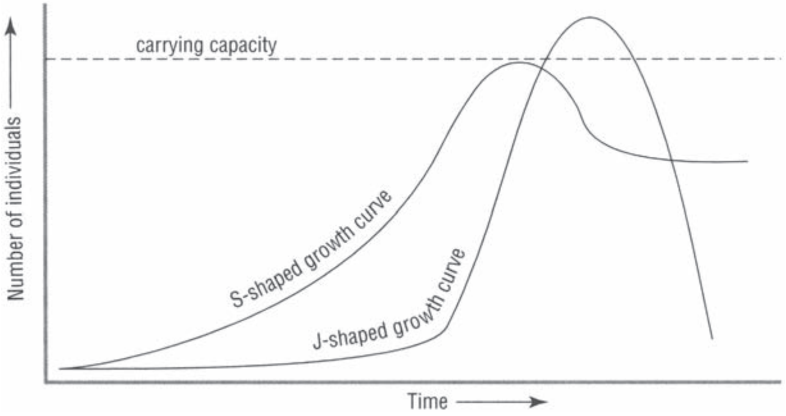

Figure 4.19 ***J- and S-shaped population growth curves***

early stage. In fact, though, their rate of increase is not so rapid as for *r*-selection species and they overshoot carrying capacity only slightly. This causes a decrease in their numbers, but only a small one followed by further even smaller increases and decreases until the population adjusts to the carrying capacity and stabilizes. This produces an S-shaped growth curve, also illustrated in Figure 4.19.

In some species the reproductive strategy changes according to circumstances. Under unstable conditions they adopt an *r*-selection strategy and under stable conditions a *K*-selection strategy, thereby optimizing their chance of survival. In these species, *r*-selection can be altered to *K*-selection by stabilizing their environment.

This is relevant to the human situation. Because we know from their reproductive strategy that humans are a *K*-selection species, we can be reasonably confident that our present population increase is located on an S-shaped growth curve, not a J-shaped one. Despite the fears of many people, it is very unlikely that human numbers will overshoot the carrying capacity of the planet by a margin large enough to generate a population collapse.

43 Simplicity and diversity

Farmers devote a great deal of time, effort, and expense to eliminating pests and weeds from their crops. Those crops comprise stands of just one plant species occupying a large area. In effect this is an ecosystem containing only one species (called a ‘monoculture’) and it appears to be unstable, because it is very vulnerable to invasion. At the other extreme, an equivalent area of tropical rain forest contains many species and it is highly resistant to invasion. With the possible exception of logging companies, it is difficult to imagine how a pest or weed species could establish itself in a tropical rain forest at the expense of the existing community: such forests are not vulnerable to pest or weed infestations.

Many people drawfrom this example the simple lesson that the more species an ecosystem supports the more stable it will be. Diversity confers stability, simplicity confers instability, and ecological successions lead to increasing diversity. It is easy to see why this should be so. An individual species can occupy only one ecological niche, defined by its physiological requirements. In a monoculture, other niches remain unoccupied and species entering the area by chance will find their needs met and will be able to establish themselves. If the ecosystem supports a wide variety of species, on the other hand, all niches will be occupied and, according to the competitive exclusion principle, two or more species with identical requirements cannot occupy the same area of habitat. Would-be invaders cannot establish themselves, therefore, and the complex system is stable because it resists invasion. A complex system is also more resistant than a simpler one to other forms of disturbance, because it is more likely to contain species, or individuals that can survive.

A problem arises immediately over the definition of ‘diversity’. It is one that returns to haunt those concerned about the maintenance of ‘biodiversity’. Counting the number of individual members of particular species is of little help, because of the huge differences in the sizes of organisms: 100 bacteria and 100 fieldmice (never mind elephants!) are not at all equal. If the diversity of plant species is being considered, not all plants are easily identified as individuals. A grove of trees may comprise plants grown from individual seeds, but it may also comprise trees growing as suckers from a single root system and, therefore, technically clones and genetically a single plant Ecologists have devised various techniques for calculating species diversity, some based on biomass rather than numbers of individuals, but the task is not simple (see box).

Measuring diversity

In 1949, E.H.Simpson devised a diversity index named after him. This is given by the formula:

$$D=1-\Sigma pi^{2}$$

where D is the diversity index, Σ means ‘the sum of’, and p_i is the proportion of individuals belonging to a particular species.

The Shannon-Wiener index of diversity (H), devised by Claude E.Shannon and Norbert Wiener, also in 1949, is given by:

$$H=-\Sigma p_i \log p_i$$

In 1980, S.F.Wratten and G.L.A.Fry devised the sequential comparison index (SCI). This is calculated as the number of runs (i.e. the number of times a sequence of individuals all of the same species occurs in a sample) divided by the total number of individuals in the sample. A run is counted by calling the first individual 1, the next individual of a different species 2, and so on. Thus, if all the individuals in the sample are of different species the SCI will be 1; if they are all of the same species the SCI will be 1 divided by the number of individuals.

‘Diversity equals stability’ seems so obvious that those who question it may be thought to fly in the face of common sense. Indeed, so many eminent ecologists once supported the idea that for many years it was the conventional view. Even then, though, ecologists recognized difficulties with the concept.

In the first place, there are examples of ecosystems that comprise relatively few species yet remain highly stable. Throughout the world, for example, salt marshes support plants belonging to a small number of cosmopolitan genera, including *Salicornia* (glassworts), *Spartina* (cord grasses), *Juncus* (rushes), *Plantago* (plantains), and *Limonium* (sea lavenders) (LONG AND MASON, 1983, p. 39). Mangrove forests often contain just one or two species of mangrove and even the most extensive contain only 5–25 species. Salt marshes and coastal mangrove forests occupy variably saline conditions few species have adapted to tolerate, so they may be thought exceptional, but there are large tropical freshwater swamp forests containing only one tree species *(Shorea alba)* and tropical montane forests with no more than five species and sometimes fewer (JANZEN, 1975, p. 45). In temperate regions, bracken covers large areas of upland, where it forms seemingly stable monocultures.

Even the vulnerability of agricultural monocultures does not necessarily establish a link between diversity and stability. When farmers plough the land they remove all vegetation, and in ecological terms the crops they plant are primary colonizers and we would expect them to be replaced by later colonizers in the ordinary course of succession. Certainly the succession will lead to greater diversity, but this does not imply that the agricultural monoculture is inherently unstable because of its simplicity.

It has also been suggested that the stability of natural communities may result partly from long periods of coevolution they, but not agricultural communities, have experienced. It is true that some, although not all, tropical rain forests are ecologically complex but, despite this, populations of insect species within them fluctuate in size just as widely as those in ecologically much simpler high-latitude forests (BEGON *ET AL.*, 1990, p. 795).

Diversity, it seems, is not related to stability in any simple way. Could it be, then, that the opposite is true and that diversity actually reduces stability? As we all know, simple devices (such as bicycles) are less likely to break down than complicated devices (such as cars).

In the early 1970s ecologists began building mathematical models of ecosystems to test the relationship between diversity and stability, and that is precisely what they discovered. The models revealed that increasing the number of species, the fraction of those species interacting with one another directly (called the 'connectance'), and the strength of those interactions made ecosystems less likely to return to equilibrium following disturbance.

It would be a mistake to substitute one sweeping assertion for another by replacing 'diversity equals stability' with 'diversity equals instability'. Different ecosystems respond to disturbance in different ways and probably no general proposition can be derived from the work that has been done so far. The truth is more likely to lie between the two extremes, and in his *Fundamentals of Ecology* (ODUM, 1984) the American ecologist E.P.Odum suggested that the confusion may be to some extent semantic. What, after all, do we mean by 'stability'?

Stability clearly concerns the response of an ecosystem to disturbance. If the system resists being disturbed its ability to preserve its essential features will be proportional to the strength of its resistance. This is one meaning of 'stability', known as 'resistance stability'. An ecosystem would exhibit high resistance stability if it offered no opportunities for invading species, tolerated parasites, and withstood prolonged periods of extreme weather with little or no change in its composition.

Other ecosystems are more easily disrupted, commonly by fire, but they recover quickly, resum-ing their former composition. This is an alternative type of stability, known as 'resilience stability', and these two stabilities may be mutually exclusive. Should an ecosystem with high resistance stability suffer serious disruption it may never recover fully, and high resilience may preclude high resistance.

Consider a ball lying on a surface. If the ball is free to roll, moving it is easy, because it offers little resistance. Glue the ball to the surface and its resistance to disturbance increases dramatically. Now consider the situation when the ball is moved. If the surface is level, the ball will move when it is pushed and remain in the position it reaches when no more energy is applied to it. It shows no sign of returning to its former position and so, if the ball represents a perturbed system, it exhibits no resilience. If the surface is curved, however, like the inside of a bowl, and the ball is pushed away from the lowest point, as soon as it is released it will roll back to its original position, showing high resilience. The situation is illustrated in the upper part of Figure 4.20, with arrows indicating the direction of movement.

Inherent stability can also be demonstrated using a ball lying on a surface, as in the lower part of Figure 4.20. In the diagram on the left, the ball is in a metastable condition. This means the system will remain stable, with the ball balanced on the small 'hill', for as long as it is not perturbed. The slightest perturbation will dislodge it, however, sending the ball to a lower and more stable position. Once in its new position it can be returned to the top of the 'hill' only by expending much more energy than was needed to dislodge it. If the ball represents an ecosystem, dislodging it from a metastable state may prove irreversible. The system to its right is extremely stable, although superficially it may appear fairly similar. Highly resilient, it will recover rapidly from disturbance. The metastable system on the left is fragile; the resilient system on the right is robust. Stability may also be described as 'local', if the system recovers from small perturbations, and 'global' if it recovers from any perturbation, no matter how severe.

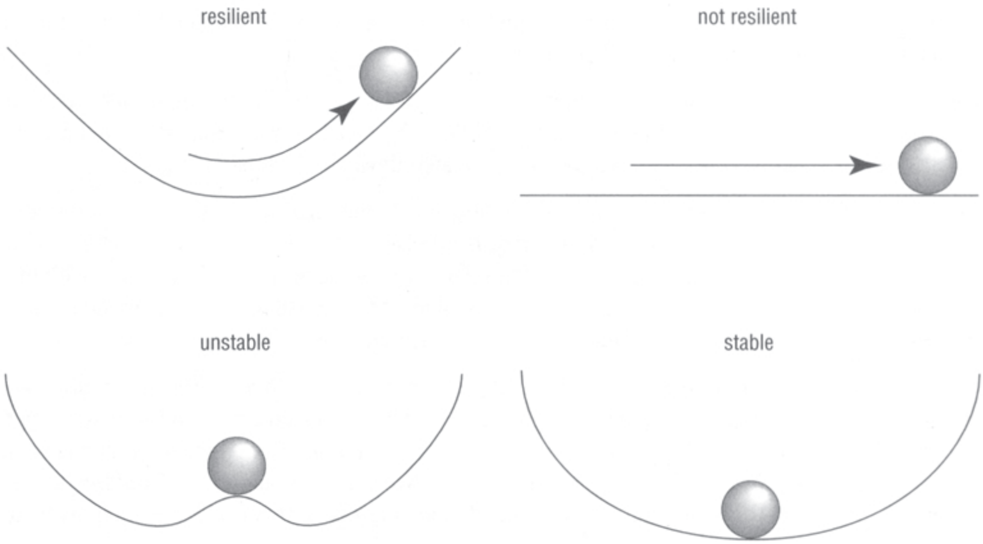

Figure 4.20 ***Resilience and stability***

With stability defined more clearly, theoretical studies and a limited number of field studies have found that adding more species generally reduces overall stability, but with some important qualifications. Increasing the number of trophic levels reduces both resistance and resilience, but increasing the interactions (connectance) among species increases them. If species are removed from a system, in most cases its stability is reduced (PIMM, 1984).

Recent research (SANKARAN AND MCNAUGHTON, 1999) in the savannah grasslands of southern India suggests that the stability of an ecosystem is more closely linked to its ecological history than to the diversity of species present in it. If the removal of species reduces the stability of an ecosystem, it does not follow that an ecosystem with little diversity is therefore inherently unstable. The species may have evolved together to withstand disturbances that occur naturally. High diversity does not necessarily imply ecological stability.

Even the concept of diversity should be treated with some caution. Ecosystems are studied as though they were discrete and isolated, but in the real world they are not. Each merges into the next and the 'edge effect' can generate an intermediate but distinct ecosystem between them. Figure 4.21 shows two ecosystems that are adjacent and overlapping. Each contains 3 species, indicated by shading, none of which is present in both systems: those in one system are indicated by circles, those in the other by squares. All 6 species occur in the intermediate zone, along with 3 more species that are confined exclusively to that zone (indicated by triangles). The intermediate zone thus contains 9 species, those to either side 3 each, yet the greater species-richness, or diversity, of the intermediate ecosystem is wholly dependent on the ecosystems bordering it. Were either of them to suffer a perturbation large enough to disrupt them, the intermediate system would necessarily be affected. In the most extreme case, the total destruction of one ecosystem would cause the intermediate system to be absorbed into the survivor and its relative diversity could not prevent its disappearance, eventually followed, of course, by the emergence of a new intermediate system as the lost system was replaced by a new community of species.

One of the few field experiments to test experimentally the relationship between ecosystem diversity and stability was conducted from 1982 to 1992. David Tilman of the University of Minnesota and John A.Downing of the Université de Montréal established 207 control and experimental

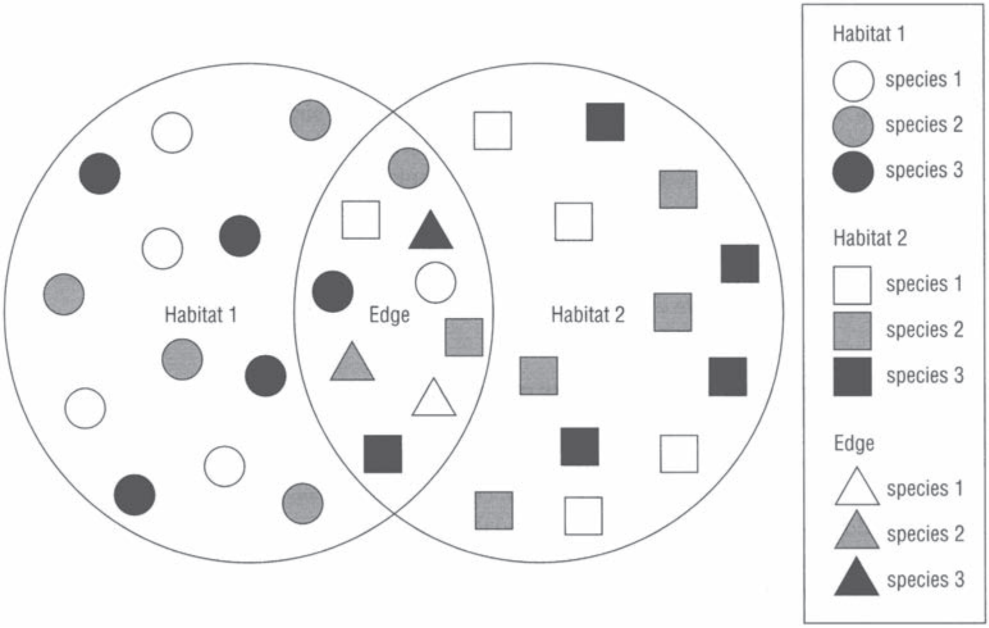

Figure 4.21 ***The edge effect***

plots in 4 fields of native grassland in Minnesota. In 1987–88, the region suffered the most severe drought for 50 years, allowing the ecologists to monitor the response of the plots to this major perturbation, which they measured as change in plant community biomass. They found that species-richness increased both drought resistance and resilience; for the 4 years following the drought, the species-poor plots remained further from their pre-drought condition than the species-rich plots (TILMAN AND DOWNING, 1994). Experiments by British scientists have reached similar conclusions using an 'Ecotron' (NAEEM *ET AL.*, 1994) (see box).

The Ectron

The Ecotron is a series of closed chambers in which environmental conditions can be closely controlled and monitored. In 1993, scientists at the NERC (Natural Environment Research Council) Centre for Population Biology, in Berkshire, England, used one containing 14 microcosms (miniature ecosystems), each 1 m^2, and varying in the number of species they contained. The experimenters found that plant productivity was higher in the more complex ecosystems, probably because the greater number of species produced a more complete canopy of leaves and so intercepted light more efficiently. Interestingly for those concerned about possible climate change, they also found the richer ecosystems absorbed more carbon dioxide for most of the time.

Theoretically, then, increasing the diversity of an ecosystem appears to reduce its stability, but the few experiments to test this suggest the opposite. They offer some support to the earlier view that diversity confers stability.

Doubtless it will be some time before the relationship between ecological diversity and stability is finally resolved, but the issue is of considerable importance and ecologists have a keen interest in the outcome. Many human activities reduce the diversity of ecosystems, by removing species from them or removing ecosystems altogether and substituting simpler ones. This is aestheti-cally displeasing: we find areas rich in species more attractive than those with few species. It would be splendid, therefore, if more tangible reasons could be found for valuing ecological diversity. There is also widespread concern over the rate at which species are being brought to extinction. Again, it would be pleasing to be able to confirm that biodiversity is of real, practical importance. We should avoid jumping to conclusions, however. Unfortunately, this is another area of environmental science in which we will have to be patient while we wait for clear answers.

44 Homoeostasis, feedback, regulation

When we are hot we sweat. Water, secreted through our skin, evaporates, obtaining the latent heat of evaporation from the skin surface and so cooling it. When we are cold, blood vessels just below the skin contract, reducing blood flow and the loss of heat through the skin; if we become still colder, we shiver, the muscular activity generating warmth. These are among the ways humans regulate body temperature. Our bodies, and those of all other organisms, also have means for regulating their internal chemistry.

The human (or non-human) body can be described as a system, an arrangement of interacting components which combine as a discrete, total entity equipped with means for regulating its own internal operating conditions. This tendency to maintain a constant state, returning to it without outside intervention in response to perturbations, is called ‘homoeostasis’. It is characteristic of individual living organisms and biological communities, but there are also many abiotic examples.

Machines are also systems. They can function efficiently only within certain tolerances and engineers have devised ways of automatically regulating their operation to prevent those tolerances being exceeded. Mechanical homoeostasis is analogous to biological homoeostasis, but much simpler, so it can provide a clear example of the way all homoeostasis works.

In the days when factory machines were all powered by a single large steam engine, it was important that the steam engine ran at constant speed. This was achieved by means of a governor, illustrated diagrammatically in Figure 4.22 and still used in all constant-speed engines, although most no longer look like the one in the diagram. Essentially, the governor comprises a set of arms (usually four, but only two are shown in the figure) weighted at the ends and pivoted. The governor spins, being driven directly by the engine. As engine speed increases, the governor spins faster and the weights are thrown outward. Because they are pivoted, as the outer, weighted ends of the arms rise, the inner ends descend, pushing down a valve that reduces engine power. If the engine slows, the opposite happens. The weights spin more slowly and fall inward, raising the inner ends of the arms and opening the valve to increase engine power. Without any attention from the human machine operator, the governor regulates the speed of the engine.

It does so by ‘negative feedback’. Feedback occurs when one component in a system alters its behaviour in response to the behaviour or condition of another component. If the effect is to counter departures from an optimal state, thus restoring equilibrium, the feedback is said to be negative, as in the case of the governor. Feedback can also be positive, acting to accelerate departure from a former state. Suppose, for example, that during an unusually cool summer some of the winter snow failed to thaw. The white snow would reflect solar radiation, preventing warming of the ground below, and the following winter would commence with the ground already cold,

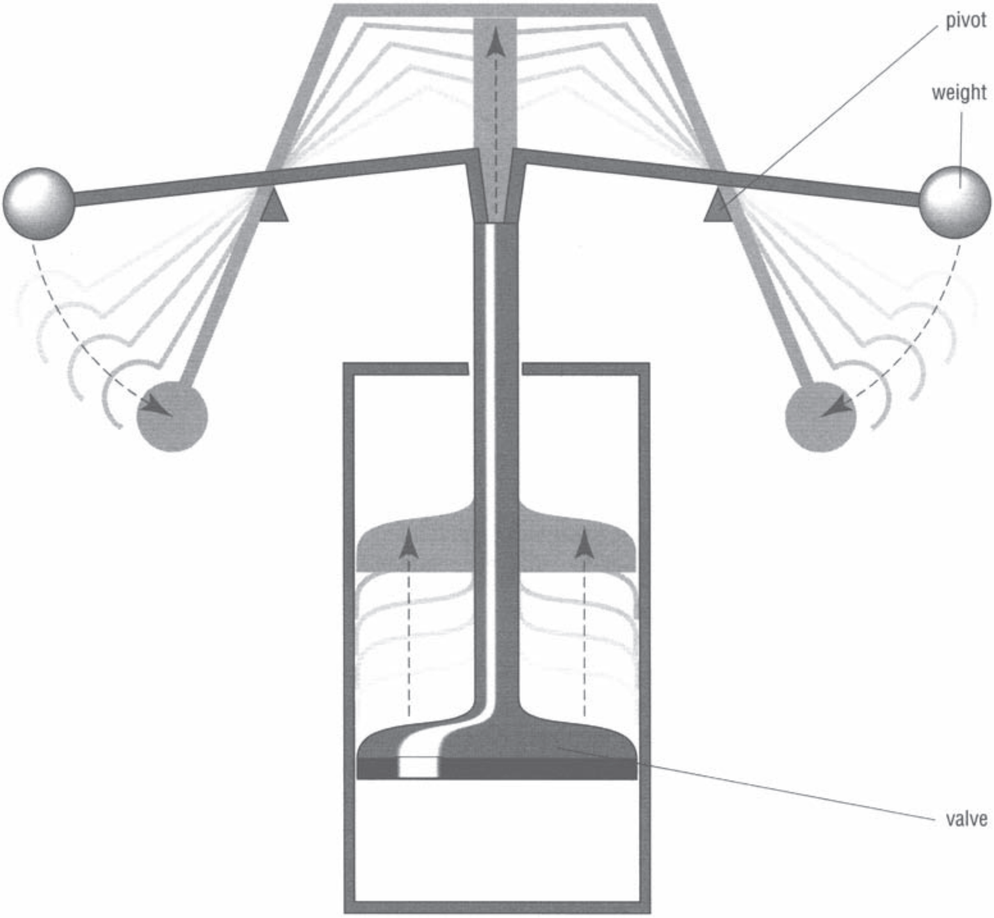

Figure 4.22 ***Speed governor of a steam engine***

so early snow would settle at once, rather than melting. This would reflect more radiation, increasing the cooling. Some climatologists believe this is how ice ages begin, in a ‘snowblitz’ during which snow accumulates rapidly, year after year, by strongly positive feedback.

Ecologists who have studied particular mature ecosystems over prolonged periods have found that the populations within them fluctuate erratically from year to year, but within quite narrow limits. Overall, the composition remains fairly constant provided the system is not severely disrupted from outside, as it might be by a major pollution incident, for example, or a disease such as myxomatosis or Dutch elm disease. This, of course, is what is meant by the stability of mature ecosystems.

Populations do not plan to control their numbers. Indeed, since natural selection favours those individuals which reproduce most successfully, homoeostasis is an entirely automatic consequence of the attempts by all organisms to maximize their reproduction. Figure 4.23 illustrates one way populations may regulate one another by feedback relationships. Allow that for some reason plant growth (primary production) increases; perhaps because of very favourable weather during the growing season. This increases the amount of food available for herbivores (primary consumers). More of their young survive and more are born, so their population increases. Since

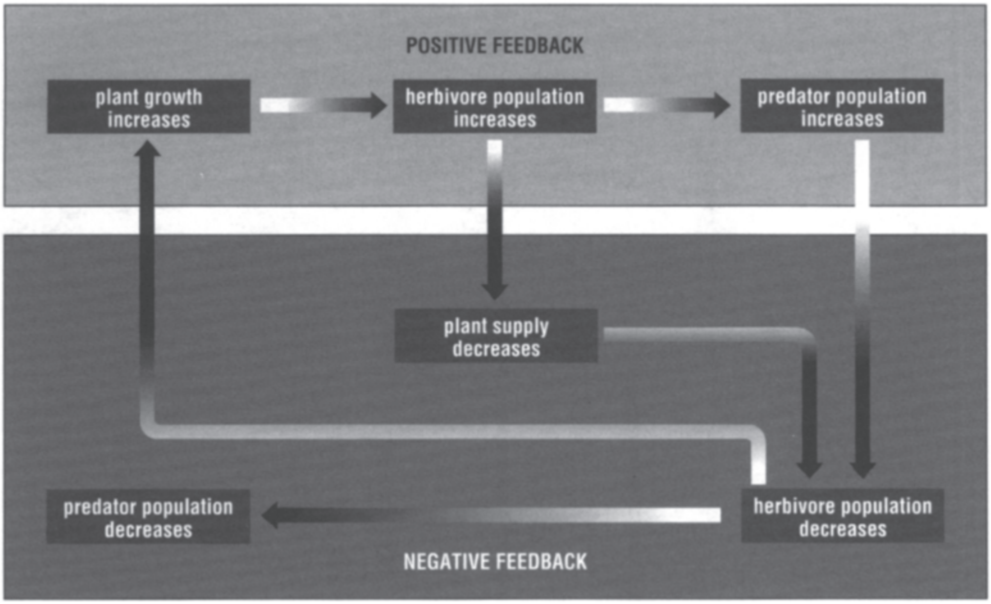

Figure 4.23 ***Feedback regulation of a population***

there are now more herbivores, more food is available for carnivores (secondary consumers) and, after a delay, their population also increases. These responses represent positive feedback: the first increase stimulates further increases. Overall, however, the system is governed by negative feedback, which soon becomes evident. Increased consumption of plants causes a decrease in the food supply to the herbivores, which are also suffering increased predation. The herbivore population decreases and, again after a delay, the carnivore population also decreases. Pressure on the plants being relieved, primary production may now start increasing again. Through cycle after cycle, populations rise a little and then fall a little, but the changes are quite minor because they are regulating one another.

The figure greatly over-simplifies the situation in a real ecosystem, of course, particularly in its omission of parasitism and the diseases associated with it, which can exert a large influence on population sizes, but it reflects the principle by which ecosystems achieve homoeostasis. It also demonstrates that herbivore numbers are controlled only partly by predation, but predator numbers are controlled to a much larger extent by herbivores. The over-simplification becomes evident when, for example, a predator species suffers from disease that reduces its population to below the level determined by the size of the herbivore population. This may encourage another predator species to enter the ecosystem and, if it can establish itself securely, to remain there after the original predators have recovered from disease and limit their population by competing successfully for a share of the food supply.

Primary production → primary consumer → secondary consumer relationships are density-dependent. That is to say, the increase in the density of population at each trophic level is what permits the proportional increase at the next higher level, and when population density at one level falls, so do those at the others.

Ecosystem homoeostasis is entirely density-dependent, but trophic relationships form only one aspect of it; it also directly affects breeding in many species. It has been observed that if the population of great tits *(Parus major)* is 1 pair per hectare, for example, the average clutch size is 14 eggs, but if there are 18 pairs of great tits per hectare, average clutch size is only 8 eggs. African

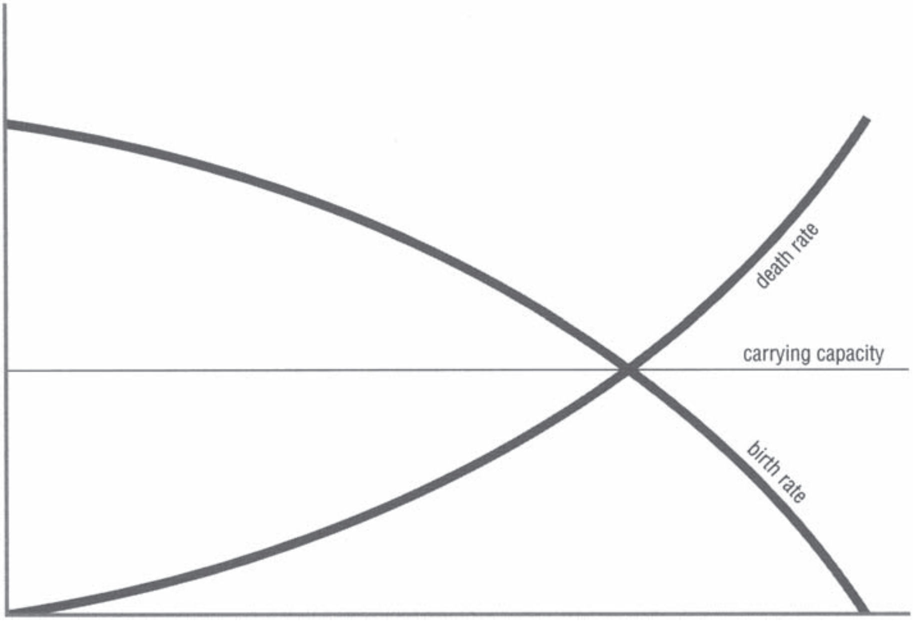

Figure 4.24 ***Density-dependent feedback regulation***

elephants reach sexual maturity at an earlier age and give birth more frequently when the population density is low than when it is high. Similar responses have been observed in many species (DAJOZ, 1975, pp. 212–213). Kept in crowded cages, mice will resorb foetuses even when the food supply is abundant.

Eventually, the usual consequence is that for each population the number born each year is approximately equal to the number dying. Birth rate and mortality strike a balance quite close to the carrying capacity of the environment for that population, as is shown in Figure 4.24. It is exceedingly difficult, and sometimes impossible, to calculate a precise value for carrying capacity and so populations are able to fluctuate somewhat in size without exceeding it or falling below it.

Density-dependent feedback maintains homoeostasis only provided it is not over-sensitive. In this respect it is a little like steering a car. When you first learn to drive there is a tendency to over-compensate when the car starts to drift across the road. Unless corrected, the result is a series of swerves from side to side that are liable to increase in magnitude. This tendency to over-compensate is even more marked among trainee pilots; because aircraft move in three dimensions and air offers much less friction than a road, over-compensation quickly sets an aeroplane bucking crazily all over the sky. Similarly in ecosystems, density-dependent over-compensation can lead to chaotic swings in numbers, producing a situation far removed from stability (BEGON *ET AL.*, 1990, pp. 222–223). Such apparently chaotic effects have been observed when systems are perturbed; although eventually they regain their stability, for a time they exhibit huge, erratic peaks and troughs (GLEICK, 1988, pp. 78–79).

Feedback mechanisms have also been proposed as the means by which living organisms regulate important aspects of their own abiotic environments, an idea that has been asserted most forcefully by James Lovelock in his Gaia hypothesis. This states that on any planet supporting life, the physical and chemical conditions necessary for life are maintained through feedback responses by the organisms themselves. If conditions begin to depart from the optimum, biological responses to those departures have the secondary effect of cancelling them and restoring equilibrium. Lovelock developed what he has called ‘Daisyworld’ computer models to demonstrate this type of homoeostatic regulation. In a world where the only living things are daisies, some white and some black, fluctuations in solar radiation favour one group or the other. When temperature rises, white daisies reflect more heat and so remain comfortably cool; when temperature falls, black daisies absorb more heat and so remain comfortably warm. With each change, the surface area covered by white or black daisies also changes as one type expands and the other contracts. This alters the planetary albedo, white daisies reflecting more radiation when radiation increases and the area they cover expands, black daisies absorbing more radiation when radiation decreases and they expand their area. These changes in albedo then raise or lower the surface temperature and hence the air temperature, so preventing the climate from becoming so warm or cool that neither type of daisy can survive (LOVELOCK, 1988, pp. 35–41).

Perhaps the highly abstract ‘Daisyworld’ story carries the efficacy of homoeostatic regulation too far. In our own, real world, however, it is a potent mechanism for maintaining ecological stability. Interference with an ecosystem will produce feedbacks. If the perturbation is small, the system will probably recover, but if it is large, the long-term consequences may be difficult and sometimes impossible to predict.

45 Limits of tolerance

Along the Pacific coast of North America, prevailing winds drive the cool California Current, flowing south with many upwellings of deep, cold water that bring nutrients close to the surface, where they feed a wide variety of marine organisms. The average temperature of the surface water, and of the breakers enjoyed by Californian surfers, used to be 13°C. Since around 1950, however, the current has warmed by 1.2–1.6°C. Too small a change to do much for the comfort of surfers, this slight warming is believed to account for an observed 80 per cent reduction in zooplankton (minute animals that drift in the surface waters) over the past forty years (HILL, 1995).

Clearly, even apparently robust ecosystems can be disrupted by quite minor changes in certain physical conditions over which they have no control. To produce such an effect, the change must affect something species need, or something that can harm them if it is present in a concentration higher than some critical value. Such a ‘something’ is known as a ‘limiting factor’.

For any limiting factor there is a minimum and a maximum value, below or above which conditions are intolerable. These boundaries are known as ‘ limits of tolerance ’. They apply directly to species and to ecosystems indirectly, through the effects on their constituent species. Somewhere between the two extremes, of ‘too little’ and ‘too much’, a limiting factor occurs at highly favourable levels. Measure the rate of growth and reproduction of a species in response to changing values of a limiting factor, and a graph displaying the resulting data will have a bell-shaped curve, as illustrated in Figure 4.25. Boundaries of the highly favourable level, where growth and reproduction reach a maximum, mark the optimum range for that limiting factor for that species.

The concept of limits of tolerance was first proposed in 1911 by the American ecologist Victor Ernest Shelford (1877–1968). In what is now known as Shelford’s law of tolerance he said that the presence and success of any organism depend on the degree to which a complete set of conditions are satisfied and that, once each of these conditions has been identified, particular organisms can be encouraged by altering those conditions which approach the limits of tolerance for those organisms. Shelford found, for example, that tiger beetles cannot reproduce unless they find suitable sites to lay their eggs, and their requirements for egg-laying and the survival of larvae are

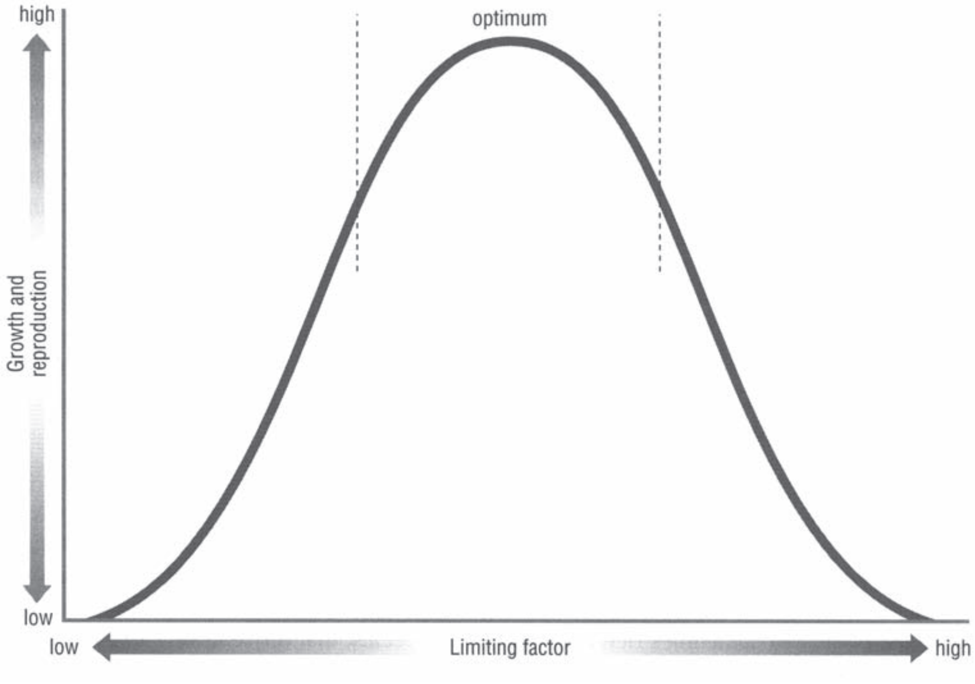

Figure 4.25 ***Limits of tolerance and optimum conditions***

quite precise. They must find sandy soil with little humus and just the right temperature and moisture, and stones to provide shade from the light. If these conditions are not present, either the females will not lay eggs or, if they do, the larvae will die (DAJOZ, 1975, p. 9).

Nutrients, of course, are the most obvious of all limiting factors, and it was from the realization of this fact, and the 'law of the minimum', that Shelford's law of tolerance was developed.

In 1840, the eminent German chemist Baron Justus von Liebig (1803–73), also perhaps the best teacher of chemistry of his day, published *Die organische Chemie in ihrer Anwendung auf Agrikulturchemie und Physiologie* ('Organic chemistry in its application to agricultural chemistry and physiology'), in which he argued that plants do not feed directly on humus, as was then generally believed, but subsisted on simple, inorganic chemicals taken directly from the air and soil. By analyzing the chemical composition of plants he was able to make a list of these substances, and he showed that plant growth ceases if the availability of just one essential nutrient falls below a certain minimum, regardless of the abundance of all other nutrients. In other words, it is the availability of the scarcest nutrient, not the most abundant, that determines success or failure for plants: if the soil is deficient, say in boron, no amount of phosphorus will remedy the lack and stimulate vigorous plant growth. This is Liebig's law of the minimum. Its acceptance by agricultural scientists led to the development of the fertilizer industry but, more generally, Liebig had identified the first limiting factor and consequently his work was of relevance to ecologists as well as agriculturists.

Plants take up soil nutrients in aqueous solution and also need water to provide their tissues with rigidity (or turgor). Water, therefore, is also a limiting factor in arid and semi-arid climates and during periods of drought in temperate climates. Deserts support sparse vegetation because for most of the time the availability of water falls below the limit of tolerance for plants not adapted to survive in arid conditions.

Some plants (called ‘xerophytes’) and animals do inhabit deserts, of course. Others thrive in habitats too saline for most and still others tolerate levels of copper that would prove lethal were it not for their adaptation to them. Copper is an essential trace nutrient, however, and in North Ronaldsay, the northernmost island of the Orkneys, off the north coast of Scotland, there is a breed of sheep that has adapted to extremely low levels of it. The sheep are confined to the foreshore by a wall surrounding the arable fields in the interior of the island, built to protect the crops from grazing. Having no choice, they feed mainly on seaweed, a diet rich in copper but also containing a substance that inhibits its uptake, so animals eating too much seaweed are prone to copper deficiency. Over the generations, North Ronaldsay sheep have evolved the ability to metabolize copper four times more efficiently than other sheep, allowing them to obtain the amount they need from an apparently deficient diet, but also exposing them to the risk of copper poisoning if they are moved on to grass. Their seaweed diet also supplies the sheep with huge amounts of iodine, their milk having been found to contain 550 times more iodine than is normal for other sheep, apparently causing them no inconvenience (ALDERSON, 1978, pp. 76–79).

The ability of certain species, or varieties within species, to thrive in circumstances beyond the limits of tolerance for most demonstrates an important evolutionary and ecological principle. If resources are present but in some respect deficient or excessive, natural selection will strongly favour those individual organisms that are tolerant of the imbalance, because their tolerance will allow them unrestricted access to the remaining resources. We should not be too surprised to learn of species, and sometimes rich communities of species, that thrive in very extreme environmental conditions. Saline lakes, which lack any outflowing river and so lose water only by evaporation, are as common in the world as a whole as freshwater lakes, and they are usually very fertile. Deep-sea hydrothermal vents support complex ecosystems thriving at temperatures of up to 40°C or even higher on a diet of sulphides and heavy metals. The topmost metre of sediment in an area of the North Pacific sea bed, 600 m×1200 m, has been found to contain 1–1.5 tonnes of uranium, 4000 tonnes of magnesium, and high concentrations of 13 other metals. Cadmium commonly occurs around vents, and some sediments are rich in hydrocarbons. Despite this, or perhaps because of it, ecosystems flourish that comprise organisms adapted to these conditions. In 1995, Greenpeace prevented the oil storage platform *Brent Spar* from being sunk to the sea bed in the deep Atlantic. Had they failed, the platform and its contents might well have nourished the ecosystem receiving it and in the opinion of many marine biologists could have caused little, if any, harm (NISBET AND FOWLER, 1995).

Temperature is an important limiting factor. Food for animals is scarce in cold weather, because at temperatures close to freezing biochemical reactions proceed so slowly that there is little or no plant growth. As Figure 4.26 shows, growth increases rapidly as the temperature rises, peaking at around 25°C and then falling rapidly. At temperatures approaching 40°C the rate of respiration exceeds that of photosynthesis and at above about 45°C many plants die.

Despite the apparently absolute chemical limitation imposed by low temperature, there are algae of the genus *Chlamydomonas* that grow on the surface of snow and die if the temperature rises above +4°C (DAJOZ, 1975, p. 69), and polar waters support diverse populations of animals. On the islands in the Arctic basin, known as the High Arctic, there are flowering plants that thrive in a climate where the soil thaws for no more than three or four weeks each year and the summer temperature seldom exceeds 4°C. Many of the plants are brown, their dark colour absorbing heat, and females of the arctic willow *(Salix arctica)* are covered in down that traps warmth and can raise their leaf temperatures to 11°C higher than the surrounding air temperature. The plants are helped by the 24 hours of summer daylight that is available to them for photosynthesis. The High Arctic ecosystem is well adapted to a cold climate, but how might it fare if the climate should become warmer? Studies have shown that the climate is already warmer than it used to be in high

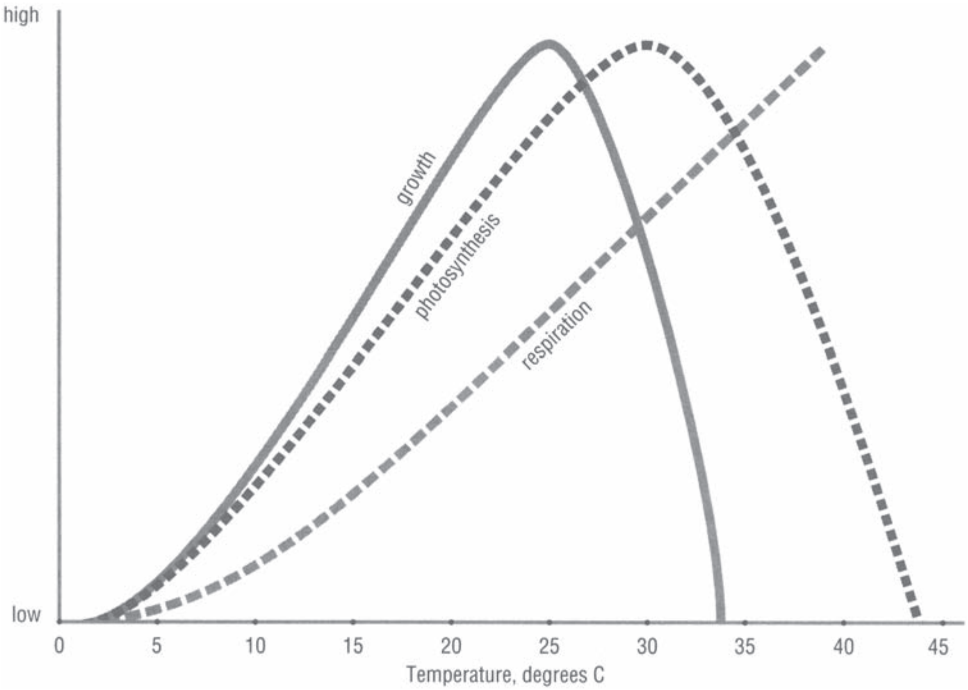

Figure 4.26 ***Plant response to temperature***

latitudes and seedlings are appearing in areas for the first time free from permanent snow and ice. At the same time, species have adapted to quite wide variation in types of habitat and seem well equipped to flourish under warmer conditions (CRAWFORD, 1995).

Brent Spar

In the spring of 1995, Shell began to tow the *Brent Spar* oil-storage platform from the North Sea to the Atlantic. There it was to be sunk in water 2000 m deep in the North Feni Ridge, which is part of the Rockall Trough, well beyond the edge of the continental shelf. This was thought to be the most environmentally satisfactory method for disposing of this particular installation, which had reached the end of its useful life.

The Greenpeace vessel *Adair* shadowed the platform as it moved north of the Shetland Islands, and on June 16 two activists boarded it by helicopter. *Solo,* a large Greenpeace tug with a helicopter landing pad, also entered the area. Greenpeace occupied the platform for 23 days, orchestrating world-wide media coverage of their protest against deep-sea disposal. Environmentalists picketed Shell petrol stations in several countries. Shots were fired at a station outside Frankfurt and a Hamburg station was firebombed. Shell backed down and the platform was towed to Erfjord, a deep inlet on the Norwegian coast while an alternative method of disposal was devised.

Greenpeace maintained that the platform contained about 5000 tons of crude oil mixed with radioactive waste and other pollutants. In fact it contained about 150 tons of oil. In September, Greenpeace admitted its mistake and apologized to Shell.

It was decided to dismantle the platform on land and to use the materials to construct a quay near Stavanger. Work began in November 1998 and was completed by September 1999.

The conversion had cost £41m (?62.2m) compared with the original estimate of £21.5m (?32.25m) and an estimated £26.25m (?39.4m) for disposal at sea. Instead of yielding a net energy gain of 48000 gigajoules it led to a net energy loss of 115000 gigajoules. This was approximately double the energy cost of disposal at sea. Most scientists agreed that deep-sea disposal of the platform would have caused no harm.

Our planet provides few habitats to which at least a few, and often many, species have not been able to adapt by expanding their limits of tolerance. These are natural habitats, however, in which natural selection has had ample time to operate. Environmental pollution presents a different situation, not because species are inherently incapable of adapting to the pollutants challenging them, but because of the rapidity with which they are exposed to them. This may disrupt established ecosystems leaving areas severely impoverished. Eventually, it is reasonable to suppose they will be recolonized, for they are seldom more inhospitable than some habitats that support rich communities, but it will take time, and this is a valid reason for minimizing the disruption we are prepared to permit. That said, most ecological effects of pollution are greatly exaggerated. While we should certainly take care to prevent avoidable pollution incidents, we should not frighten ourselves into supposing industrial or other pollution could bring life on Earth to an end. Organisms are more robust than some people believe and better able to stretch their limits of tolerance.

End of chapter summary

Physical and chemical resources are used by plants and animals, including ourselves, and any adverse effect that arises from their exploitation and use is felt by living organisms. Indeed, it is difficult to imagine what ‘environmental harm’ might mean if it does not mean harm to living organisms.

Before we can measure, monitor, and predict the environmental consequences of events we need to understand how living organisms function and how they relate to each other and to their abiotic surroundings. This involves acquiring a grasp of the way nutrients move through cycles and how the basic processes of respiration and photosynthesis work.

Relationships among populations provide the subject matter of ecology. Those relationships are based on the transfer of nutrients or energy from group to group. In this context the concepts of nutrients and energy may be considered interchangeable. Ecological systems are complex, but research has revealed a limited number of processes that underlie them. From an environmental point of view, possibly the most important ecological discovery is that there are definable limits to the conditions each species can tolerate.

End of chapter points for discussion

What is the relationship between photosynthesis and respiration?
What are the advantages and disadvantages of ecological pyramids?
Does greater species diversity imply greater ecological stability?
Is the climax concept always valid?

See also

Greenhouse effect (section 13)
Climatic regions and floristic regions (section 21)
Eutrophication (section 23)
Nutrient cycles (section 33)
Respiration and photosynthesis (section 34)
Trophic relationships (section 35)
Energy, numbers, biomass (section 36)
Ecosystems (section 37)
Succession and climax (section 38)
Biodiversity (section 50)
Human populations and demographic change (section 54)

Further reading

The Ages of Gain. James Lovelock. 1988. Oxford University Press, Oxford. A description of the Gaian hypothesis by its originator.

Biogeography: A Study of Plants in the Ecosphere, 3rd edn. Joy Tivy. 1993. Longman Scientific & Technical, Harlow, Essex. An excellent introduction to biogeography and the subjects related to it.

Ecology: Individuals, Populations and Communities, 2nd edn. Michael Begon, John L.Harper, and Colin R. Townsend. 1990. Blackwell Science, Oxford. A standard textbook on its subject, and an excellent one.

Gaia: The Growth of an Idea. Lawrence E.Joseph. 1990. Arkana, London. Explains the Gaian hypothesis clearly and also the criticisms it has encountered.

Methods of Study in Quantitative Soil Ecology: Population, Production and Energy Flow. J.Phillipson. 1971. International Biological Programme, London, and Blackwell Scientific Publications, Oxford. Provides detailed information on sampling soil organisms.

Waste and Pollution: The Problem for Britain. Kenneth Mellanby. 1992. HarperCollins, London. Describes simply the character and effects of waste. The late Professor Mellanby was one of the foremost authorities on environmental pollution.

References

Alderson, Lawrence. 1978. *The Chance to Survive.* Cameron and Tayleur in association with David and Charles, Newton Abbot.

Allaby, Michael. 1981. *A Year in the Life of a Field.* David and Charles, Newton Abbot.

Baron, Stanley. 1972. *The Desert Locust.* Eyre Methuen, London.

Begon, Michael, Harper, John L., and Townsend, Colin R. 1990. *Ecology: Individuals, populations and communities,* 2nd edn. Blackwell Science, Oxford.

Bowler, Peter J. 1992. *The Fontana History of the Environmental Sciences.* Fontana Press, London.

Brewer, Richard. 1988. *The Science of Ecology,* 2nd edn. Saunders College Publishing, Fort Worth, Texas.

Carson, Rachel. 1962. *Silent Spring.* Penguin Books, Harmondsworth.

Cooke, G.W. 1972. *Fertilizing for Maximum Yield.* Crosby Lockwood, London.

Copley, Jon. 1999. 'Indestructible', in *New Scientist,* 23 Oct., pp. 45–46.

Corbet, G.B. and Southern, H.N. 1977. *The Handbook of British Mammals,* 2nd edn. Blackwell Scientific Publications, Oxford.

Crawford, R.M.M. 1995. 'Plant survival in the High Arctic', *Biologist,* 42, 3, 101–105. Institute of Biology, London.

Dajoz, R. 1975. *Introduction to Ecology,* 3rd edn. Hodder and Stoughton, London.

Dowdeswell, W.H. 1984. *Ecology: Principles and practice.* Heinemann Educational Books, Oxford.

Gimingham, C.H. 1975. *An Introduction to Heathland Ecology.* Oliver and Boyd, Edinburgh.

Gleick, James. 1988. *Chaos: Making a new science.* Heinemann, London.

Godwin, Sir Harry. 1975. *History of the British Flora: A factual basis for phytogeography.* 2nd edn. Cambridge University Press, Cambridge.

Graham, Jeffrey B., Dudley, Robert, Agullar, Nancy M., and Gans, Carl. 1995. 'Implications of the late Palaeozoic oxygen pulse for physiology and evolution'. *Nature,* 375, 117–120.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.* John Wiley and Sons, Chichester.

Harman, Denham, 1992. 'Role of free radicals in aging and disease', in Fabris, Nicola, Harman, Denham, Knook, Dick L., Steinhagen-Thiessen, Elizabeth, and Zs.-Nagy, Imre, eds. *Physiopathological Processes of Aging,* Annals of the NY Acad. of Sciences, Vol. 673. NY Adac. of Sciences, New York. pp. 126–141.

Hill, David K. 1995. 'Pacific warming unsettles ecosystems', *Science,* 267, 1911–1912.

Hillstead, A.F.C. 1945. *The Blackbird.* Faber and Faber, London.

Huck, U.William. 1995. 'Lemming migrations', in Macdonald, David (ed.) *The Encyclopedia of Mammals,* Andromeda Oxford, Abingdon, Oxon., pp. 656–657.

Hutchins, Ross E. 1966. *Insects.* Prentice-Hall, Englewood Cliffs, New Jersey.

Janzen, Daniel H. 1975. *Ecology of Plants in the Tropics.* Studies in Biology No. 58 (Institute of Biology). Edward Arnold, London.

Johnson, C.G. 1963. 'The aerial migration of insects', in Eisner, Thomas and Wilson, Edward O. (eds) *The Insects.* W.H.Freeman & Co., San Francisco.

Joseph, Lawrence E. 1990. *Gaia: The Growth of an Idea.* Arkana, London.

Kendeigh, S.Charles, 1974. *Ecology with Special Reference to Animals and Man.* Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Kupchella, Charles E. and Hyland, Margaret C. 1986. *Environmental Science,* 2nd edn. Allyn and Bacon, Needham Heights, Mass.

Long, Steven P. and Mason, Christopher F. 1983. *Saltmarsh Ecology.* Blackie, Glasgow and London.

Lovelock, James. 1988. *The Ages of Gaia.* Oxford University Press, Oxford.

Marshall, N.B. 1979. *Developments of Deep-Sea Biology.* Blandford Press, Poole, Dorset.

Mellanby, Kenneth, 1992. *The DDT Story.* British Crop Protection Council, Farnham.

——. 1992a. *Waste and Pollution: The problem for Britain.* HarperCollins, London.

Moore, David M. 1982. *Green Planet.* Cambridge University Press, Cambridge.

Naeem, Shahid, Thompson, Lindsey J., Lawler, Sharon P., Lawton, John H., and Woodfin, Richard M. 1994. 'Declining biodiversity can alter the performance of ecosystems', *Nature,* 368, 734–737.

Nisbet, E.G. and Fowler, C.M.R. 1995. 'Is metal disposal toxic to deep oceans?', *Nature,* 375, 715.

Odum, E.P. 1984. *Fundamentals of Ecology.* W.B.Saunders, Philadelphia.

Parkes, R.John. 1999. 'Oiling the wheels of controversy', book review in *Nature,* 401, 644.

Phillipson, J. 1971. *Methods of Study in Quantitative Soil Ecology: Population, production and energy flow.* International Biological Programme, London, and Blackwell Scientific Publications, Oxford, p. 89

Pimm, Stuart L. 1984. 'The complexity and stability of ecosystems', *Nature,* 307, 321–326.

Pollard, E., Hooper, M.D., and Moore, N.W. 1974. *Hedges.* Collins New Naturalist, London.

Post, Eric, Peterson, Rolf O., Stenseth, Nils Chr., and McLaren, Brian. 1999. ‘Ecosystem consequences of wolf behavioural response to climate’, *Nature,* 401, 905–907.

Sankaran, Mahesh and McNaughton, S.J. 1999. ‘Determinants of biodiversity regulate compositional stability of communities’, *Nature,* 401, 691–693.

Tansley, A.G. 1946. *Introduction to Plant Ecology.* George Allen and Unwin, London.

Thompson, H.V. and Worden, A.N. 1956. *The Rabbit.* Collins New Naturalist, London.

Tilman, David and Downing, John A. 1994. ‘Biodiversity and stability in grasslands’, *Nature,* 367, 363–365.

Tivy, Joy. 1993. *Biogeography: A study of plants in the ecosphere,* 3rd edn. Longman Scientific and Technical, Harlow, Essex.

Wilson, Edward O. 1992. *The Diversity of Life.* Penguin Books, London.

Young, J.Z. 1981. *The Life of Vertebrates,* 3rd edn. Clarendon Press, Oxford.