a high efficiency (Figure 11.8a). In contrast, the decomposer system plays its greatest role where vegetation is woody – forests, shrublands and mangroves (Figure 11.8b). Grasslands and aquatic systems based on large plants [seagrasses, freshwater weeds and macroalgae (seaweeds)] occupy intermediate positions.

The live consumer system holds little sway in terrestrial communities because of low herbivore consumption efficiencies and assimilation efficiencies, and it is almost non-existent in many small streams and ponds simply because primary productivity is so low (Figure 11.7d). The latter often depend for their energy base on dead organic matter that falls or is washed or blown into the water from the surrounding terrestrial environment. The deep-ocean benthic community has a trophic structure very similar to that of streams and ponds. In this case, the community lives in water too deep for photosynthesis and energy is derived from dead phytoplankton, bacteria, animals and feces that sink from the autotrophic community in the euphotic zone above. From a different perspective, the ocean bed is equivalent to a forest floor beneath an impenetrable forest canopy.

11.4 The process of decomposition

Given the profound importance of the decomposer system, and thus of decomposers (bacteria and fungi) and detritivores, it is important to appreciate the range of organisms and processes involved in decomposition.

Immobilization is what occurs when an inorganic nutrient element is incorporated into organic form, primarily during the growth of green plants: for example, when carbon dioxide becomes incorporated into a plant's carbohydrates. Energy (coming, in the case of plants, from the sun) is required for this. Conversely, decomposition involves the release of energy and the *mineralization* of chemical nutrients – the conversion of elements from organic back to an inorganic form. Decomposition is defined as the gradual disintegration of dead organic matter (i.e. dead bodies, shed parts of bodies, feces) and is brought about by both physical and biological agencies. It culminates with complex, energy-rich molecules being broken down by their consumers (decomposers and detritivores) into carbon dioxide, water and inorganic nutrients. Ultimately, the incorporation of solar energy in photosynthesis, and the immobilization of inorganic nutrients into biomass, is balanced by the loss of heat energy and organic nutrients when the organic matter is mineralized.

> decomposition defined

11.4.1 Decomposers: bacteria and fungi

If a scavenging animal, a vulture or a burying beetle perhaps, does not take a dead resource immediately, the process of decomposition usually starts with colonization by bacteria and fungi. Bacteria and fungal spores are always present in the air and the water, and are usually present on (and often in) dead material before it is dead. The early colonists tend to use soluble materials, mainly amino acids and sugars that are freely diffusible. The residual resources, though, are not diffusible and are more resistant to attack. Subsequent decomposition therefore proceeds more slowly, and involves microbial specialists that can break down structural carbohydrates (e.g. celluloses, lignins) and complex proteins such as suberin (cork) and insect cuticle.

> bacteria and fungi are early colonists of newly dead material

11.4.2 Detritivores and specialist microbivores

specialist microbivores feed on bacteria and fungi, but most detritivores consume detritus too

The *microbivores* are a group of animals that operate alongside the detritivores, and which can be difficult to distinguish from them. The name microbivore is reserved for the minute animals that specialize at feeding on bacteria or fungi but are able to exclude detritus from their guts. In fact, though, the majority of detritivorous animals are generalist consumers, of both the detritus itself and the associated bacterial and fungal populations. The invertebrates that take part in the decomposition of dead plant and animal materials are a taxonomically diverse group. In terrestrial environments they are usually classified according to their size (Figure 11.9). This is not an arbitrary basis for classification, because size is

Figure 11.9

Size classification by body width of organisms in terrestrial decomposer food webs. Bacteria and fungi are decomposers. Animals that feed on dead organic matter (plus any associated bacteria and fungi) are detritivores. Carnivores that feed on detritivores include Opiliones (harvest spiders), Chilopoda (centipedes) and Araneida (spiders).

AFTER SWIFT ET AL., 1979
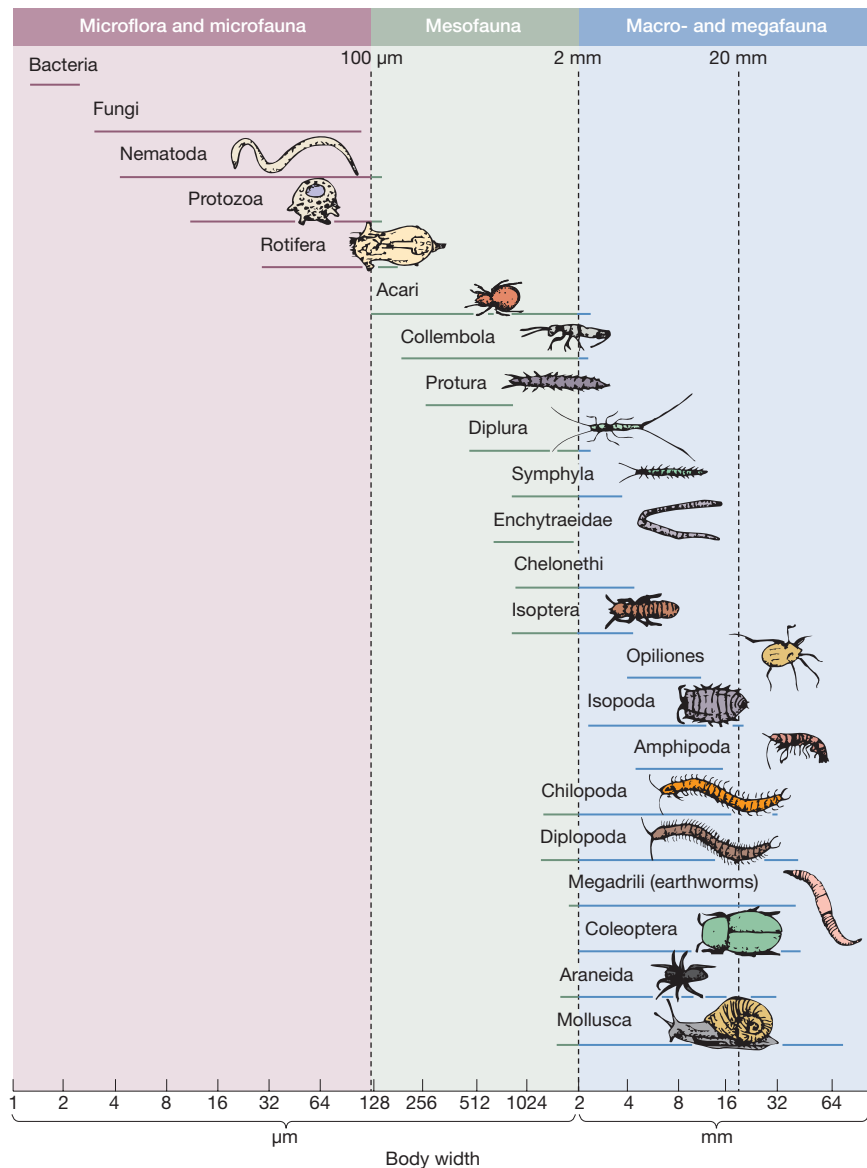
an important feature for organisms that reach their resources by burrowing or crawling among cracks and crevices of litter or soil.

In freshwater ecology, on the other hand, the study of detritivores has been concerned less with the size of the organisms than with the ways in which they obtain their food (refer back to Figure 4.16). For example, *shredders* are detritivores that feed on coarse particulate organic matter, such as tree leaves fallen into a river – these animals fragment the material into finer particles. On the other hand, *collector–filterers*, such as larvae of blackflies in rivers, consume the fine particulate organic matter that otherwise would be carried downstream. Because of very high densities (sometimes as many as 600,000 blackfly larvae per square meter of riverbed) a very large quantity of fine particulate matter is converted by the larvae into fecal pellets that settle on the bed and provide food for other detritivores (estimated at an amazing 429 tonnes dry mass of fecal pellets per day in a Swedish river; Malmqvist et al., 2001).

> aquatic detritivores are usually classified according to their feeding mode

11.4.3 Consumption of plant detritus

Two of the major organic components of dead leaves and wood are cellulose and lignin. These pose considerable digestive problems for animal consumers. Digesting cellulose requires *cellulase* enzymes but, surprisingly, cellulases of animal origin have been definitely identified in only one or two species. The majority of detritivores, lacking their own cellulases, rely on the production of cellulases by associated bacteria or fungi or, in some cases, protozoa. The interactions are of a range of types: (i) *obligate mutualisms* between a detritivore and a specific and permanent gut microflora (e.g. bacteria) or microfauna (e.g. termites); (ii) *facultative mutualisms*, where the animals make use of cellulases produced by a microflora that is ingested with detritus as it passes through an unspecialized gut (e.g. woodlice); or (iii) 'external rumens', where animals simply assimilate the products of the cellulase-producing microflora associated with decomposing plant remains or feces [e.g. springtails (Collembola)].

A variety of detritivores may be involved in fragmenting a single leaf. In experiments involving larvae of shredding stoneflies in streams, three different species were very similar in the efficiency with which they decomposed leaves of the alder tree, *Alnus incana*. However, average leaf loss was significantly greater when pairs of species were involved and was faster still when all three species were feeding on the leaf (Figure 11.10). The same number of stonefly larvae were

> the presence of more species of detritivore increases decomposition rate

AFTER JONSSON & MALMQVIST, 2000
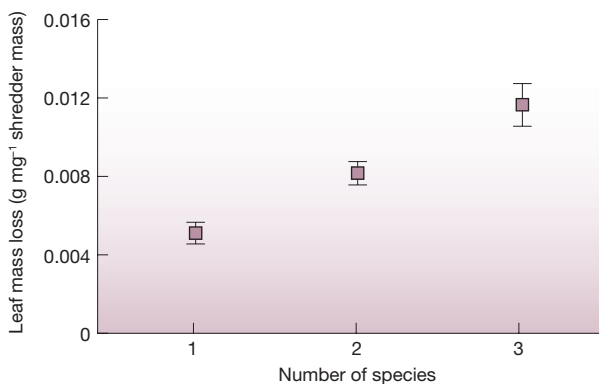
Figure 11.10

Variation in rate of loss of alder leaf mass in replicated stream experiments (per gram of leaf per milligram of shredder ± SE) caused by three species of shredder: larvae of the stoneflies *Protonemura meyeri*, *Nemoura avicularis* and *Taeniopteryx nebulosa*. The results are averaged for species acting on their own, for pairs of species in all possible combinations, and for all three species together (means ± SE). The decomposition rate was significantly faster when species operated in pairs, and was fastest of all when all three species were together.

included in every experiment (12 of a single species, six each in the species pairs, and four each when all three species were present) and the results were expressed in a standard way (leaf mass loss per gram of leaf per milligram of shredder in a 46-day experiment) so the result directly reflects the species richness present. These results are indicative of *complementarity* (each species feeds in a slightly different way so their combined effect is enhanced). Studies such as these have significant implications for the role that biological diversity plays in ecosystem functioning. Given current concerns about the extinction of species worldwide (see Chapter 14), we need to know whether diversity loss will have major consequences for the way ecosystems work. This is an important and controversial area (Box 11.2).
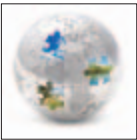
11.2 *Topical ECOncerns*

The importance of biological diversity in ecosystem functioning

Ecologists agree that some experimental evidence points to a significant role for biological diversity (biodiversity) in ecosystem functioning. Figure 11.10, for example, showed how decomposition rate is slower when fewer species are involved in the process. But some disagree about how much this matters – in other words, whether these kinds of result prove that biodiversity is critical to ecosystem health. This is a significant question at a time when global biodiversity is declining.

The following quotation comes from a commentary by Jocelyn Kaiser that appeared in 2000 in one of the major academic scientific journals, *Science* (289, 1282–1283).

Rift over biodiversity divides ecologists
A long-simmering debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war. Opposing camps are dueling over the quality of key experiments, and some are flinging barbs at meetings and in journals.

What lay behind such bellicose language? The disagreement began as part of the normal debate that should occur about any piece of research. To what extent are the conclusions justified from the results and how far can they be generalized from the special circumstances of the experiment to other situations in nature? Various studies around the world seemed to show that the loss of plant or animal species might adversely affect ecosystem function; for example, the productivity of grassland communities appears to be higher when more species are present. This could mean that biodiversity *per se* matters to productivity. But might variables other than species diversity have given rise to increased productivity? For example, perhaps such a result was a statistical artefact – higher productivity with higher species diversity might be explained simply by the addition of a more productive species to the list (and a more productive species is more likely to be present when more species are included in the experiment).

This kind of debate is healthy, but it took on a new dimension when one of the world's leading learned societies, the Ecological Society of America (ESA), published a pamphlet and sent copies to members of Congress. One of a series called 'Issues in Ecology', the pamphlet concerned the importance of biodiversity for ecosystem functioning. It summarized the results of several studies but with little discussion of doubts raised by skeptics in the ESA.

The commentator noted:

Other ecologists safely outside the fray say there is more at stake in this dispute than personalities and egos. Beyond the legitimate scientific question about how much can be learned from experiments is the nagging question – by no means limited to biodiversity – of when scientific data are strong enough to form the basis of policy decisions.

This debate was not really about the quality of the science (since every study has its limitations), but rather the document that the ESA sent to Congress, which some said tended to present opinion as fact. Do you think scientists should remain entirely outside the political arena? If not, how would you ensure that balanced and generally accepted positions would be presented? Read the article by Hooper et al. (2005) 'Effects of biodiversity on ecosystem functioning: a consensus of current knowledge' in Ecological Monographs 75, 3–35. Decide whether the opposing factions have found an effective way forward – the list of authors includes people who were on different sides of the original debate.

The decomposition of dead material is not simply due to the sum of the activities of decomposers and detritivores; it is largely the result of interaction between the two (Lussenhop, 1992). This can be illustrated by taking an imaginary journey with a leaf fragment through the process of decomposition, focusing attention on a part of the wall of a single cell. Initially, when the leaf falls to the ground, the piece of cell wall is protected from microbial attack because it lies within the plant tissue. The leaf is now chewed and the fragment enters the gut of a woodlouse. Here it meets a new microbial flora in the gut and is acted on by the digestive enzymes of the woodlouse. The fragment emerges, changed by passage through the gut. It is now part of the woodlouse's feces and is much more easily attacked by microorganisms, because it has been fragmented and partially digested. While microorganisms are colonizing the fecal pellet, it may again be eaten, perhaps by a springtail, and pass through the new environment of the springtail's gut. Incompletely digested fragments may again appear, this time in springtail feces, yet more easily accessible to microorganisms. The fragment may pass through several other guts in its progress from being a piece of dead tissue to its inevitable fate of becoming carbon dioxide and minerals.

11.4.4 Consumption of feces and carrion

The dung of carnivorous vertebrates is relatively poor-quality stuff. Carnivores assimilate their food with high efficiency (usually 80% or more is digested) and their feces retain only the least digestible components; their decomposition is probably caused almost entirely by bacteria and fungi. In contrast, herbivore dung still contains an abundance of organic matter and is sufficiently thickly spread in the environment to support its own characteristic fauna, consisting of many occasional visitors but with several specific dung-feeders. A good example is provided by elephant dung; within a few minutes of dung deposition the area is alive with beetles. The adult dung beetles feed on the dung but they also bury large quantities along with their eggs to provide food for developing larvae.

All animals defecate and die, yet feces and dead bodies are not generally very obvious in the environment. This is because of the efficiency of the specialist

Figure 11.11

The influence of woodlice on the rate of breakdown of feces of herbivorous caterpillars (*Operophthera fagata* – which feed on leaves of beech trees, *Fagus sylvatica*). After 6 weeks, twice as much of the fecal material had decomposed when woodlice were present.
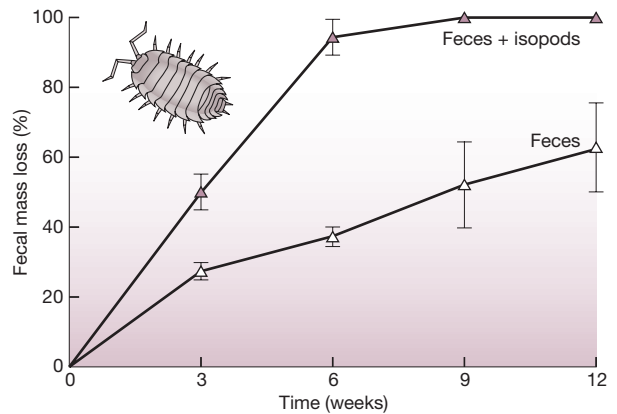
AFTER ZIMMER & TOPP, 2002

consumers of these dead organic products. On the other hand, where consumers of feces are absent, a build-up of fecal material may occur. Figure 11.11 shows how feeding by woodlice (*Porcellio scaber* and *Oniscus asellus*) speeds the breakdown of invertebrate feces. A more dramatic example is provided by the accumulation of cattle dung where these domestic animals have been introduced to locations lacking appropriate dung beetles. In Australia, for example, during the past 200 years, the cow population increased from just seven individuals (brought over by the first English colonists in 1788) to 30 million or so, producing 300 million cowpats per day. The lack of native dung beetles led to losses of up to 2.5 million hectares per year under dung. The decision was made in 1963 to establish in Australia beetles of African origin, able to dispose of bovine dung under the conditions where cattle are raised; more than 20 species have been introduced (Doube et al., 1991).

When considering the decomposition of dead bodies, it is helpful to distinguish three categories of organisms that attack carcasses. As before, decomposers (bacteria and fungi) and invertebrate detritivores have roles to play, but, in addition, scavenging vertebrates are often of considerable importance. Many carcasses of a size to make a single meal for one of a few of these scavenging detritivores will be removed completely within a very short time of death, leaving nothing for bacteria, fungi or invertebrates. This role is played, for example, by Arctic foxes and skuas in polar regions; by crows, gluttons and badgers in temperate areas; and by a wide variety of birds and mammals, including kites, jackals and hyenas, in the tropics.

11.5 The flux of matter through ecosystems

Chemical elements and compounds are vital for the processes of life. When living organisms expend energy (as they all do, continually), they do so, essentially, in order to extract chemicals from their environment, and hold on to them and use them for a period before they lose them again. Thus, the activities of organisms profoundly influence the patterns of flux of chemical matter.

The great bulk of living matter in any community is water. The rest is made up mainly of carbon compounds and this is the form in which energy is accumulated

and stored. Carbon enters the food web of a community when a simple molecule, carbon dioxide, is taken up in photosynthesis. Once incorporated in NPP, it is available for consumption as part of a sugar, a fat, a protein or, very often, a cellulose molecule. It follows exactly the same route as energy, being successively consumed and either defecated, assimilated or used in metabolism, during which the energy of its molecule is dissipated as heat while the carbon is released again to the atmosphere as carbon dioxide. Here, though, the tight link between energy and carbon ends.

Once energy is transformed into heat, it can no longer be used by living organisms to do work or to fuel the synthesis of biomass. The heat is eventually lost to the atmosphere and can never be recycled: life on Earth is only possible because a fresh supply of solar energy is made available every day. In contrast, the carbon in carbon dioxide can be used again in photosynthesis. Carbon, and all other nutrient elements (nitrogen, phosphorus, etc.), are available to plants as simple organic molecules or ions in the atmosphere (carbon dioxide), or as dissolved ions in water (nitrate, phosphate, potassium, etc.). Each can be incorporated into complex carbon compounds in biomass. Ultimately, however, when the carbon compounds are metabolized to carbon dioxide, the mineral nutrients are released again in simple inorganic form. Another plant may then absorb them, and so an individual atom of a nutrient element may pass repeatedly through one food chain after another.

energy cannot be cycled and reused – matter can

Unlike the energy of solar radiation, moreover, nutrients are not in unalterable supply. The process of locking some up into living biomass reduces the supply remaining to the rest of the community. If plants, and their consumers, were not eventually decomposed, the supply of nutrients would become exhausted and life on Earth would cease.

We can conceive of pools of chemical elements existing in compartments. Some compartments occur in the *atmosphere* (carbon in carbon dioxide, nitrogen as gaseous nitrogen, etc.), some in the rocks of the *lithosphere* (calcium as a constituent of calcium carbonate, potassium in the rock called feldspar) and others in the waters of soil, streams, lakes or oceans – the *hydrosphere* (nitrogen in dissolved nitrate, phosphorus in phosphate, carbon in carbonic acid, etc.). In all these cases the elements exist in inorganic form. In contrast, living organisms (the biota) and dead and decaying bodies can be viewed as compartments containing elements in organic form [carbon in cellulose or fat, nitrogen in protein, phosphorus in adenosine triphosphate (ATP), etc.]. Studies of the chemical processes occurring within these compartments and, more particularly, of the fluxes of elements between them, comprise the science of biogeochemistry.

Nutrients are gained and lost by communities in a variety of ways (Figure 11.12). A nutrient budget can be constructed if we can identify and measure all the processes on the credit and debit sides of the equation.

biogeochemistry and biogeochemical cycles

## 11.5.1 Nutrient budgets in terrestrial ecosystems

Weathering of parent bedrock and soil, by both physical and chemical processes, is the main source of nutrients such as calcium, iron, magnesium, phosphorus and potassium, which may then be taken up via the roots of plants.

nutrient inputs

Atmospheric carbon dioxide is the source of the carbon content of terrestrial communities. Similarly, gaseous nitrogen from the atmosphere provides most

Components of the nutrient budgets of a terrestrial and an aquatic system. Inputs are shown in blue and outputs in black. Note how the two communities are linked by streamflow, which is a major output from the terrestrial system but a major input to the aquatic one.
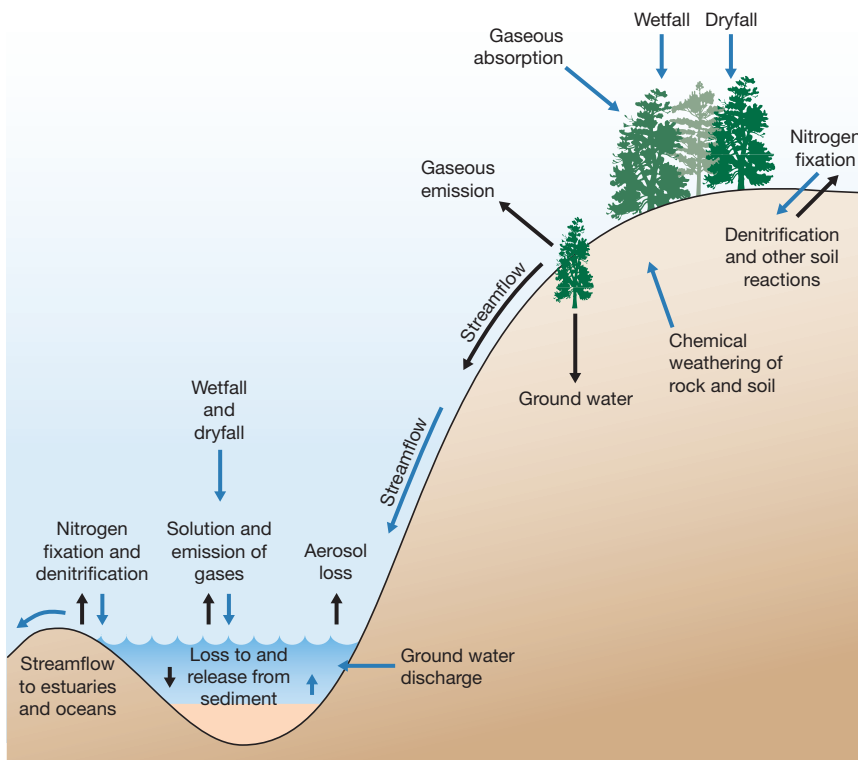
of the nitrogen content of communities. Several types of bacteria and blue-green algae possess the enzyme nitrogenase, which converts gaseous nitrogen to ammonium ions (NH_4^+) that can then be taken up through the roots and used by plants. All terrestrial ecosystems receive some available nitrogen through the activity of free-living, nitrogen-fixing bacteria, but communities containing plants such as legumes and alder trees (*Alnus* spp.), with their root nodules containing symbiotic nitrogen-fixing bacteria (see Section 8.4.6), may receive a very substantial proportion of their nitrogen in this way.

Other nutrients from the atmosphere become available to communities in *dryfall* (settling of particles during periods without rain) or *wetfall* (in rain, snow and fog). Rain is not pure water but contains chemicals derived from a number of sources: (i) trace gases, such as oxides of sulfur and nitrogen; (ii) aerosols, produced when tiny water droplets from the oceans evaporate in the atmosphere and leave behind particles rich in sodium, magnesium, chloride and sulfate; and (iii) dust particles from fires, volcanoes and windstorms, often rich in calcium, potassium and sulfate. Nutrients dissolved in precipitation mostly become available to plants when the water reaches the soil and can be taken up by plant roots.

nutrient outputs

Nutrients may circulate within the community for many years. Alternatively, the atom may pass through the system in a matter of minutes, perhaps without interacting with the biota at all. Whatever the case, the atom will eventually be lost through one of the variety of processes that remove nutrients from the system (Figure 11.12). These processes constitute the debit side of the nutrient budget equation.

Figure 11.13

Annual carbon budget for a ponderosa pine (*Pinus pondersosa*) forest in Oregon, USA, where the trees are up to 250 years old. The numbers above ground represent the amount of carbon contained in tree foliage, in the remainder of forest biomass, in understorey plants and in dead wood on the forest floor. The numbers just below the ground surface represent tree roots (left) and litter (right). The lowest numeral is for soil carbon. The amounts of carbon stored in each of these elements of biomass are in g C m^{-2}. Values for net primary production (NPP) and for respiratory heat loss from heterotrophs (R_h) (i.e. microorganisms and animals) are in g C m^{-2} yr^{-1} (arrows). There is an approximate balance in the rate at which carbon is taken up in NPP and the rate at which it is lost as respiratory heat loss.
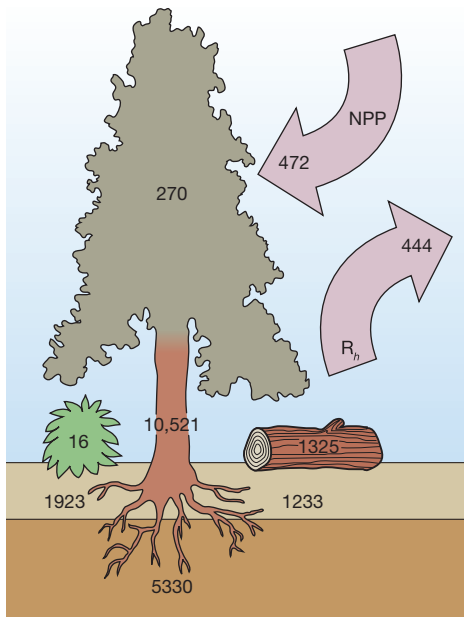
Release to the atmosphere is one pathway of nutrient loss. In many communities there is an approximate annual balance in the carbon budget; the carbon fixed by photosynthesizing plants is balanced by the carbon released to the atmosphere as carbon dioxide from the respiration of plants, microorganisms and animals (Figure 11.13). Plants themselves may be direct sources of gaseous and particulate release. For example, forest canopies produce volatile hydrocarbons (e.g. terpenes) and tropical forest trees appear to emit aerosols containing phosphorus, potassium and sulfur. Finally, ammonia gas is released during the decomposition of vertebrate excreta. Other pathways of nutrient loss are important in particular instances. For example, fire (either natural, or when, for instance, agricultural practice includes the burning of stubble) can turn a very large proportion of a community's carbon into carbon dioxide in a very short time, and the loss of nitrogen, as volatile gas, can be equally dramatic.

For many elements, the most substantial pathway of loss is in streamflow. The water that drains from the soil of a terrestrial community into a stream carries a load of nutrients that is partly dissolved and partly particulate. With the exception of iron and phosphorus, which are not mobile in soils, the loss of plant nutrients is predominantly in solution. Particulate matter in streamflow occurs both as dead organic matter (mainly tree leaves) and as inorganic particles.

It is the movement of water under the force of gravity that links the nutrient budgets of terrestrial and aquatic communities (see Figure 11.12). Terrestrial systems lose dissolved and particulate nutrients into streams and ground waters; aquatic systems (including the stream communities themselves, and ultimately the oceans) gain nutrients from streamflow and groundwater discharge. Refer to Section 1.3.3 for discussion of a study (at Hubbard Brook) that explored the chemical linkages at the land–water interface.

## 11.5.2 Nutrient budgets in aquatic communities

Aquatic systems receive the bulk of their supply of nutrients from stream inflow. In stream and river communities, and also in lakes with a stream outflow, export in outgoing stream water is a major factor. By contrast, in lakes without an outflow (or where this is small relative to lake volume), and also in oceans, nutrient accumulation in permanent sediments is often the major export pathway.

Many lakes in arid regions, lacking a stream outflow, lose water only by evaporation. The waters of these *endorheic* lakes (the word means 'internal flow') are thus more concentrated than their freshwater counterparts, being particularly rich in sodium but also in other nutrients such as phosphorus. Saline lakes should not be considered as oddities; globally, they are just as abundant in terms of numbers and volume as freshwater lakes (Williams, 1988). They are usually very fertile with dense populations of blue-green algae, and some, such as Lake Nakuru in Kenya, support huge aggregations of plankton-filtering flamingoes (*Phoeniconaias minor*).

The largest of all endorheic 'lakes' is the world ocean – a huge basin of water supplied by the world's rivers and losing water only by evaporation. Its great size, in comparison to the input from rain and rivers, leads to a remarkably constant chemical composition. The main transformers of dissolved inorganic carbon (essentially carbon dioxide dissolved from the atmosphere) are small phytoplankton cells, whose carbon is mainly recycled near the ocean surface via consumption by microzooplankton, release of dissolved organic substances and their mineralization by bacteria (Figure 11.14). In contrast, pathways involving larger phytoplankton and macrozooplankton are responsible for the majority

Figure 11.14

Pathways of carbon atoms in the ocean. Small phytoplankton, microzooplankton and bacteria recycle carbon in the mixed surface layer. Most of the carbon that moves to the deep ocean follows pathways involving larger phytoplankton and macrozooplankton, to be recycled again. A small proportion of remineralized inorganic carbon and particulate organic carbon is lost to the ocean sediment.

AFTER FASHAM ET AL., 2001
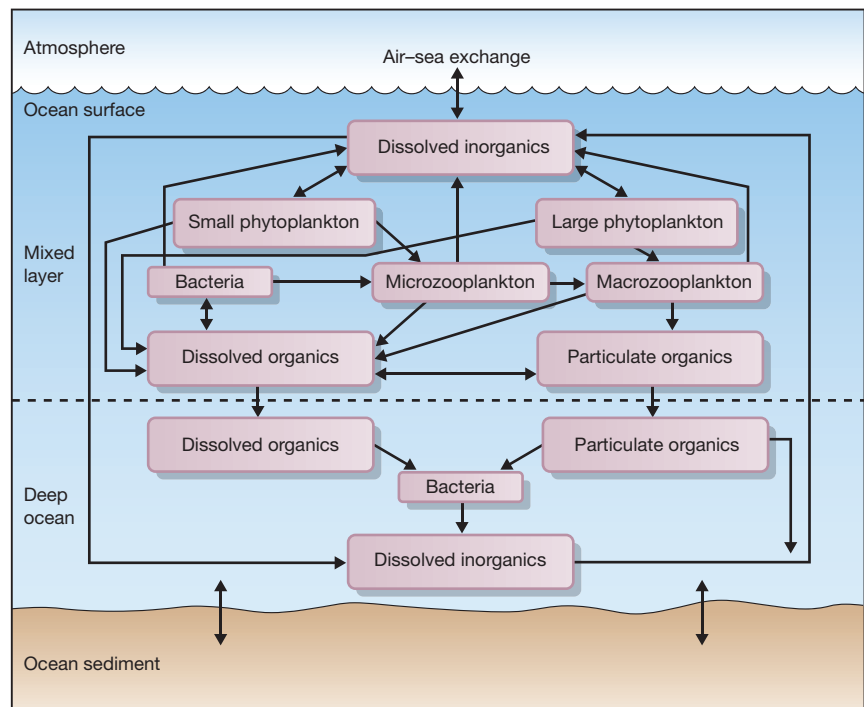
of carbon flux to the deep ocean floor. Some of this organic material is consumed by deep-sea animals, some is mineralized to inorganic form by bacteria and recirculated, and a small proportion becomes buried in the sediment. Figure 11.14 is essentially the ocean equivalent of the forest system in Figure 11.13. In contrast to the atmospheric source of carbon, nutrients such as phosphorus come from two sources – river inputs and water welling up from the deep. Phosphorus atoms in the surface water follow a similar set of pathways to carbon atoms, with about 1% of detrital phosphorus being lost to the deep sediment during each oceanic mixing cycle.

All water bodies receive nutrients, in inorganic and organic form, in the water draining from the land. It is no surprise, therefore, that human activities are responsible for dramatic changes in nutrient fluxes both locally (Box 11.3) and globally. We turn to global biogeochemical cycles in the next section.
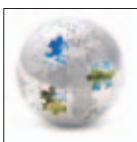
11.3 *Topical ECOncerns*

Nutrient enrichment of aquatic ecosystems: a major problem for lakes and oceans

The excess input of nutrients from sources such as agricultural runoff and sewage has caused many 'healthy' *oligotrophic* lakes (low nutrients, low plant productivity with abundant water weeds, and clear water) to switch to a *eutrophic* condition where high nutrient inputs lead to high phytoplankton productivity (sometimes dominated by toxic bloom-forming species), making the water turbid, shading out large plants and, in the worst situations, leading to anoxia and fish kills. This process of *cultural eutrophication* of lakes has been understood for some time. But it was only recently that people noticed huge 'dead zones' in the oceans near river outlets, particularly those draining large catchment areas such as the Mississippi in North America and the Yangtze in China. The following extracts are from a news item posted by Associated Press on March 29, 2004.

Ocean dead zones on the increase

So-called 'dead zones', oxygen-starved areas of the world's oceans that are devoid of fish, top the list of emerging environmental challenges, the United Nations Environment Program [UNEP] warned Monday in its global overview.

The new findings tally nearly 150 dead zones around the globe . . . The main cause is excess nitrogen run-off from farm fertilizers, sewage and industrial pollutants. The nitrogen triggers blooms of microscopic algae known as phytoplankton. As the algae die and rot, they consume oxygen, thereby suffocating everything from clams and lobsters to oysters and fish.

'Human kind is engaged in a gigantic, global, experiment as a result of inefficient and often overuse of fertilizers, the discharge of untreated sewage and the ever rising emissions from vehicles and factories', UNEP Executive Director Klaus Toepfer said in a statement. 'Unless urgent action is taken to tackle the sources of the problem, it is likely to escalate rapidly.'

Suggest some 'urgent actions' that could be taken to alleviate the problem.