of species anywhere along the continuum is likely to decrease long-term average productivity. Removal of strong competitors should result in less complete or efficient resource use, while a loss of good colonizers should lead to decreased production through incomplete establishment in recently disturbed areas (Tilman *et al.* 1994).

These three factors (spatial variability, temporal variability, and variation in time since disturbance) all tend to make average annual production an initially increasing function of biodiversity, without necessarily requiring more than one species of the dominant life form per habitat type. For a biome populated with a random selection of the possible species and genotypes, duplication of functional types or suites of adaptations would increase the number of species and genotypes at which long-term average production saturates (Figure 6.2-1).

Given these mechanisms that favour an increase in production with an increase in biodiversity, at what level of biodiversity should production reach a maximum, and how should this vary across biomes? In general, production should saturate at lower levels of biodiversity in biomes with lower levels of spatial and temporal complexity. Biomes certainly differ in the source and scale of the major modes of variation, but differences in the total amount or importance of variation are less clear. In tropical rain forests, the dominant sources of variation are probably related to small-scale gap dynamics (Martínez-Ramos *et al.* 1988) while in Arctic tundra, variation due to topography and soils is especially important (Chapin and Shaver 1989). In other biome types, year-to-year climate variation is a dominant source of variation. The response of grassland production to rainfall is a clear example of this (Sala *et al.* 1994). Precise quantitative estimates of the number of distinctive zones of habitat, climate and disturbance within each major biome are not yet possible. A rough but reasonable estimate is in the order of 10 substantially different zones per biome, with a range of perhaps 4 to 40. Additional experiments will be necessary before it is feasible to develop a more detailed accounting.

### 6.2.1.4 Production and resource augmentation
The mechanisms discussed above do not address the response to biodiversity of production at a single site in a single year. This topic is not well studied and neither the shape nor the quantitative limits of the response is generally known. In some cases, biological and biogeochemical characteristics related to production appear to saturate with a few species, even in a complex ecosystem like a tropical forest (Ewel *et al.* 1991). But when low-diversity ecosystems fail to develop complete canopies, as a consequence of the suite of plant species present or of interactions across trophic levels, increased diversity can lead to increased production (Naeem *et al.* 1994). Most of

the current hypotheses on the role of biodiversity in production at one site in one year are summarized by a resource augmentation model, which states that adding a species should increase production only if that species has access to, or prevents losses of, previously unused light, water or nutrients. Examples of mechanisms for increasing resource access or decreasing loss include symbiotic nitrogen fixation (for increased access to nutrients (Vitousek *et al.* 1987), increased rooting depth (for increased access to water; Davis and Mooney 1986), improving the temporal match between nutrient release and uptake (Swift and Anderson 1993), releasing extracellular phosphatases into the soil solution (to increase phosphorus availability), faster canopy development (for increased light capture), increased leaf longevity (for decreased nutrient loss), and providing a refuge for ants or other defenders against herbivory (for decreased nutrient loss).

The resource augmentation model predicts that only a fraction of the many possible species additions should lead to increased production. But it also presents the possibility that many of the consequences of additions and deletions should be predictable on the basis of a species' pattern of resource utilization (Hobbie *et al.* 1993) or its relative abundance (Sala *et al.* 1996).

Anthropogenic impacts on the biosphere often result in changes in resource availability, in the efficiency with which resources are used for growth, or in the dynamics of resource turnover (Field *et al.* 1992). In some cases, these impacts may change the response of NPP to biodiversity. If for example, anthropogenic nutrient deposition changes the relative availability of limiting nutrients (Schulze 1989), or if a change in climate eliminates one or more species, potentially available resources may go unused without an increase in biodiversity. On the other hand, a change in resources or species composition could also make it possible for a smaller number of species to capture the available resources or to use the available resources more efficiently. It is also likely that the response of NPP to changes in biodiversity will differ with different anthropogenic impacts and that, for any particular anthropogenic impact, the NPP/biodiversity relationship will vary among biomes. Developing the understanding necessary to predict changes in the response of NPP to biodiversity in ecosystems impacted by altered climate, elevated $CO_2$, nutrient deposition, oxidants or species introductions should be a central objective of future studies. The role of biodiversity in regulating production at one site in one year involves different mechanisms from those governing the role of biodiversity across the whole array of habitats within a biome, and it is unlikely that relationships among species are the same in the two contexts. Thus, the response of production to biodiversity almost certainly saturates more slowly when both site-to-site and within-site mechanisms are operating. The quantitative response is not

yet known, but it is possible that species complementarity through resource augmentation could lead to increased production with two to several species or genotypes per site. A conservative minimum estimate is that accounting for resource augmentation for each site and year doubles the biodiversity necessary to saturate ecosystem production. Thus, the combination of the mechanisms related to resource augmentation and temporal and spatial diversity should lead to increasing production until the total reaches on the order of 20 species and/or genotypes in the dominant life-form of primary producers. The uncertainty of this estimate is very large. In addition, the persistence of these dominant life-form primary producers may depend on a number of other species, including pollinators, dispersers, nitrogen fixers, decomposers, herbivores and pathogens.

## 6.2.1.5 Biomass and disturbance

The role of biodiversity in regulating standing biomass is poorly studied. In most biomes, the major control on standing biomass is the frequency of disturbance, including fire, severe weather, and pest and pathogen attacks (e.g. Bonan and Shugart 1989). Disturbance frequency regulates not only the size of the dominant plants but also the species present and, in some cases, the presence or absence of a major growth form, e.g. trees (Hughes *et al.* 1991). Effects of single species on disturbance frequency have been documented (D'Antonio and Vitousek 1992), and resistance to pests and pathogens is one of the best-known benefits of multi-crop agriculture.

Increasing biodiversity could potentially decrease the frequency or intensity of many types of disturbance. Effects of biodiversity on disturbance by pests and pathogens are relatively well known, at least for agriculture. Biodiversity could decrease fire frequency, especially in ecosystems where single species enhance flammability (D'Antonio and Vitousek 1992). While increased biodiversity would not reduce the frequency or intensity of severe weather, it could reduce the intensity of disturbance through interspecific or population differences in tolerance to the extreme weather.

To the extent that increasing biodiversity decreases the frequency and intensity of disturbance, it should lead to increased standing biomass. It is not feasible, at this point, to even speculate on the number of species required to saturate the long-term average standing biomass.

## References

Bonan, G.B. and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* **20**: 1–28.

Chabot, B.F. and Mooney, H.A. (eds) 1985. *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.

Chapin, F.S., III 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**: 233–260.

Chapin, F. S., III, and Shaver, G.R. 1989. Differences in growth and nutrient use among arctic plant growth forms. *Functional Ecology* **3**: 73–80.

Chapin, F.S., III Walker, L.R., Fastie, C.L. and Sharman, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**: 149–175.

D'Antonio, C.M. and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.

Davis, S.D. and Mooney, H.A. 1986. Water use patterns of four co-occuring chaparral shrubs. *Oecologia* **70**: 172–177.

Ewel, J.J., Mazzarino, M.J. and Berish, C.W. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications* **1**: 289–302.

Field, C.B., Chapin F.S. III, Matson, P.A. and Mooney, H.A. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics* **23**: 201–235.

Francis, C.A. 1986. *Multiple Cropping Systems*. Macmillan, New York.

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

Hobbie, S., Jensen, D. and Chapin, F.S. III 1993. Global changes in resources and disturbance: predictions for biodiversity. In: Schulze E.-D. and Mooney H.A. (eds), *Ecosystem Function and Biodiversity*. 385–408. Springer-Verlag, Berlin.

Hobbs, R.J .and Mooney, H.A. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**: 59–68.

Hughes, R.F., Vitousek, P.M. and Tunison, T. 1991 Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* **72**: 743–746.

Martínez-Ramos, M., Alvarez-Buylla, E., Sarukhán, J. and Piñero, D. 1988. Treefall age determination and gap dynamics in a tropical forest. *Journal of Ecology* **76**: 700–716.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734–737.

Sala, O. E., Lauenroth, W.K. and Burke, I.C. 1994. Carbon budgets of temperate grasslands and the effects of global change. In: Melillo, J.M. and Breymeyer, A. (eds). *Global Change: Effects on coniferous forests and grasslands*. John Wiley, Chichester (in press).

Sala, O.E., Lauenroth, W.K., McNaughton, S.J., Rusch, G. and Zhang, X. 1996. Biodiversity and ecosystem function in grasslands. In: Mooney, H.A., Cushman, J.A., Medina, E., Sala, O.E. and Schulze E.-D. (ed.,) *Functional Roles of Biodiversity: A global perspective*. John Wiley, New York (in press).

Schulze, E.-D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* **244**: 776–783.

Swift, M.J. and Anderson, J.M. 1993. Biodiversity and ecosystem function in agricultural systems. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 15–41. Springer-Verlag, Berlin.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Function*

*of Plant Communities*. Princeton University Press, Princeton, NJ.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation. *Ecology* 74: 2179–2191.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.

Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65–66.

Vandermeer, J.H. 1988. *The Ecology of Intercropping*. Cambridge University Press, Cambridge.

Vitousek, P.M., Walker, L.R., Whiteacre, L.D., Mueller-Dombois, D. and Matson, P.A. 1987 Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802–804.

Williams, M.E. and Levings, C.S., III 1992. Molecular biology of cytoplasmic male sterility. *Plant Breeding Reviews* 10: 23–51.

## 6.2.2 The soil system

### 6.2.2.1 Introduction

The widespread effects of human activities on soils are of global concern because of increased emissions of 'greenhouse' gases, accelerated erosion and desertification, and declining fertility in soils supporting some of the highest population densities in developing countries (World Resources Institute 1992-3). Human-induced soil degradation by wind, water and pollution amounts to about 24% of the inhabited land area of the globe (Oldeman 1994). Changes in climate, atmospheric $CO_2$ concentrations and UV radiation are affecting soils and vegetation in regions of the world remote from direct effects of human activities (IPCC 1992). Disruption of soil processes from atmospheric pollution, changes in landuse, management practices and intensive use of agrochemicals are also affecting freshwater and marine systems as a consequence of increased transfers of sediment, nutrients and toxins from land to water.

Losses of genetic and species diversity below ground resulting from human impacts on the biosphere are largely undocumented in comparison with estimates of extinction rates above ground. Biodiversity in soils, however, is not simply an attribute of the living biota. Unlike above-ground systems, the physical and biochemical properties of dead organic matter (litter and soil organic matter fractions) confer important functional attributes on soils which are integral to biogeochemical cycles. The structural and biochemical characteristics of soils vary both with depth in the profile and in relation to the parent materials, topographic variation, climate gradients and vegetation cover within and between systems. This spatial heterogeneity constitutes a mosaic of sinks and sources for surface water, sediment and trace gases which is important for stabilizing soil processes at aggregate, patch, plot, ecosystem and landscape scales.

The functional importance of biodiversity for the maintenance of soil fertility remains one of the most fundamental gaps in current understanding of terrestrial ecosystems (Swift and Anderson 1993; Anderson 1994). Indeed, the total diversity of the soil biota, as a starting point for this assessment, has not yet been determined for any natural system (Lee 1991). As a consequence of this dearth of comparable information on biodiversity in soils for the different biomes, this review has been developed in the style of a biome essay rather than a cross-biome synthesis as originally intended.

### 6.2.2.2 Lessons from agriculture

*Human impacts on biodiversity.* Most of the annual flux of carbon and nutrients in soils from tundra to tropical rain forest occurs in the top 5–10 cm of the profile despite the considerable variation in biomass and primary productivity above ground along this gradient. Structural characteristics of litter cover and the soil surface to a few millimeters depth partition the beneficial or destructive effects of rainfall (Papendick 1994). The animal and microbial communities occupying these critical soil interfaces are highly complex even in natural systems with low biodiversity of plant species. At the molecular and organism level, biodiversity in soils is very high. A single gram of temperate forest soil could contain $10^9$ individual cells comprising 4000–5000 bacterial types, of which less than 10% have been isolated and are known to science (Torsvik *et al.* 1990; Klug and Tiedje 1994). More than 500 species of soil invertebrates have been recorded from a beech (*Fagus sylvatica*) forest (Schaefer and Schauermann 1990) and new records are still being added to a list of 2500 species of fungi from a nature reserve covering a few hectares in southwest England (Hawksworth 1992). Species richness declines towards the poles but assumptions regarding the simplicity of communities at high latitudes generally ignore the complexity of below-ground systems. Even simple moss tussock communities in the Antarctic Peninsula have complex food webs linking over a hundred species of algae, protozoa, nematodes, tardigrades, collembola and mites plus unknown numbers of fungal and bacteria species (Davis 1981).

Significant loss of biodiversity can occur when natural habitats are modified or converted to intensive permanent cultivation (Paoletti *et al.* 1992; Anderson and Swift 1993; Freckman and Ettema 1993; Lavelle *et al.* 1994). The larger, surface-living invertebrates disappear first with the destruction of litter habitats which provide food and living space. Dead tree boles and branches containing many wood-decomposing invertebrates and fungi can be eliminated under intensive extractive forest management or plantation forestry (Gilot *et al.* 1992). Conversion of tropical forest to tree plantations or smallholder farming

systems can also result in changes in termite communities with the loss of highly diverse humivorous groups and an increase in wood/litter feeders which include damaging pest species (Wood *et al.* 1977). In New Zealand, improvement of temperate pastures with legumes and exotic grasses eliminated indigenous earthworm species and enabled European lumbricids to become established (Lee 1985). In contrast, European lumbricids maintained marginal populations in US prairies in relation to native *Diplocardia* species because of their intolerance of high summer temperatures (James 1991). However, these exotic earthworms have invaded many mesic habitats where there is a low diversity of indigenous species (Hendrix *et al.* 1992).

Communities of smaller invertebrates live within the highly complex microscopic structure of litter and soil habitats. Anderson (1978) showed that the diversity of mite (Cryptostigmata) species was closely related to microhabitat diversity in organic soils developed under a single tree species. Changes in litter quality or the introduction of plant species with faster decay rates reduces habitat complexity. Improvement of pasture quality to support higher stock densities reduces the thatch of litter on the soil surface and thus the habitat space for the associated micro-arthropod communities (Hutchinson and King 1980), but earthworms living within the mineral soil respond positively to increased grass and dung quality (Knight *et al.* 1992; James 1992).

Mechanical cultivation is highly destructive to most invertebrate groups. The microbiota (nematodes, protozoa, micro-fungi and bacteria) are the main groups surviving in intensively tilled soils (Hendrix *et al.* 1986; Freckman and Ettema 1993). Agrochemicals also reduce the taxonomic and genetic diversity of soil micro-organisms (Domsch *et al.* 1983; Atlas *et al.* 1991). Even so, total biodiversity in agricultural soils is likely to be greater than the total above-ground diversity of plants and animals in the natural systems from which they were derived. The adoption of zero or minimum tillage practices allows the resurgence of biodiversity in agricultural soils provided that sources of colonists are present in habit refugia around the field margins (Hendrix *et al.* 1986).

*Ecosystem consequences of human impacts.* Most soil organisms are small (<2 mm diameter) and manifest their specific effects at spatial and temporal scales orders of magnitude below those where process measurements are made in most ecological studies (Anderson 1988). As a consequence there is a poor understanding of the links between their proximate roles in biological transformations and processes operating at larger scales and over longer time intervals.

The roles of the soil biota can be described in terms of allogenic and autogenic processes proposed by Jones and Lawton (1995). The allogenic processes, such as carbon and nitrogen mineralization, are direct products of soil organism metabolism. These are modified by changes in the quality of the resources they are processing as a consequence of changes in plant species composition, $CO_2$ and N enrichment of plants, or pollution. Autogenic processes involve the modulating effects of organisms where the consequences of their activities, such as removing litter, creating soil macropores or the release of prey from predation, influence mass or energy transfers much larger than their allogenic effects (Anderson 1995).

Microcosm studies have shown that different species and combinations of invertebrates and microorganisms have specific effects on the rates and products of carbon and nutrient fluxes. The feeding activities of collembola, mites, nematodes and protozoa have also been shown to change the composition and activities of bacterial and fungal communities in ways analogous to the effects of herbivores in above-ground communities (reviews by Anderson 1988; Verhoef and Brussaard 1990). The specific nature of allogenic and autogenic effects could be taken to support the 'Rivet Hypothesis' that the removal of each species deletes unique properties from community functions (Ehrlich and Ehrlich 1981; see Section 5.1). However, at an ecosystem level, the attributes of complexity in food webs are not apparent and fumigation treatments, which eliminate much of the biotic diversity in soils, usually show transient effects on soil processes; at least in the short term (Rovira 1976; Ridge 1976; Ingham *et al.* 1986). These results suggests that there is a high level of functional overlap in soil biological processes, with many organisms producing similar metabolic end products able to compensate for changes in community structure. On the other hand, microbial processes such as nitrogen fixation, which are carried out by a group of bacteria with intrinsically low diversity in soils, are susceptible to heavy metal contamination of soils (Brookes and Verstraete 1989). McGrath *et al.* (1988) have shown that the activity of *Rhizobium* associations with white clover (*Trifolium repens*) was drastically reduced by heavy metal concentrations from sewage sludge which were within legislative limits set by the European Community.

The activities of soil fauna are evident at the ecosystem level where functional groups are dominated by one or two species creating persistent artifacts (aggregates, burrows, incorporation of organic matter into soil) which have cumulative effects on soil properties (Anderson 1995). The elimination of earthworms, or the introduction of exotic species with different attributes to the indigenous community, has been shown to alter soil structure, aeration, surface water infiltration, the distribution of organic matter, pesticides and heavy metals, and total crop production (Lee 1985; Lavelle 1988; Clements *et al.* 1991). In Peru, the conversion of forest to improved pasture eliminated most of the soil macrofauna and populations of an exotic tropical

earthworm species, *Pontoscolex corethrurus*, then developed a biomass of 4 t/ha and dominated soil processes (Lavelle and Pashanasi 1989). Termites in semi-arid systems have similar key effects on soil structure and hydrology which can shift from beneficial to deleterious as a consequence of changes in climate or management. In the overgrazed grasslands of Ethiopia, scavenging of the little remaining grass and litter cover by termites leaves soil bare and susceptible to erosion (Wood 1991). Similarly, the bare ground around termite mounds in grassland fallows of West Africa can initiate erosion and land degradation when they reach high densities (Janeau and Valentin 1987). Conversely, the elimination of a single termite species in the Chiuhuahuan desert altered the soil water balance and resulted in shrubs replacing grass cover in experimental plots over a period of eight years (Elkins *et al.* 1986).

### 6.2.2.3 Soil organic matter

*Components of diversity.* Soil organic matter (SOM) contains on average twice the amount of carbon found in vegetation above ground and is a resource of extraordinary physical and biochemical complexity (Theng *et al.* 1989; Anderson 1991). Dead organic matter is essential to the functioning of most natural and derived soils not only as a complex habitat and resource base for a diverse biota, but also because it maintains the physical and chemical integrity of the system. Litter resource types (fruits, leaves, twigs, branches, coarse and fine roots) from species with different chemical compositions and decomposition rates regulate the rates of carbon and nutrient mineralization (Swift and Anderson 1993). Litter cover also protects the soil from wind and rain erosion, and influences water and heat transfer to the underlying soil (Lal 1994). During the process of decomposition, soil organic matter (SOM) is formed which can be chemically or physically stabilized by soil minerals to form different fractions with turnover rates ranging from years to centuries. The whole range of SOM fractions, operationally defined as fast, slow and passive, confer particular attributes on soil such as aggregate stabilization, complexing free aluminium, regulating soil moisture, forming ion exchange complexes and constituting sinks/sources of plant nutrients (Duxbury *et al.* 1989). There are, however, very different time scales over which these effects are manifested. Changes in litter and fast SOM fractions have rapid effects on soil physical processes and nutrient cycling but the slow and passive fractions have turnover rates ranging from decades to millenia. Consequently, the restitution of soil profile characteristics under natural vegetation cover following catastrophic disturbance can effectively operate outside the human time frame.

*Ecosystem consequences of human impacts.* The effects of changing resource diversity on soil properties fits the asymptotic model of Vitousek and Hooper (1993; see Figure 5.2-1A) relating species richness to ecosystem functioning. Adding (or removing) resources until all the key resource types are represented has larger effects on a given process than further additions of representatives of those groups. For example, erosion control depends on the amount of litter cover for soil protection rather than the diversity of plant species making up the litter (Mbakaya *et al.* 1988). Similarly, the amount of soil organic matter depends upon the quality and quantity of resource inputs and not on vegetation diversity. Hence SOM accumulation in forests is related to the inherent fertility of the parent soil and not to tree species diversity.

Where resource types are the product of a keystone species the effects of changing diversity can be profound. Davies (1981) has described two Antarctic moss communities: a tall turf community dominated by two moss species and a moss carpet dominated by three species. The decomposition-resistant (low quality) stems of one moss in the tall turf contributed to SOM accumulation to a depth of 2 m under this community against only 0.2 m SOM accumulated under the moss carpet with more rapidly decomposing (high quality) species. Analagous effects on soil carbon pools are associated with changes in landuse between high quality broad-leaf woodlands and low-quality conifer plantations; or the introduction new keystone species with contrasting litter quality into communities with low diversity (Anderson 1991). In Hawaii, organic soils have developed under stands of a single tree species, *Metrosideros polymorpha* which produces a low-quality litter in response to limited N availability. The invasion of the monospecific stands by an introduced nitrogen-fixing tree, *Myrica faya*, which produces a rapidly decomposing litter, has changed the nutrient and organic matter balances of the ecosystem (Vitousek *et al.* 1987). The consequences of these changes for the biodiversity of soil organisms are unknown but are likely to be profound. More gradual increases in litter quality and SOM turnover are occurring over much of Europe where anthropogenic sources of N are saturating forest ecosystems leading to increased nitrate leaching and nitrous oxide emissions (Aber *et al.* 1989; Rosen *et al.* 1992). Conversely, increased C/N ratios in litter as a consequence of $CO_2$ enrichment of N-limited systems may be increasing carbon storage in SOM on a global scale (Allen 1990; Bazzaz 1990).

### 6.2.2.4 Functional importance of spatial complexity

*Spatial components of biodiversity.* Soils under undisturbed vegetation cover have high resilience to natural perturbations, such as storm events, cataclysmic litter inputs and extreme seasonality, so that losses of suspended solids or solutes are usually small in relation to the pools and fluxes within the system boundaries. The mass balance of carbon and nutrients in the system is maintained by transfers between sinks and sources which operate at

different scales from microsites to landscapes (Anderson 1995). Reciprocal processes, which stabilize the overall dynamics of the system, are manifest in soil organism populations (natality/mortality; emigration/immigration), nutrient cycling (mobilization/immobilization), carbon fluxes (plant growth/decomposition), water balances (runoff/ infiltration) and soil development (erosion/weathering). These sink/source interactions are considered in other essays in this volume and are only briefly reviewed here.

The balance between processes of nitrogen mineralization/immobilization, and nitrification/ denitrification, are important in regulating nitrate leaching and nitrous oxide emissions from soils. These N transfers occur between adjacent bacteria, on gradients within soil aggregates (Groffman *et al.* 1987; Parkin 1987), at the level of resource patches integrated by fungal hyphae on the forest floor ( Rayner and Boddy 1988), in forest gaps (Vitousek and Denslow 1986) and between hill-slope and riparian zones of catchments (Peterjohn and Correll 1984; Gregory *et al.* 1991). Sinks and sources for methane similarly exhibit scaling related to aerobic and anaerobic regimes in soils (Crutzen 1991) from microsites within aggregates (King and Adamsen 1992), and between surface and underlying soil horizons (Whalen and Reeburgh 1990) through the patch scales associated with plant communities (Whalen *et al.* 1990) up to the landscape scale (Moore *et al.* 1990).

Hydrological processes are also buffered by spatial heterogeneity of surface water sources and sinks. In rain forest, high intensity storm events, combined with funnelled stemflow as a result of branching patterns of canopy emergents, may create saturated areas around the trunk bases and overland flow downslope from these areas. Exposed roots and buttresses, however, can act as effective barriers to downslope soil wash (Spencer *et al.* 1990). Van Hooff (1982) showed that splash erosion and overland flow in a deciduous woodland was determined by the differential palatability to earthworms of litter from the two tree species. Consumption of the more palatable litter in patches of one tree species in spring caused splash erosion, while patches of the less palatable species, where litter cover remained intact, formed sinks for surface water and sediment so that there were no net losses of sediment across the forest boundary. Soil loss rates are generally low under forest cover but severe erosion can occur in extensive plantations of teak (*Tectona grandis*) where ground cover vegetation is suppressed and the rapidly decomposing leaves give no soil protection from the high kinetic energy of canopy throughfall (Bell 1973).

Spatial heterogeneity of soil properties reduces the amplitude of sediment, solute and trace gas losses from terrestrial systems. Extreme events which exceed sink strengths at local scales may be contained with the patch mosaic sinks at ecosystem or landscape scales. Human activities have major impacts on the heterogeneity of soils

which affect terrestrial, aquatic and atmospheric processes.

*Ecosystem consequences of human impacts.* Changes in landuse resulting from traditional agricultural practices can increase spatial heterogeneity of ecosystems within the landscape as a consequence of habitat fragmentation. Further intensification of landuse reduces the patch heterogeneity of sources and sinks for trace gases and solutes, and increases the periodicity and amplitude of biogeochemical fluxes within the landscape (Burke and Lauenroth; see 6.2.4). As larger areas of arable agriculture, plantation forestry and pastures come under the same soil management practices and cropping cycles, trace gas fluxes and nutrient leaching can be synchronized across whole landscapes with knock-on effects for atmospheric and aquatic systems on regional and even wider geographic scales.

Extensive development of intensive agricultural practices has increased soil erosion by wind and water in many regions of Europe and North America (Lal 1994; Papendick 1994). The removal of hedgerows and buffer strips, levelling of field systems and intensive tillage have reduced sinks for transported material. Soil channelling and compaction also result in surface runoff exceeding the infiltration capacity and particle retention by the microtopography of inter-rill areas (Boardman 1991). Similarly, Hutsch *et al.* (1993) have shown that sink strengths for methane in agricultural systems are related to the use of inorganic fertilizer (decreased sink) and organic manures (increased sink). Uniform agricultural practices using inorganic fertilizers can therefore reduce sinks for methane across agricultural landscapes (Mosier *et al.* 1991). Atmospheric N deposition also reduces the sink strength of forest soils (Steudtler *et al.* 1989).

### 6.2.2.5  *Summary and relevance to human activities*
Soils contain high biological, biochemical and physical complexity which can be defined across all scales from the microscopic to landscape level. The biotic diversity below ground may be orders of magnitude higher than that above ground but total microbial diversity has not been fully documented in any system. Human activities reduce the diversity of species, resources and spatial heterogeneity through changes in land-use and the effects of pollutants but the functional importance of these changes are largely unknown. Processes dominated by a few species representing functional groups are at risk from the direct and indirect effects of human activities. Source/sink dynamics within systems buffer mineral element, trace gas and sediment fluxes. These processes become synchronized with increasing intensity of landuse and reduction of spatial heterogeneity. As a consequence the amplitude and periodicity of biogeochemical fluxes can override sinks within landscapes and result in net transfers between the atmosphere and adjacent systems which would otherwise

be accommodated within system boundaries. It is concluded that there is a high degree of uncertainty over the consequences of reducing biodiversity below ground to undefined threshold levels in any terrestrial systems.

## References

Aber, J.D., Nadelhoffer, K., Steudler, P. and Melillo, J.M. 1989. Nitrogen saturation in Northern forest ecosystems. *Bioscience* 39: 378–386.

Allen, L.H. 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. *Journal of Environmental Quality* 19: 15–34.

Anderson, J.M. 1978. Inter- and intra-habitat relationships between woodland *Cryptostigmata* species diversity and the diversity of soil and litter habitats. *Oecologia* 32: 341–346.

Anderson, J.M. 1988. Spatiotemporal effects of invertebrates on soil processes. *Biology and Fertility of Soils* 6: 216–227.

Anderson, J.M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications* 1: 326–347.

Anderson, J.M. 1994. Functional attributes of biodiversity in land use systems. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*. 267–290. CAB International, Wallingford.

Anderson, J.M. 1995. Soil organisms as engineers: microsite modulation of macroscale processes. In: Jones, C.G. and Lawton, J.H. (eds), *Linking Species to Ecosystems*. 94–106. Chapman and Hall, New York.

Atlas, R.M., Horowitz, A., Kritchevsky, M. and Bej, A.K. 1991. Response of microbial populations to environmental disturbance. *Microbial Ecology* 22: 249–256.

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising $CO_2$ levels. *Annual Review of Ecology and Systematics* 21: 167–196.

Bell, T.I.W. 1973. Erosion in Trinidad teak plantation. *Commonwealth Forestry Review* 52: 233–233.

Boardman, J. 1991. Land use, rainfall and erosion risk on the South Downs. *Soil Use and Management* 7: 34–38.

Brookes, P.C. and Verstraete, W. 1989. The functioning of soil as an ecosystem. *Soil Quality Assessment. State of the Art Report on Soil Quality*. Report to Commission of the European Communities Directorate-General DG XII. Contract EV4A/0008/NL, 41.

Clements, R.O., Murray, P.J. and Sturdt, R.G. 1991. The impact of 20 years' absence of earthworms and three levels of N fertilizer on a grassland soil environment. *Agriculture Ecosystems and Environment* 36: 75–85.

Crutzen, P.J. 1991. Methane's sinks and sources. *Nature* 350: 380–381.

Davis, R.C. 1981. Structure and function of two Antarctic terrestrial moss comm    .es. *Ecological Monographs* 51: 125–143.

Domsch, K.H., Jagnow, G. and Anderson, T.H. 1983. An ecological concept for the assessment of side effects of agrochemicals on soil microorganisms. *Residue Review* 86: 65–105.

Duxbury, J.M., Scott Smith, M. and Doran, J.W. 1989. Soil organic matter as a source and sink of plant nutrients. In: Coleman, D.C., Oades, J.M. and Uehara, G. (eds), *Tropical Soil Organic Matter*. 33–68. University of Hawaii Press, Hawaii.

Ehrlich, P.R. and Ehrlich, A.H. 1981. *Extinction. The causes and consequences of the disappearence of species*. Random House, New York.

Ehrlich, P.R. 1991. Population diversity and the future of ecosystems. *Science* 254: 175.

Elkins, N.Z., Sabol, G.V., Ward, T.J. and Whitford, W.G. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia* 68: 521–528.

Freckman, D.W. and Ettema, C.H. 1993. Assessing communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems and Environment* 45: 239–261.

Gilot, C., Lavelle, P., Kouassi, Ph. and Guillaume, G. 1992. Biological activity of soils in *Hevea* stands of different ages. *Acta Zoologica Fennica*.

Gregory, S.V., Swanson, F.J., McKee, W.A. and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *BioScience* 41: 540–550.

Groffman, P.M., Tiedje, J.M., Robertson, G.P. and Christiansen, S. 1987. In: Wilson, J.R. (ed.), *Advances in Nitrogen Cycling in Agricultural Systems*. 174–192. CAB International, Wallingford.

Hawksworth, D.L. 1992. In: Solbrig, O.T., van Emden, H.M. and van Oordt, P.G.W.J. (eds), *Biodiversity and Global Change*. 83–93. International Union of Biological Sciences, Paris.

Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P. and Groffman, P.M. 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36: 374–380.

Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W. and Parmelee, R.W. 1992. Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont, USA. *Soil Biology and Biochemistry* 24: 1357–1361.

Hutchinson, K.J. and King, K.L. 1980. The effects of sheep stocking level on invertebrate abundance, biomass and energy in a temperate, sown grassland. *Journal of Applied Ecology* 17: 369–387.

Hutsch, B.W., Webster, C.P. and Powlson, D.S. 1993. Long term effects of nitrogen fertilization on methane oxidation in soil of the Broadbalk wheat experiment. *Soil Biology and Biochemistry* 25: 1307–1315.

Ingham, E.R., Trofymow, J.A., Ames, R.N., Hunt, H.W., Morley, C.R., Moore, J.C. and Coleman, D.C. 1986. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. II. System responses to the removal of different groups of soil microbes or fauna. *Journal of Applied Ecology* 23: 615–630.

Intergovernmental Panel on Climate Change 1992. Houghton, J.T., Callander, B.A. and Varney, S.K. (eds), *Climate Change 1992: The supplementary report to the IPCC Scientific Assessment*.Cambridge University Press, Cambridge.

James, S.W. 1991. Soil nitrogen, phosphorus and organic matter processing by earthworms in tallgrass prairie. *Ecology* 72: 2101–2109.

James, S.W. 1992. Localised dynamics of earthworm populations in relation to bison dung in North American tallgrass prairie. *Soil Biology and Biochemistry* 24: 1471–1476.

Janeau, J.L. and Valentin, C. 1987. Relations entre des termitières Trinervitermes spp. et la surface du sol; réorganizations, ruissellment et erosion. *Revue Ecologie et de Biologie du Sol* 24: 637–647.

Jones, C.G. and Lawton, J.H. (ed.) 1995. *Linking Species and Ecosystems; Fifth Cary Conference, Millbrook, New York, May 8–12, 1993.* Chapman and Hall, New York.

King, G.M. and Adamsen, A.P.S. 1992. Effects of temperature on methane consumption in in a forest soil and in pure cultures of the methanotroph *Methylomomas rubra*. *Applied and Environmental Microbiology* 58: 2758–2763.

Klug, M.J. and Tiedje, J.M. 1994. Responses of microrganisms to changing environmental conditions; chemical and physiological approaches. In: Guerrero, R. and Pedros-Alio, C. (eds), *Trends in Microbial Ecology*, 371–378. Spanish Society for Microbiology, Barcelona.

Knight, D., Elliott, P.W. and Anderson, J. M. 1992. The role of earthworms in a managed, permanent pasture in South West England. *Soil Biology and Biochemistry* 24: 1511–1519.

Lal, R. 1994. Sustainable land use systems and soil resilience. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*, 41–67. CAB International, Wallingford.

Lavelle, P. 1988. Earthworm activities and the soil system. *Biology and Fertility of Soil* 6: 237–251.

Lavelle, P., Gilot, C., Fragoso, C. and Pashanasi, B. 1994. Soil fauna and sustainable land use in the humid tropics. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*, 291–300. CAB International, Wallingford.

Lavelle, P. and Pashanasi, B. 1989. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia* 33: 283–291.

Lee, K.E. 1985. *Earthworms: Their ecology and relationships with land use*. Academic Press, Sydney.

Lee, K.E. 1991. The diversity of soil organisms. In: Hawksworth, D.L. (ed.), *The Role of Biodiversity in Agricultural Systems*, 73–88. CAB International, Wallingford.

Mbakaya, B.S., Blackburn, W.H., Skovlin, J.M. and Child, R.D. 1988. Infiltration and sediment production of a bushed grassland as influenced by livestock grazing systems, Buchama, Kenya. *Tropical Agriculture* 65: 99–105.

McGrath, S.P., Brookes, P.C. and Giller, K.E. 1988. Effects of potentially toxic metals in soil derived from past applications of sewage sludge on nitrogen fixation by *Trifolium repens*. *Soil Biology and Biochemistry* 20: 415–424.

Moore, T., Roulet, N. and Knowles, R. 1990. Spatial and temporal variations of methane flux from sub-Arctic/northern boreal fens. *Global Biogeochemical Cycles* 4: 29–46.

Mosier, A.R., Schimel, D.S., Valentine, D., Bronson, K.F. and Parton, W.J. 1991. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature* 350: 330–332.

Oldeman, L.R. 1994. The global extent of soil degradation. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Land Use*, 99–118. CAB International, Wallingford.

Paoletti, M.G., Pimentel, D., Stinner, B.R. and Stinner, D. 1992. Agroecosystem biodiversity: matching production and conservation biology. *Agriculture, Ecosystems and Environment* 40: 3–23.

Papendick, R.I. 1994. Maintaining soil physical conditions. In:

Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*, 215–234, CAB International, Wallingford.

Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society America Journal* 51: 1194–1199.

Peterjohn, W.T. and Correll, D.L. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* 65: 1466–1475.

Rayner, A.D.M. and Boddy, L. 1988. *Fungal Decomposition of Wood; Its biology and ecology.* John Wiley, Chichester.

Ridge, E.H. 1976. Studies on soil fumigation. II. Effects on bacteria. *Soil Biology and Biochemistry* 8: 249–253.

Rosen, K., Gundersen, P., Tegnhammar, L., Johansson, M. and Frogner, T. 1992. Nitrogen enrichment of Nordic forest ecosystems. *Ambio* 21: 364–368.

Rovira, A.D. 1976. Studies on soil fumigation. I. Effects on ammonium, nitrate and phosphate in soil and on the growth, nutrition and yield of wheat. *Soil Biology and Biochemistry* 8: 241–247.

Schaefer, M. and Schauman, J. 1990. The soil fauna of a beech forests – comparison between a mull and moder soil. *Pedobiologia* 34: 299–314.

Spenser, T., Douglas, I, Greer, T. and Sinun, W. 1990. Vegetation and fluvial geomorphic processes in South East Asian Tropical rain forests. In: Thornes, J.B. (ed.), *Vegetation and Erosion*, 451–469. John Wiley, Chichester.

Steudler, P.A., Bowden, R.D., Melillo, J.M. and Aber, J.D. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. *Nature* 341: 314–316.

Swift, M.J. and Anderson, J.M. 1993. Biodiversity and ecosystem function. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 15–41. Springer-Verlag, Heidelberg.

Theng, B.K.G., Tate, K.R. and Sollins, P. 1989. Constituents of organic matter in temperate and tropical soils. In: Coleman, D.C., Oades, J.M. and Uehara, G. (eds), *Tropical Soil Organic Matter*, 5–32. University of Hawaii Press, Hawaii.

Torsvik, V., Goksoyr, J. and Daae, F.L. 1990. High diversity of DNS of soil bacteria. *Applied and Environmental Microbiology* 56: 782–787.

Van Hooff, P. 1982. Earthworm activity as a cause of splash erosion in a Luxembourg forest. *Geoderma* 31: 195–204.

Verhoef, H.A. and Brussaard, L. 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. *Biogeochemistry* 11: 175–211.

Vitousek, P.M. and Denslow, J.S. 1986. Nitrogen and phosphorus availability in tree fall gaps of a lowland forest. *Journal of Ecology* 74: 1167–1178.

Vitousek, P.M. and Hooper, D.U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 3–14. Springer-Verlag, Heidelberg.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., Matson, P.A. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802–804.

Whalen, S.C., Reeburgh, W.S. and Sanbeck, K.A. 1990. Rapid

methane oxidation in landfill cover soil. *Applied and Environmental Microbiology* **56**: 3405–3411.

Whalen, S.C. and Reeburgh, W.S. 1990. Consumption of atmospheric methane by tundra soils. *Nature* **346**: 160–162.

Wood, T.G. 1991. Termites in Ethiopia: the environmental implications of their damage and and resultant control measures. *Ambio* **20**: 136–138.

Wood, T.G., Johnson, R.A., and Ohiagu, C.E. 1977. Populations of termites (Isoptera) in natural and agricultural systems in southern Guinea savannah near Mokwa, Nigeria. *Geo Ecol Trop* **1**: 139–148.

World Resources Institute 1992–1993. *Towards Sustainable Development. A guide to the global environment.* WRI, Washington, DC.

### 6.2.3 Effects of biodiversity on water distribution and quality in ecosystems

#### 6.2.3.1 Introduction

Water is essential to all living organisms, and in turn the biosphere plays a crucial role in the transportation, transformation and redistribution of water on local and regional scales. In terrestrial ecosystems, vegetation plays the primary role in transferring water from the soil to the atmosphere; plants and animals also have significant effects on the movement of water into the soil. In terrestrial systems, living organisms often regulate the magnitude and rate of flow of water from one site to another; similar effects occur in some aquatic ecosystems. In both terrestrial and aquatic systems the biota can have measurable impacts on water quality (e.g. on composition of solutes, abundance and nature of particulates). Unfortunately there are few experimental studies exploring the links between biodiversity and water. Clearly, though, differences among organisms and communities in physiology, phenology and structure determine the type and magnitude of biotic effects. The text below summarizes some of the major influences of species and communities on water fluxes and water quality.

#### 6.2.3.2 Distribution of water

In terrestrial ecosystems, precipitation landing in one place is either evaporated again into the atmosphere, absorbed or infiltrated into the soil, or transferred by surface flow as runoff to another spot on the landscape. At the landscape scale, the types, relative abundances, and relative spatial locations of ecosystem types affect the amount of water moving from one point to another. For example, diverse land-use and management practices in water catchments in South Africa have been shown to affect stream-flow behaviour differently by altering runoff surface and water storage capacity in different ways (Braune and Wessels

1981). Conversion of vegetation within a watershed from forest or shrubland to grassland is known to have both short- and long-term effects on stream flow out of the watershed, in both temperate and tropical systems (Knight *et al.* 1985; Heimsath 1993); these effects could be due both to differences in the balance between infiltration and run-off, and to differences in the water use of the different communities (see discussion of evapotranspiration, below). In stream ecosystems, the presence of tree species can influence the rate of water flow with consequent effects on hydrology, sedimentation and stream channel structure (Graf 1978; Blackburn *et al.* 1982). Similarly, the presence of coral reefs offshore, and of estuarine or coastal vegetation, moderates the energy of water and reduces erosive action along shorelines (Walsh 1967; Twilley 1988). Lagoons within 'closed' coral atolls experience different water circulation, nutrient dynamics and productivity than do waters adjacent to 'open' reefs (Birkeland 1987).

Biodiversity at the scale of functional groups or species also plays an important role in determining the distribution and rate of movement of water. In terrestrial systems, differences in canopy and stem architecture among plants result in differences in the amount of precipitation intercepted, the proportion of precipitation converted to stem-flow, and the proportion of precipitation that infiltrates the soil rather than running off. For example, in arid lands a vegetative cover of shrubs has a very different effect from one of grasses: a semi-arid grassland has relatively homogeneous, complete capture of precipitation leading to shallow infiltration, while a shrubland has bare areas with high runoff interspersed with other areas where stem-flow leads to deep percolation (Schlesinger *et al.* 1990). Among woody species in semi-arid systems, differences in, for example, stem angle and leaf display lead to differences in the impact energy of precipitation (throughfall), and in infiltration rates, etc. (Nulsen *et al.* 1986; Wood *et al.* 1987; Navar and Bryan 1990). The movement of water through lotic (flowing) systems may also be affected by species differences. Water flow in streams moving through coniferous forests is more frequently slowed by large logs in the stream bed, with resulting influences on water chemistry, temperature and invertebrate communities (Bilby and Likens 1980), because of the slow decomposition of conifer wood relative to that of deciduous hardwood (Molles 1982). Other organisms redistribute moisture in even more subtle ways: Keeley and Swift assert that oaks on coastal slopes in Mediterranean climates act to collect fog and dew, which significantly increases water availability at the site. Even single animal species can affect water distribution: for example, the presence or absence of beavers in northern forest ecosystems creates extremely different distributions of surface waters (Naiman *et al.* 1994).

### 6.2.3.3 Groundwater fluxes

The movement of water from the atmosphere and shall' soil layers to deeper portions of the soil profile i important determinant of the structure and function of a terrestrial ecosystem, and also influences the 'loss' or leaching of nutrients from the surface layers of the soil. This flux to the groundwater, and removals from that groundwater which serve as sources of water elsewhere, is largely regulated at the functional group scale of plant diversity. Addition or removal of trees and phreatophytes (plants whose deep root systems reach the water table) has the capacity to alter the depth of the water table locally. For example, in Australia an introduced pathogen has killed trees and shrubs, reducing evapotranspiration and causing a rise in the water table (Shea *et al.* 1975). Deliberate removal of woody vegetation (to be replaced by seasonal agriculture) in Australia has resulted in a similar reduction of evapotranspiration, raising the water table, and salinization over large regions (McFarlane *et al.* 1993; Lyons *et al.* 1993). Reduced diversity of landscapes and of plant growth forms has reduced the systems' ability to absorb and buffer storms, so that peak flows after extreme precipitation events have increased (Nulsen *et al.* 1986; McFarlane *et al.* 1993). Species differences within a functional group can be significant: for example, the phreatophytic invader *Tamarix* has the ability to draw water from unsaturated alluvial soil, an ability missing in native phreatophytic trees of the southwestern USA (Busch *et al.* 1992). This difference affects the species' relative competitive abilities as well as their overall effect on soil and stream hydrology. Other examples of species' or functional group differences influencing flux to the groundwater come from the forestry and watershed management literature: for example, conversion of deciduous forest to conifers can reduce the flow of water to the groundwater (Schulze 1982), in part because interception of precipitation (and subsequent loss to evaporation) is greater (Swift *et al.* 1975). Hamilton and King (1983) reviewed the conflicting reports that changes in tropical forest cover did (or did not) alter groundwater percolation and streamflows.

Animal functional groups are important to groundwater fluxes as well: for example, the earthworms (which can be divided into different sub-groups by soil depth) are responsible for aeration and porosity in soils, which in turn affect the water storage capacity of the profile and the infiltration rates (Al Addan 1990; Joschko *et al.* 1992; Smettem 1992). Agricultural activities also have altered or reduced the soil macrofauna in many areas, changing the impacts of animals on the physical properties of soil profiles (including porosity; e.g. Abbott *et al.* 1979; Lobry de Bruyn 1990). In semi-arid and arid zones, where earthworms may be unimportant, termites and ants play a similar role (see Section 6.2.2). Plots of semi-desert where ants and termites had been removed have demonstrated 'ng-term decreases in infiltration and increases in runoff (Elkins *et al.* 1986; Whitford 1991).

### 6.2.3.4 Evapotranspiration

The transfer of water from the substrate to the atmosphere by vegetation is undoubtedly the single largest flux from biosphere to atmosphere (Schlesinger 1991). Carbon dioxide cannot be fixed into primary production without the loss of water molecules from the leaves of plants. At the functional group level, the phenology, root structure and physiology of plants have direct implications for the amount and timing of water transfer to the atmosphere via transpiration. For example, tilling and the resultant changes in *fynbos* vegetation (including a reduction of plant species diversity) resulted in greater moisture content in the soil during summer months (Davis 1992). Plant functional groups may influence water flux to the atmosphere even in aquatic systems. The presence of a surface aquatic macrophyte, the invasive water hyacinth, results in leafy cover over the lake surface, which decreases surface evaporation but greatly increases transpirational losses (due to the great surface area of mesophyll). The net balance between the two processes can alter water levels. In terrestrial systems, diversity of root morphology and depth (including the tendency of some species to form roots at or even above the soil surface) results in the extraction of soil moisture from different parts of the soil profile, and thus more complete exploitation of received precipitation (e.g., Patric 1961; Dodd *et al.* 1984; Knoop and Walker 1985; Sala *et al.* 1989; Golluscio and Sala 1993). Differences in the depth of rooting zones and thus of water use result in differences in the depth of carbonate deposition in arid land soils (Schlesinger *et al.* 1987). Diversity at the species level may also be important. Within a group of plants, individual species differ in their resistance to water loss, their efficiency of water uptake from the soil, and so on. Even genetic diversity can have measurable effects: in agricultural ecosystems, varietal differences in water use efficiency, stomatal resistance and the like are the focus of selection in some crop breeding programmes. Certainly at a landscape level, evaporation/transpiration from one ecosystem or patch can have an effect on microclimate (especially relative humidity) downwind. It has even been suggested that inputs of moisture by transpiration are significant enough to increase local probability of precipitation (Anthes 1984). Work in the Amazon Basin suggests that roughly half of local precipitation is derived from moisture transpired locally (the rest coming from oceanic air masses), and that forest vegetation also contributes by intercepting moisture that would not otherwise fall as precipitation; thus deforestation is expected to decrease local moisture availability considerably (Franken and Leopoldo 1984; Salati 1985).

Effects on the hydrological cycle may be indirect as well: climate models suggest that the effect of boreal forest in warming the soil (compared with bare soil or with tundra vegetation) regulates formation of permafrost, snow accumulation and persistence, and soil moisture (Bonan *et al.* 1992).

### 6.2.3.5 Filtration and assimilative capacity

Biological organisms also serve to alter water quality by performing various filtration, uptake or excretory processes, all of which affect the composition and concentration of various dissolved gases, solutes and particulates. Diversity at the landscape scale (that is, the types, relative abundances, and relative spatial locations of ecosystem types) affects the quality of water moving from one point to another. For example, the width of strips of native vegetation bordering a stream in an agricultural area will affect the sediment and nutrient loads in runoff reaching the stream (Peterjohn and Correll 1984), suggesting that the presence of belts of riparian vegetation in a largely agricultural landscape is important in limiting the eutrophying effects of agricultural runoff into freshwater ecosystems . Changes in landscape structure in dry tropical forest increase runoff, erosion and nutrient loss in runoff (Maass *et al.* 1988). Beaver activity determines the inundation of land in the Great Lakes region of North America, with consequent changes to nutrient cycling, sediment accretion, aeration and other properties of flowing water (Naiman *et al.* 1988). In shallow coastal marine areas, seagrass beds are known to serve as buffers, minimizing the sediment and nutrient loads that reach coral reefs from eutrophied waters (Ogden and Gladfelter 1983; Ogden 1988). Estuarine and floodplain vegetation is known to exert a strong influence on the chemical composition of water (e.g. Amazon River: Junk and Furch 1985; estuarine mangroves: Twilley 1988). At the level of functional groups and of species, a diversity of uptake mechanisms and metabolic pathways (in both plants and microbial assemblages) allows more complete and efficient processing of nutrients and pollutants. There is a burgeoning industry pursuing the use of wetland communities (both natural and 'constructed') for the treatment of water pollution (Tourbier and Pierson 1976). There is ample documentation of the effects of species-level differences on water quality in aquatic systems. For example, there were differences among tree species and among nutrients for the uptake of N and P from waste water 'processed' by cypress swamps in Florida (Ewel and Odum 1986), and the presence of floating macrophytes was an important additive effect. Introductions of non-native macrophytes can affect lake chemistry significantly (Lodge *et al.* 1988) Differences among species of mangroves result in differences in the decomposition of organic matter and thus shifts in the balance between particulate organic carbon and

dissolved organic carbon (Boto and Bunt 1981; Snedaker 1989). On a smaller scale, *Sphagnum* mosses are known for their ability to pump cations from surrounding water, thus regulating water pH and quality (Hutchinson 1975). Species effects may be significant in terrestrial systems too; where pollution has altered the abundance or the composition of trees, forested ecosystems have exhibited alterations of groundwater quality (Schulze *et al.* 1989; Last and Watling 1991).

### 6.2.3.6 Trophic cascades and other biotic influences on water quality

Consumption and trophic patterns of primary consumers and secondary consumers also represent the influences of biodiversity at the functional group/species level. In lakes without fishery exploitation, the fish assemblage will be dominated by large individuals; smaller, zooplanktivorous fish will be strongly regulated by predation. Then predation on zooplankton is light; these attain high densities and effectively regulate phytoplankton. With heavy fishery exploitation, though, the fish community becomes dominated by smaller individuals with varying levels of zooplanktivory. The net result is an increase in algal biomass, sometimes causing blooms and water quality problems (Carpenter *et al.* 1985; Carpenter and Kitchell 1993). A similar story involves the introduction of Nile Perch to Lake Victoria, resulting in the elimination of many native cichlid fishes, a disruption of local fishery patterns, an increase in algal blooms, and eventually increased erosion from surrounding landscapes due to altered patterns of fuelwood consumption for drying the larger fish (Ogutu-Ohwayo 1990; Witte *et al.* 1992). The composition of the fish community ultimately determines whether the system's productivity is limited by nitrogen or by phosphorus (Elser *et al.* 1988; Carpenter and Kitchell 1993).

Human activity (particularly nutrient enrichment) has apparently increased the incidence of toxic blooms of algae (e.g. red tides, flagellate outbreaks) in shallow seas. These species-level effects in turn have dramatic effects on water quality and on fisheries (higher trophic levels), as well as on the shellfish industry (Smayda 1990, 1992). Another example of a species-level impact is the invasion of zebra mussels into North American lakes and rivers, where the rapid population growth of this filter-feeding mollusc has affected food particle density and the abundance and diversity of native filter-feeding organisms (Nalepa and Schloesser 1992).

### 6.2.3.7 Summary and implications

Because of the great magnitude of the transpiration flux through vegetation, and because of the diversity of plant physiology and water use, changes in the diversity of vegetation at almost any scale can have dramatic effects on

the rate of movement of water from the soil into the atmosphere (with resulting impacts on soil and atmospheric water content). Diversity of the biota at the functional group level can also have significant impacts on the movement of water in the opposite direction, into the soil. And because water availability is such a basic constraint to primary productivity and other facets of ecosystem functioning, considerations of potential impacts should accompany any actions that could have the effect of altering vegetative cover or soil macro-organisms. In aquatic systems, organisms affect water quality more than distribution (although there are biotic influences on the hydrology and geomorphology of streams). In most cases a greater diversity of biological organisms leads to a higher water quality, as perceived by humans, and in this sense aquatic biota (from microbes to fish and macrophytes) perform valuable ecosystem services. While the appropriate comparisons have not yet been made, current understanding allows several predictions about the relative impact of biodiversity alterations on water distribution and quality in different ecosystem types:

- Effects of biodiversity changes on local water distribution are predicted to be greatest in arid and semi-arid systems, for several reasons: the low availability of water in general, the large effects of organisms in regulating infiltration and surface flow, and the relatively low diversity of functional groups and of species within functional groups. Similarly, the magnitude of biodiversity effects on water flow in aquatic systems will probably be in inverse proportion to the magnitude of water flow itself (i.e. greater in small streams than in large open-water seas).

- Biodiversity effects on groundwater flux (especially the presence or absence of phreatophytes in the vegetation) are predicted to be important in almost any terrestrial system where precipitation exceeds potential evapotranspiration and there is significant flow of water from the soil profile into the groundwater.

- Biodiversity effects on evapotranspiration at the landscape scale are probably more dependent on geography than on biome type. That is, the effects are predicted to be most significant where (1) climate allows the development of sufficient vegetation to maintain high rates of transpiration, and (2) regional geography results in local moisture supply being significant in relation to moisture transported by air masses from distant regions.

- An important question to be addressed is whether water quality is most affected by biodiversity where biomass (or some other index of the rate of biological

activity) is high relative to the volume of water. That is, one might argue that the chemistry of water in a large lake will be less sensitive to changes in biodiversity than in a small pond, or in the soil solution of a well-developed forest.

In summary, there is strong evidence that biological diversity at the level of functional groups has significant effects on major fluxes in the hydrological cycle (infiltration, percolation to the groundwater, evapotranspiration), with the magnitude of the flux usually being positively related to the number of functional groups represented. It is, however, premature to draw conclusions about the effects of different numbers of species within functional groups. Species-level differences in physiology can be more directly related to differences in their effects on water quality (which can be either positive or negative). We conclude that biological diversity plays a substantial role in the ecosystem services of water supply and filtration, so critical to human welfare.

## References

Abbott, I., Parker, C.A., and Sills, I.D. 1979. Changes in abundance of large soil animals and physical properties of soils following cultivation. *Australian Journal of Soil Research* **17**: 343–353.

Al Addan, F. 1990. Biophysique du sol. Etude Quantitative de la Regulation, par le Travail Lombricien, des Propriétés Structurales en Milieu Mediterranéen. PhD, USTL, Montpellier.

Anthes, R.A. 1984. Enhancement of convective precipitation by mesoscale variations in vegetative covering in semiarid regions. *Journal of Climatology and Applied Meteorology* **23**: 541–554.

Bilby, R.E. and Likens, G.E. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* **61**: 1107–1113.

Birkeland, C. (ed.) 1987. Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity. *UNESCO Reports in Marine Science* **46**.

Blackburn, W.H., Knight, R.W. and Schuster, J.L. 1982. Saltcedar influence on sedimentation in the Brazos River. *Journal of Soil and Water Conservation* **37**: 298–301.

Bonan, G.B., Pollard, D. and Thompson, S.L. 1992. Effects of boreal forest vegetation on global climate. *Nature* **359**: 716–718.

Boto, K.G. and Bunt, J.S. 1981. Tidal export of particulate organic matter from a Northern Australian mangrove system. *Estuarine, Coastal and Shelf Science* **13**: 247–250.

Braune, E. and Wessels, H.P.P. 1981. Effects of landuse on runoff from catchments and yield from present and future storage. In: Maaron, H. (ed.), *Workshop on the effect of rural land use and catchment management on water resources.* Department of Water Affairs, Pretoria **113**: 133–187.

Busch, D.E., Ingraham, N.L. and Smith, S.D. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecological Applications* **2**: 450–459.

Carpenter, S.R., Kitchell, J.F. and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

Carpenter, S.R. and Kitchell, J.F. (eds) 1993. The Trophic Cascade in Lakes. Cambridge University Press, Cambridge.

Davis, G.W. 1992. Effects of tillage on heathland soil: disturbance of a natural mountain fynbos system in the southwestern Cape, South Africa. Soil and Tillage Research 24: 29–45.

Dodd, J., Heddle, E.M., Pate, J.S. and Dixon, K.W. 1984. Rooting patterns of sandplain plants and their functional significance. In: Pate, J.S. and Beard, J.S. (eds), Kwongan: Plant life of the sandplain. 146–177. University of Western Australia Press, Nedlands.

Elkins, N.Z., Sabol, G.V., Ward,T.J. and Whitford, W.G. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. Oecologia 68: 521–528.

Elser, J.J., Elser, M.M., MacKay, N.A., and Carpenter, S.R. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. Limnology and Oceanography 33: 1–14.

Ewel, K.C. and Odum, H.T. (eds) 1986. Cypress Swamps. University Presses of Florida, Gainesville.

Franken, W. and Leopoldo, P.R. 1984. Hydrology of catchment areas of Central-Amazonian forest streams. In: Sioli, H. (ed.), The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin. 501–519. Dr W. Junk, Dordrecht.

Golluscio, R.A. and Sala, O.E. 1993. Plant functional types and ecological strategies in Patagonian forbs. Journal of Vegetation Science 4: 839–846.

Graf, W.L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin 89: 1491–1501.

Hamilton, L.S. and King, P.N. 1983. Tropical Forested Watersheds: Hydrologic and soils response to major uses or conversions. Westview Press, Boulder, Colorado.

Heimsath, A.M. 1993. A comparison of streamflow from agricultural and forested watersheds in the Middle Hills, Nepal. Tropical Resources Institute News 12: 14–17.

Hutchinson, G.E. 1975. A Treatise on Limnology. Vol. III, Limnological Botany. John Wiley, New York.

Joschko, M., Sochtig, W. and Larink, O. 1992. Functional relationship between earthworm burrows and soil water movement in column experiments. Soil Biology and Biochemistry 24: 1545–1543.

Junk, W.J. and Furch, K. 1985. The physical and chemical properties of Amazonian waters and their relationships with the biota. In: Prance, G.T. and Lovejoy, T.E. (eds), Amazonia. Key Environments Series. 3–17. Pergamon Press, Oxford.

Keeley, J.E. and Swift, CC. 1995. Biodiversity and ecosystem functioning in mediterranean-climate California. In: Davis, G.W. and Richardson, D.M. (eds), Mediterranean-type Ecosystems: Functions of biodiversity. Ecological Studies Series. Springer-Verlag, Heidelberg.

Knight, D.H., Fahey, T.J. and Running, S.W. 1985. Water and nutrient outflow from contrasting lodgepole pine forests in Wyoming. Ecological Monographs 55: 29–48.

Knoop, W.T. and Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a Southern African savannah. Journal of Ecology 73: 235–253.

Last, F.T. and Watling, R. 1991. Acid Deposition: Its nature and impacts. The Royal Society of Edinburgh.

Lobry de Bruyn, L.A. 1990. The role of ants and termites in modifying soil properties in naturally vegetated and agricultural environments. PhD dissertation, University of Western Australia, Nedlands.

Lodge, D.M., Barko, J.W., Strayer, D., Melack, J.M., Mittelbach, G.G., Howarth, R.W., Menge, B. and Titus, J.E. 1988. Spatial heterogeneity and habitat interactions in lake communities. In: Carpenter, S.R. (ed.), Complex Interactions in Lake Communities. 181–208. Springer-Verlag, New York.

Lyons, T.J., Schwerdtfeger, P., Hacker, J.M., Foster, I.J., Smith, R.C.G. and Xinmei, H. 1993. Land-atmosphere interaction in a semiarid region: the bunny fence experiment. Bulletin of the American Meteorological Society 74: 1327–1334.

McFarlane, D.J., George, R.J. and Farrington, P. 1993. Changes in the hydrological cycle. In: Hobbs, R.J. and Saunders, D.A. (eds). Reintegrating Fragmented Landscapes: Towards sustainable production and nature conservation. 146–186. Springer-Verlag, New York.

Maass, J.M., Jordan, C. and Sarukhán, J. 1988. Soil erosion and nutrient losses in seasonal tropical agroecosystems under various management techniques. Journal of Applied Ecology 25: 595–607.

Molles, M.C. Jr 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology 63: 1–6.

Naiman, R.J., Johnston, C.A. and Kelley, J.C. 1988. Alteration of North American streams by beaver. BioScience 38: 753–763.

Naiman, R.J., Pinay, G., Johnston, C.A. and Pastor, J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75: 905–921.

Nalepa, T.F. and Schloesser, D.W. 1992. Zebra Mussels: Biology, impacts, and control. Lewis Publishers, Boca Raton, Fla.

Navar, J. and Bryan, R. 1990. Interception loss and rainfall redistribution by three semi-arid growing shrubs in northeastern Mexico. Journal of Hydrology 115: 51–63.

Nulsen, R.A., Bligh, K.J., Baxter, I.N., Solin, E.J. and Imrie, D.H. 1986. The fate of rainfall in a mallee and heath vegetated catchment in southern Western Australia. Australian Journal of Ecology 11: 361–371.

Ogden, J.C. 1988. The influence of adjacent systems on the structure and function of coral reefs. Proceedings of the 6th International Coral Reef Symposium 1: 123–129.

Ogden, J.C. and Gladfelter, E.H. (eds). 1983. Coral reefs, seagrass beds and mangroves: their interactions in the coastal zones of the Caribbean. UNESCO Reprints in Marine Science 23.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. Environmental Biology of Fishes 27: 81–96.

Patric, J.H. 1961. The San Dimas large lysimeters. Journal of Soil and Water Conservation 16: 13–17.

Peterjohn, W.T. and Correll, D.L. 1984. Nutrient dynamics in an

agricultural watershed: observations on the role of a riparian forest. *Ecology* 65: 1466–1475.

Sala, O.E., Golluscio, R.A., Lauenroth, W.K., and Soriano, A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81: 501–505.

Salati, E. 1985. The climatology and hydrology of Amazonia. In: Prance, G.T. and Lovejoy, T.E. (eds), *Amazonia, Key Environments* series. 18–48. Pergamon Press, Oxford.

Schlesinger, W.H. 1991. *Biogeochemistry: An analysis of global change.* Academic Press, San Diego.

Schlesinger, W.H., Fonteyn, P.J. and Marion, G.M. 1987. Soil moisture content and plant transpiration in the Chihuahuan desert of New Mexico. *Journal of Arid Environments* 12: 119–126.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043–1048.

Schulze, E.-D. 1982. Plant life forms as related to plant carbon, water and nutrient relations. In: Lange, O.L., Nobel, P.S., Osmond, C.B., and Ziegler, H. (eds), *Encyclopedia of Plant Physiology. Physiological Plant Ecology.* Vol. 12B, *Water relations and photosynthetic productivity.* 615–676. Heidelberg, Berlin.

Schulze, E.-D., de Vries, W., Hauhs, M., Rosen, K., Rasmussen, L., Tamm, C.O. and Nilsson, J. 1989. Critical loads for nitrogen deposition on forest ecosystems. *Water, Air and Soil Pollution* 48: 451–456.

Shea, S.R. Hatch, A.B., Havel, J.J. and Ritson, P. 1975. The effect of changes in forest structure and composition on water quality and yield from the northern Jarrah forest. *Proceedings of the Ecological Society of Australia* 9: 58–73.

Smayda, T.J. 1990. Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: Granéli, E., Sundström, B., Edler, L. and Anderson, D.M. (eds), *Toxic Marine Phytoplankton.* 29–40. Elsevier, New York.

Smayda, T.J. 1992. Global epidemic of noxious phytoplankton blooms and food chain consequences in large ecosystems. In: Sherman, K., Alexander, L.M. and Gold, B.D. (eds), *Food Chains, Yields, Models, and Management of Large Marine Ecosystems.* 275–307. Westview Press, Boulder, Colorado.

Smettem, K.R.J. 1992. The relation of earthworms to soil hydraulic properties. *Soil Biology and Biochemistry* 24: 1539–1543.

Snedaker, S.C. 1989. Overview of ecology of mangroves and information needs for Florida Bay. *Bulletin of Marine Science* 44: 341–347.

Swift, L.W., Swank, W.T., Mankin, J.B., Luxmoore, R.J., and Goldstein, R.A. 1975. Simulation of evapotranspiration and drainage from mature and clearcut deciduous forests and young pine plantations. *Water Resources Research* 11: 667–673.

Tourbier, J. and Pierson P.W. Jr, (eds). 1976. *Biological Control of Water Pollution.* University of Pennsylvania Press, Philadelphia.

Twilley, R.R. 1988. Coupling of mangroves to the productivity of estuarine and coastal waters. In: Jansson, B.O. (ed.) *Coastal-Offshore Ecosystem Interactions.* 155–180. Springer-Verlag, Berlin.

Walsh, G.E. 1967. An ecological study of a Hawaiian mangrove swamp. In: Lauff, G.H. (ed.), *Estuaries.* 420–431. AAAS Press, Washington, DC.

Whitford, W.G. 1991. Subterranean termites and long-term productivity of desert rangelands. *Sociobiology* 19: 235–243.

Witte, D., Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., Oijen, M.J.P. and Wanink, J.H. 1992. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology* 42: 214–232.

Wood, J.C., Wood, M.K. and Tromble, J.M. 1987. Important factors influencing water infiltration and sediment production on arid lands in New Mexico. *Journal of Arid Environments* 12: 111–118.

## 6.2.4 Atmospheric feedbacks

### 6.2.4.1 Introduction

The biosphere interacts with the atmosphere in various ways with respect to biodiversity and ecosystem functioning. As a source of atmospheric constituents the biosphere contributes significantly to the chemical composition of the atmosphere and thus has a strong influence on important atmospheric properties and, hence, on climate. Vice versa, changes of climate will have a strong feedback on ecosystem functioning and biodiversity, and thereby will influence biogenic emissions. Biogenic emissions of atmospheric constituents may be entirely dependent on a few species or a single functional group of species. As a consequence, particular ecosystem functions constitute a high environmental risk; minor changes in species composition will produce a direct feedback on atmospheric properties, which will then affect other aspects of ecosystem functioning and biodiversity. The term 'biodiversity risk' is used here for this pattern of biosphere/atmosphere interaction. As the biosphere is also the most important sink for numerous atmospheric constituents, the flux of injurious compounds from the atmosphere to the biosphere can reduce biodiversity and impair essential ecosystem functioning, which may then feed back into the atmosphere. The following text summarizes the biosphere/atmosphere interactions that can affect biodiversity and ecosystem functioning and/or constitute a high biodiversity risk.

### 6.2.4.2 Biogenic emissions and atmospheric properties

The biosphere is the most important source of several atmospheric trace constituents, including dimethylsulphide (DMS), carbonylsulphide (COS), methane ($CH_4$) and nitrous oxide ($N_2O$), as well as non-methane hydrocarbons such as terpenes and isoprene (Table 6.2-1). DMS is the major biogenic sulphur compound emitted by planktonic algae in marine environments (Barnard *et al.* 1982; Bates *et al.* 1987). In the atmosphere DMS is rapidly oxidized by OH radicals to form sulphate aerosols (Graedel 1979; Niki *et al.* 1983) which are the most important source of cloud

condensation nuclei (CCN) in the marine atmosphere and thus have a strong influence on the type and abundance of clouds over the oceans (Charlson et al. 1987). Since the growth of planktonic algae is highly dependent on environmental conditions, DMS emissions from the open oceans are considered a regulatory factor of the climate that can feed back on biodiversity and ecosystem functioning. Although many marine algae contain and release significant amounts of DMS (Keller et al. 1989), high rates of production and emission are restricted to a few classes of marine phytoplankton (mainly Dinophyceae and Prymnesiophyceae). As a consequence, high DMS concentrations in marine water ('hot spots') are superimposed on relatively constant concentration levels of 1–3 nM and result from blooms of certain species, e.g. *Phaeocystis poucheti* (Bates et al. 1987; Berresheim et al. 1989; Saltzman and Cooper 1989). Therefore, DMS emissions and, hence, CCN formation over the open oceans constitute a high biodiversity risk. DMS is also emitted from terrestrial ecosystems (Rennnenberg 1991); however, it will not have a significant impact on cloud formation over the continents because of the high CCN formation by the oxidation of sulphur dioxide ($SO_2$) emitted by fossil fuel burning (Schwartz 1988; Wigley 1989).

The relatively long-lived biogenic sulphur compound COS and its atmospheric precursor $CS_2$ (Jones et al. 1983;

Hynes and Wine, 1989) represent the major sources of sulphur in the stratosphere (Crutzen 1976; Lazrus and Gandrun 1977; Inn et al. 1979; Khalil and Rasmussen 1984; Hofman 1990). Oxidation of COS in the stratosphere results in the production of sulphate aerosols (Lazrus and Gandrun 1977), which influence the Earth's radiation budget by scattering sunlight back into space and interfere with stratospheric ozone (Hofman 1990). Therefore, biogenic emission of COS and $CS_2$ contributes to climate as well as to the intensity and spatial distribution of UV-B radiation reaching the Earth's surface (Charlson et al. 1987) which will feed back on biodiversity and ecosystem functioning. In marine environments, COS and $CS_2$ emission is dominated by coastal environments that are considered highly vulnerable to anthropogenic disturbance (Aneja et al. 1979). Emission of COS from terrestrial ecosystems seems to be restricted to bare soils. COS released from vegetated soils is rapidly taken up and metabolized by vegetation and thus does not reach the atmosphere (Rennenberg 1991). Recent requirements for sulphur fertilization in agroecosystems due to the prolonged use of low-sulphur fertilizers, and the increasing cultivation of high-sulphur crops such as rape, may be linked to increasing biogenic emissions of COS (Hofman 1990) which now constitute a significant biodiversity risk.

Next to $CO_2$, $CH_4$ is presently thought to be the most

Table 6.2-1: Biogenic emissions affecting atmospheric properties.[1]

| Biome | DMS[2] | COS[3] | $CH_4$[4] | $N_2O$[5] | Terpenes[6] | Isoprene[6] |
|---|---|---|---|---|---|---|
| Mediterranean-type | | | + | | +++ | ++ |
| Tropical forest | | | + | | ++ | ++ |
| Savannahs | | | + | | | |
| Arctic alpine | | | ++ | | ++ | ? |
| Coral reefs | | | | | | |
| Islands | | | | | | |
| Coastal systems | + | +++ | | | | |
| Temperate forest | | | | ++ | ++ | ++ |
| Temperate grasslands | | | +++ | | | |
| Agroecosystems | | ++ | +++ | ++ | | |
| Lakes and rivers | | | | | | |
| Open ocean | +++ | | | | | |
| Boreal forests | | | ++ | | ++ | ++ |
| Estuaries, lagoons and mangroves | + | +++ | | | | |

1. The number of (+) indicates differences in the source strength of biomes for individual trace gases.
2. Barnard et al. 1982; Bates et al. 1987; Keller et al. 1989; Berresheim et al. 1989; Saltzman and Cooper 1989;
3. Aneja et al. 1979; Rennenberg 1991;
4. Heyer 1990; Schutz et al. 1991; Green 1992; Wassmann et al. 1993;
5. Papen and Rennenberg 1990; Bouwman et al. 1993; Papen et al. 1993;
6. Monson et al. 1991; Tingey et al. 1991.

important greenhouse gas (IPCC 1992) and is released into the atmosphere predominantly from biogenic sources (IPCC 1992). Biogenic $CH_4$ production is mediated by a single functional group of approximately 100 species of bacteria that require strictly anaerobic conditions (Heyer 1990). Therefore, biogenic $CH_4$ emission is restricted to anaerobic environments, i.e. natural and human-made wetlands such as rice paddy fields and the digestive tracts of ruminants and termites (IPCC 1992). Many other biomes may become transient sources of atmospheric $CH_4$ when temporarily flooded. The actual amount of methane emitted is not only dependent on $CH_4$ production, but also on $CH_4$ oxidation in aerobic zones of the corresponding environment: $CH_4$ oxidation by methylotrophic bacteria, a functional group of approximately 25 species (Green 1992), may consume as much as 80% of the $CH_4$ produced (Wassmann *et al.* 1993). In vegetated wetland soils, $CH_4$ is released into the atmosphere mainly via transport through the aerenchyma of the plants which may provide resistance to the $CH_4$ flux (Schutz *et al.* 1991). Thus, $CH_4$ emission from wetlands is determined by the balance of microbial populations and their interaction with vegetation. Because of the low number of species involved, this balance is highly vulnerable to disturbance at the ecosystem functioning and landscape diversity level.

Another important greenhouse gas is $N_2O$. It is accumulating in the atmosphere at an increasing rate (IPCC 1992) and may therefore become even more important in the future. Global $N_2O$ production has almost doubled within the last 100 years by anthropogenic activities, and because of the long (150-year) residence time of $N_2O$ in the atmosphere, the atmospheric $N_2O$ concentration will only stabilize in about 250 years from now, even if $N_2O$ production were to be maintained at the present level. As for $CH_4$, a major part of the atmospheric $N_2O$ is of biogenic origin (IPCC 1992): it is produced in aerobic soils by chemolithotrophic and heterotrophic nitrification and in anaerobic soils by denitrification (Papen and Rennenberg 1990; Bouwman *et al.* 1993), but may also originate from other processes so far not identified (Papen *et al.* 1993). As $N_2O$ emission is dependent on the availability of substrates for these processes, biomes that are exposed to high loads of nitrogen by direct application of N-fertilizer (e.g. agroecosystems) or by its incidental input through the atmosphere via dry and wet deposition (e.g. temperate forests) are major sources of biogenic $N_2O$ (IPCC 1992; Papen *et al.* 1993). In addition to interfering with ecosystem functioning and biodiversity by climate forcing, $N_2O$ emission also constitutes a biodiversity risk, as chemolithotrophic nitrification is restricted to a small number of microbial species (Papen and Rennenberg 1990).

Volatile organic compounds, especially terpenes and isoprene, are produced and released into the atmosphere by a large number of plant species (Monson *et al.* 1991; Tingey *et al.* 1991), especially by woody plants including Mediterranean shrubs, eucalypts and conifers which determine particular landscape patterns in several biomes (Table 6.2-1). This heterogeneous group of volatile compounds affects the chemical composition of the atmosphere by controlling the oxidation capacity of the troposphere (Chameides *et al.* 1988). Changes in the photo-oxidation capacity of the atmosphere will influence the abundance and the distribution of other radiative trace constituents such as ozone. Apparently, terpene emissions are dominated by *Pinus* species which constitute a functional group for the emission of these atmospheric trace gases (Tingey *et al.* 1991).

### 6.2.4.3 Fluxes of atmospheric constituents into the biosphere

The biosphere is not only a source, but also a sink of radiatively active trace gases and atmospheric pollutants. Depositions of atmospheric sulphur and nitrogen compounds of anthropogenic origin severely affect biodiversity and ecosystem functioning in temperate and boreal forests and grasslands, as well as in lakes and rivers, by acidifying of water and soils and unbalancing nitrogen and sulphur nutrition (Lauenroth and Preston 1984; Reuss and Johnson 1986; Schulze *et al.* 1989; Wellburn 1990; Pearson and Stewart 1993; Rennenberg and Polle 1994). In particular, the diversity and abundance of ectomycorrhizal fungi and lichens can be reduced in the presence of atmospheric sulphur and nitrogen compounds (Kozlowski 1985; McCool 1987). Air pollution by photochemical oxidants can cause severe species-specific damage in agroecosystems and horticulture (Guderian *et al.* 1985). Deposition of atmospheric pollutants also affects the diversity and functioning of microbial populations in the soil and, as a consequence, changes interactions between the soil and the atmosphere as feedback reactions. Acidification of forest soils eliminates chemolithotrophic nitrification, a significant source of atmospheric $N_2O$ (Johnsrud 1978; Papen *et al.* 1993). Nitrogen input into forest soils reduces the oxidation of atmospheric methane and, thus, the sink strength of forest soils for this radiatively active trace gas (Keller *et al.* 1983; Steudler *et al.* 1989).

### 6.2.4.4 Climate change and biosphere/atmosphere interactions at the level of biodiversity and ecosystem functioning

The depletion of stratospheric ozone with the consequence of increasing UV-B radiation and the increase in radiatively active trace gases in the atmosphere with the consequence of global warming are considered to be the most important changes in climate presently occurring (German Bundestag 1989). Increasing UV-B radiation will have direct effects

on biosphere/atmosphere interactions at the level of biodiversity and ecosystem functioning. Impairment of photosynthesis, nitrogen metabolism and orientation of marine phytoplankton by enhanced UV-B radiation (Tevini 1994) may affect DMS emission into the marine atmosphere, and hence CCN formation, an important factor in the global climate. In particular, the generation of hotspots of DMS emission connected with the blooming of a few classes of marine phytoplankton may be a sensitive process. Changes in marine phytoplankton will also affect marine food chains and thus the vertical flux of atmospheric $CO_2$ into the deep ocean layers (biogenic $CO_2$ pump). This will in turn have a severe impact on the atmospheric $CO_2$ concentration, and hence on climate. In terrestrial ecosystems, increasing UV-B radiation may affect not only biogenic emission from sensitive vegetation (Tevini 1994), but also the production and emission of radiatively active trace gases by nitrification in the upper soil (Hooper and Terry 1974; Endo *et al.* 1986). As biogenic emissions are temperature-dependent processes, global warming is expected generally to increase the biogenic production of atmospheric trace constituents, which will cause a significant negative feedback on global warming. Species-specific responses and interactions with ecosystem functioning have to be expected as a direct consequence of elevated atmospheric $CO_2$. Functional studies and model estimations indicate that changes in growth rates and biomass production due to elevated $CO_2$ levels are dependent on environmental factors such as nutrient supply and climate and differ between species (Jarvis 1989; Mooney *et al.* 1991; Woodward *et al.* 1991; Bazzaz and Fajer 1992; Gilford 1992; Bowes 1993; Korner 1993). These factors will also affect ecosystem functioning at increasing atmospheric $CO_2$ concentrations and, hence, the sink and source strength of the biosphere for atmospheric trace constituents.

### 6.2.4.5 Conclusions and management implications

The biosphere is an essential factor in determining the budget, abundance and distribution of the most important environmentally relevant trace gases in the atmosphere. As these atmospheric constituents play a central role in global climate, changes in the source or sink strength of the biosphere will strongly affect biodiversity and ecosystem functioning. In addition, the emission of atmospheric trace gases by, and their deposition in, the biosphere is itself an important ecosystem function, highly dependent on biodiversity. The prevention of changes in ecosystem functioning and biodiversity that will affect the composition of the atmosphere is likely to be one of the most important environmental policy issues of the immediate future. To support policy decisions in this direction, intensive research is required on biosphere/atmosphere exchange processes and their interaction with ecosystem functioning and biodiversity. Studies on soil microbial/atmosphere interactions may be of particular significance in this respect.

## References

Aneja, V.P., Overton, J.H., Cupitt, L.T., Durham, L.J. and Wilson, L.E. 1979. Carbon disulphide and carbonyl sulphide from biogenic sources and their contribution to the global sulphur cycle. *Nature* 282: 493–496.

Barnard, W.R., Andreae, M.O., Watkins, W.E., Bingemer, H. and Georgii, H.W. 1982. The flux of dimethylsulfide from the oceans to the atmosphere. *Journal of Geophysical Research* 87: 8787–8793.

Bates, T.S., Cline, J.D., Gammon, R.H. and Kelley-Hansen, S.R. 1987. Regional and seasonal variations in the flux of oceanic dimethylsulfide to the atmosphere. *Journal of Geophysical Research* 92: 2930–2938.

Bazzaz, F.A. and Fajer, E.D. 1992. Plant life in a $CO_2$-rich world. *Scientific American* 266: 68–74.

Berreshein, H., Andreae, M.O., Ayers, G.P. and Gillet, R.W. 1989. Distribution of biogenic sulfur compounds in the remote southern hemisphere. In: Saltzman, E.S. and Cooper, W. J. (eds), *Biogenic Sulfur in the Environment*, 352–366. American Chemical Society, Washington, DC.

Bouwman, A.F., Fung, I., Matthews, E. and John, J. 1993. Global analysis of the potential for $N_2O$ production in natural soils. *Global Biogeochemical Cycles* 7: 557–597.

Bowes, G. 1993. Facing the inevitable: plants and increasing atmospheric $CO_2$. *Annual Review of Plant Physiology and Plant Molecular Biology* 44: 309–332.

Chameides, W.L., Lindsay, R.W., Richardson, J. and Kiang, C.S. 1988. The role of biogenic hydrocarbons in urban photochemical smog: Atlanta as a case study. *Science* 241: 1473–1475.

Charlson, R.J., Lovelock, J.E., Andreae, M.O. and Warren, S.G. 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326: 655–661.

Crutzen, P.J. 1976. The possible importance of COS for the sulfate layer of the stratosphere. *Geophysical Research Letters* 3: 73–76.

Endo, M., Minami, K., and Fukushi S 1986. Effects of the interception of near ultraviolet radiation on nitrifier activity and nitrification process in a fertilized andosol under field conditions. *Soil Science Plant Nutrition* 32: 365–372.

German Bundestag 1989. *Protecting the Earth Atmosphere. An International Challenge*. Universitäts-Buchdruckerei, Bonn.

Gifford, R.M. 1992. Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: implications for the global carbon cycle. *Advances in Bioclimatology* 1: 24–58.

Graedel, T.E. 1979. Reduced sulfur emission from the open oceans. *Geophysical Research Letters* 6: 329–331.

Green, P.N. 1992. Taxonomy of methylotrophic bacteria. In: Murrell, J. C. and Dalton, H. (eds), *Methane and Methanol Utilizers*, 23–84.

Guderian, R., Tingey, T.D. and Rabe, R. 1985. Effects of

photochemical oxidants on plants. In: Guedrian, R. (ed.) *Air Pollution by Photochemical Oxidants*. 129–296. Springer-Verlag, Berlin.

Heyer, J. 1990. *Der Kreislauf des Methans*. Akademie-Verlag, Berlin.

Hofman, D.J. 1990. Increase in stratospheric background of sulfuric acid aerosol mass in the past 10 years. *Science* **248**: 996–1000.

Hooper, A.B. and Terry, K.R. 1974. Photoinactivation of ammonium oxidation in *Nitrosomonas*. *Journal of Bacteriology* **119**: 899–906.

Hynes, A.J. and Wine, P.H. 1989. OH-initiated oxidation of biogenic sulfur compounds: kinetics and mechanisms under atmospheric conditions. In: Satzman, E.S. and Cooper, W.J. (eds), *Biogenic Sulfur in the Environment*. 424–436. American Chemical Society, Washington, DC.

Inn, E.C.Y., Vedder, J.F. and Tyson, B.J. 1979. COS in the stratosphere. *Geophysical Research Letters* **6**: 191–193.

Intergovernmental Panal on Climate Change 1992. Houghton, J.T., Callandar, S.K. and Varney, S.K. (eds), *Climate Change 1992 – The Supplementary Report to the IPCC Scientific Assessment*. Cambridge University Press, Cambridge.

Jarvis, P.G. 1989. Atmospheric carbon dioxide and forests. *Philosophical Transactions of the Royal Society of London* **324**: 369–392.

Johnsrud, S.C. 1978. Heterotrophic nitrification in acid forest soils. *Holartic Ecology* **1**: 27–30.

Jones, B.M.R., Cox, R.A. and Penkett, S.A. 1983. Atmospheric chemistry of carbon disulphide. *Journal of Atmospheric Chemistry* **1**: 65–86.

Keller, M.D., Bellows, W.K. and Guillard, R.R.L. 1989. Dimethyl sufide production in marine phytoplankton. In: Saltzman, E.S. and Cooper, W.J. (eds), *Biogenic Sulfur in the Environment*. 167–182. American Chemical Society, Washington, DC.

Keller, M., Goreau, T.J., Woffsy, S.C., Kaplan, W.A. and McElroy, M.B. 1983. Production of nitrous oxide and consumption of methane by forest soils. *Geophysical Research Letters* **10**: 1156–1159.

Khalil, M.A.K. and Rasmussen, R.A. 1984. Global sources, lifetimes and mass balance of carbonyl sulfide (OCS) and carbon disulfide ($CS_2$) in the earth's atmosphere. *Atmos. Environm.* **18**: 1805–1813.

Körner, Ch. 1993. $CO_2$ fertilization: the great uncertainty in future vegetation development. In: Solomon, A.H. and Shugart, H.H. (eds), *Vegetation Dynamics and Global Change*. 53–70. Chapman and Hall, New York.

Kozlowski, T.T. 1985. $SO_2$ effects on plant community structure. In: Winner, W.E., Mooney, H.A. and Goldstein, R.A. (eds), *Sulfur Dioxide and Vegetation. Physiology, ecology, and policy issues*. 431–453. Stanford University Press, Stanford, Calif.

Lauenroth, W.K. and Preston, E.M. 1984. *The Effects of $SO_2$ on a Grassland. A Case Study in the Northern Great Plains of the United States*. Springer-Verlag, New York.

Lazrus, A.L. and Gandrun, B.W. 1977. Stratospheric sulfate at high altitudes. *Geophysical Research Letters* **4**: 521–522.

McCool, P.M. 1987. Effect of air pollutants on mycorrhizae. In: Schulte-Hostede, S., Darrall, N.M., Blank, L.W. and Wellburn,

A.R. (eds), *Air Pollution and Plant Metabolism*. 356–365. Elsevier, London.

Monson, R.K., Guenther, A.B. and Fall, R. 1991. Physiological reality in relation to ecosystem- and global-level estimates of isoprene emission. In: Sharkey, T.D., Holland, E.A. and Mooney, H.A. (eds), *Trace Gas Emissions by Plants*.185–207. Academic Press, San Diego.

Mooney, H., Drake, B., Luxmoore, W., Oechel, W. and Pitelka, L.F. 1991. Predicting ecosystem response to elevated $CO_2$ concentrations. *BioScience* **41**: 96–104.

Niki, H., Maker, P.D., Savage, C.M. and Breitenbach, L.P. 1983. An FTIR study of the mechanism for the reaction $HO + CH_3SCH_3$. *International Journal of Chem Kinet*. **15**: 647–654.

Papen, H. and Rennenberg, H. 1990. Microbial processes involved in emissions of radiatively important trace gases. In: *Transactions of the 14th International Congress of Soil Science*, Vol. II, Kyoto. 232–237.

Papen, H., Hellmann, B., Papke, H. and Rennenberg, H. 1993. Emission of N-oxides from acid irrigated and limed soils of a coniferous forest in Bavaria. In: Oremland, R.S. (ed.), *Biogeochemistry of Global Change. Radiatively active trace gases*. 245–260. Chapman and Hall, London.

Pearson, J. and Stewart, G.R. 1993. The deposition of atmospheric ammonia and its effects on plants. *New Phytologist* **125**: 283–305.

Rennenberg, H. 1991. The significance of higher plants in the emission of sulfur compounds from terrestrial ecosystems. In: Sharkey, T.D., Holland, E.A. and Mooney, H.A. (eds), *Trace Gas Emissions by Plants*. 217–260. Academic Press, San Diego.

Rennenberg, H. and Polle, A. 1994. Metabolic consequences of atmospheric sulphur influx into plants. In: Welburn, A. and Alscher, R. (eds), *Proceedings of the 3rd International Symposium on Air Pollution and Plant Metabolism*, Chapman and Hall, London, (in press).

Reuss, J.O. and Johnson, D.W. 1986. *Acid Deposition and the Acidification of Soils and Waters*. Springer-Verlag, New York.

Saltzman, E.S. and Cooper, D.J. 1989. Dimethyl sulfide and hydrogen sulfide in marine air. In: Saltzman, E.S. and Cooper, W.J. (eds), *Biogenic Sulfur in the Environment*. 330–351, American Chemical Society, Washington, DC.

Schutz, H., Schröder, P. and Rennenberg, H. 1991. Role of plants in regulating the methane flux to the atmosphere. In: Sharkey, T.D., Holland, E.A. and Mooney, H.A. (eds), *Trace Gas Emissions by Plants*. 29–63. Academic Press, San Diego.

Schulze, E.-D., Lange, O.L. and Oren, R. 1989. *Forest Decline and Air Pollution. A study of spruce* (Picea abies) *on acid soils*. Springer-Verlag, Berlin.

Schwartz, S.E. 1988. Are global cloud albedo and climate controlled by marine phytoplankton? *Nature* **336**: 441–445.

Steudler, P.A., Bowden, R.D., Melillo, J.M. and Aber, J.D. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. *Nature* **341**: 314–316.

Tevini, M. 1994. UV-B effects on terrestrial plants and aquatic organisms. *Progress in Botany* **55**: 174–190.

Tingey, D.T., Turner, D.P. and Weber, J.A. 1991. Factors controlling the emissions of monoterpenes and other volatile organic compounds. In: Sharkey, T.D., Holland, E.A. and

Mooney, H.A. (eds), *Trace Gas Emissions by Plants.* 93–119. Academic Press, San Diego.

Wassmann, R., Papen, H. and Rennenberg, H. 1993. Methane emission from rice paddies and possible mitigation strategies. *Chemosphere* 26: 201–217.

Wellburn, A.R. 1990. Why are atmospheric oxides of nitrogen usually phytotoxic and not alternative fertilizers? *New Phytol.* 115: 395–429.

Wigley, T.M.L. 1989. Possible climate change due to SO₂-derived cloud condensation nuclei. *Nature* 339: 365–367.

Woodward, F.I., Thompson, G.B. and McKee, I.F. 1991. The effect of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany* 67: 23–38.

### 6.2.5 The influence of biodiversity on landscape structure

#### 6.2.5.1 Introduction

Here, we explore how changes in biodiversity can affect landscapes and the way they function. A landscape can be defined scientifically as a heterogeneous area made up of a cluster of interacting ecosystems that is repeated in similar form throughout (Forman and Godron 1986). Although we usually think of landscapes as covering tens to hundreds of square kilometres, they can be of any size and can be defined hierarchically. At one scale we might recognize a riverine landscape consisting of clumps of trees, grassy patches, bank habitats, reed beds and so on. From a broader perspective this landscape is subsumed as a riverine landscape element in a larger landscape consisting of rivers, valleys, ridges and so on. From the perspective of an aquatic insect, the bank habitat is a landscape in itself, made up of small communities of different terrestrial and aquatic plants, bare patches and so on.

Landscape structure consists of the spatial layout of the different landscape elements and the linakges between them. The way a landscape functions is determined by the interactions between the spatial elements, the most important of these being mediated by flows of materials, energy and organisms. Landscape structure is primarily determined by the geomorphological and edaphic features of an area, but is also modified by the complex of interactions between the elements of the landscape itself. Changes in biological diversity that affect the exchange of material, energy or organisms between the elements have the potential to disrupt existing landscape structure and functioning.

The many different species found in a landscape are, of course, essential components of that landscape. Thus, any change in biodiversity affecting a large number of species is likely to affect landscape structure and functioning. The conversion of forests or grasslands to agriculture are examples of such changes in biodiversity. These types of land cover changes are well documented along with the

changes in ecosystem functioning (e.g. Waring and Schlesinger 1985). They usually involve major human activity to bring about the initial change and sometimes also to maintain the modified landscape. They will not be discussed further in this essay, but instead we will concentrate on the less deliberate anthropogenic modification of biodiversity, and on cases where changes in biodiversity in one element of the landscape lead to changes in other elements.

In assessing the impact on landscapes of changes in biodiversity it is important to keep in mind the chain of causality that we are discussing. This is shown in Figure 6.2-2*a* where some event, action or impact leads to a change in biodiversity and this subsequently causes changes in the landscape. However, it is often difficult to distinguish this chain from that in Figure 6.2-2*b* where the impact affects both biodiversity and landscape but with no strong causal connection between biodiversity and landscape in either direction, or from Figure 6.2-2*c* where the chain of causality is reversed. Further combinations of chains of causality can be described but these are the main three. In this summary we have sought examples that
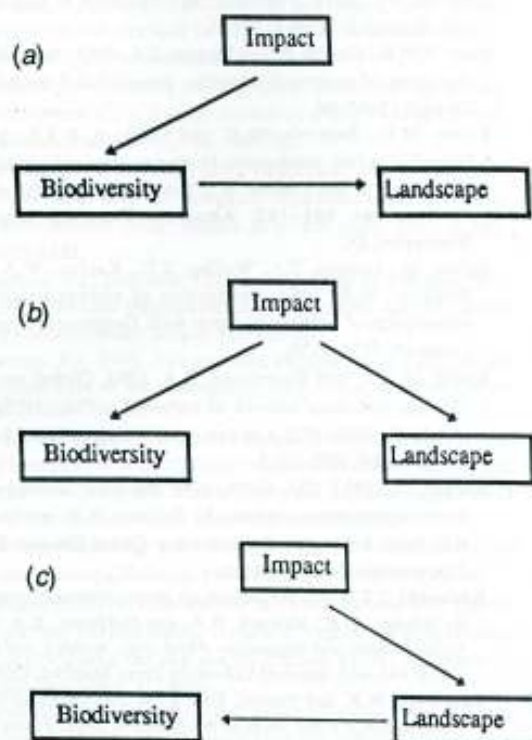


**Figure 6.2-2:** Chains of causality in assessing the impact of changes in biodiversity.

appear to be best described by Figure 6.2-2*a* but accep than in some cases other interpretations may be valid.

### 6.2.5.2 *Specific systems*

*6.2.5.2.1 Arid systems.* In arid ecosystems the redistribution and concentration of water, nutrients and sediments are important at several scales in achieving adequate growing conditions for plants. For example, in arid shrublands, each individual shrub is a 'fertile island' where nutrients and water are concentrated (Garcia-Moya and McKell 1970; Noy Meir 1985; Garner and Steinberger 1989; Friedel *et al.* 1990). Introduced herbivores, or changes in the concentration of domestic and native herbivores, around new watering points for example, can disrupt these fertile islands and lead to changes in biodiversity and eventually the structure of the surrounding landscape. Introduced species that occupy the transfer areas, such as shrubs and trees invading watercourses, can disrupt the concentration process and lead to the loss of other species.

The stripe process, which is found in many arid regions of the world (White 1971), is an example of the resource concentration process at a larger scale. In these systems vegetation is clumped in parallel, narrow bands and the soil between the bands of vegetation is usually almost bare. In heavy rainfalls water quickly runs off bare areas but is trapped in vegetated areas. These systems occur in landscapes with slopes of less than 0.6° and relatively impervious soil surfaces. Measurements have shown that the stripe process can effectively double the amount of water received in the stripes and the development pattern in stripes is species-dependent (Montaña *et al.* 1990). The pattern of stripes can develop initially either from the loss of surrounding vegetation in previously vegetated areas or from the spread of vegetation around an initial colonizer in previously bare areas (White 1971). The system can be disrupted by changed herbivory patterns that break the runoff surfaces (e.g. sheep tracks; Tongway and Ludwig 1990), by introduced species colonizing the runoff surfaces, or by grazing in the stripe vegetation.

At a larger scale the resource concentration process has been described as an 'erosion cell' (Pickup 1985). Arid lands are often a mosaic of erosion cells each consisting of erosional, transfer and sink areas. Changes in grazing patterns bought about by human activity can increase the susceptibility of land surfaces to erosion (e.g. by removing plant cover or by breaking up soil crusts), so initiating new erosional cells and thus altering landscape patterns.

*6.2.5.2.2 Temperate and boreal forests and grasslands.* In more mesic systems the concentration process described for arid systems is not as important. Instead, the main effect of changes in biodiversity is through the disruption of disturbance regimes leading to changes in the landscape patterns that result from disturbance.

common examples involve fire. Any gain or loss of species that contributes to heavy fuel loads is likely to affect fire regimes and these changes in disturbance regime can lead to significant changes in landscapes. An example is the impact of introduced herbivores (sheep) to native pastures in temperate to semi-arid areas of eastern Australia. Increased grazing pressure has reduced the grass biomass (and possibly diversity) and, coupled with fire suppression activities by landowners, fire frequencies have been reduced. This has led to dramatic increases in the density of many shrubby species previously kept in check by fires, and the conversion of large areas from a mosaic of grass and shrublands to shrub thickets (Griffin and Friedel 1984).

Beavers (*Castor canadensis*) provide an example of the loss of a single species leading to major changes in landscapes (Hammerson 1994; Naiman *et al.* 1994). It has been estimated that in parts of North America the density of beavers was 0.8/km along streams of all sizes (Jenkins and Busher 1979) and that they were the major element in creating patches of 0.5 to 24 ha in forested landscapes (Remillard *et al.* 1987). They do so by creating ponds, affecting stream flow, opening the forest canopy, changing nutrient distribution and creating habitats favourable to some species (e.g. willows, waterfowl) and unfavourable to others (e.g. aspen, cottonwood, running-water invertebrates). Their loss leads to a reduction in landscape heterogeneity, although their influence on the landscape may persist for centuries. For example, beavers disappeared from England about 1000 years ago but their influence can still be traced in the distribution of fens and peat areas (Darby 1956).

Moose (*Alces alces*) and Alaskan snowshoe hares (*Lepus americanus*) also play a keystone role in the composition and structure of boreal forests, and their presence or absence can affect the distribution and abundance of many other species (see 6.1.6).

*6.2.5.2.3 Tropical savannahs.* The complex interactions leading to the unstable balance of trees and grasses in savannah systems have been summarized by Walker (1987). In the alternating wet and dry tropical systems, changes in biodiversity can affect landscape functioning both by changing nutrient concentrating processes and by changing the fire regime as described above. Also, the loss of a few species can lead to a significant flow-on of effects that results in changes in landscape structure. An example is the role of termite mounds in acting as sites for the establishment of tree clumps (Menaut and Cesar 1982). Abandoned termitaria provide higher nutrient concentrations, greater water availability and local protection from fire, and thus favour the establishment of tree seedlings over those of grasses. The number of such mounds can be reduced by domestic

stock, so reducing tree regeneration and changing the nature of the savannah landscape towards a grassland.

Large native herbivores, such as elephants (*Loxodonta africana*) and hippopotamuses (*Hippopotamus amphibius*) affect savannah structure directly (Cumming 1982). Elephants physically remove trees and both species create paths that can eventually lead to new erosional cycles. Hippopotamus trails have a major influence in drainage patterns and thus on wetland landscapes (Laws 1981). The loss of these large species and their replacement by smaller or domestic herbivores usually leads to an homogenization of the savannah landscape.

*6.2.5.2.4 Wet tropics.* In wet tropical systems it appears that landscape patterns are less affected by changes in biodiversity *per se*, and that the biological diversity of most functional groups is so high that the loss of one or a few species has little effect (Janzen 1981). Landscape pattern is a consequence of topography and small-scale events such as blow-downs. Human activity, such as shifting agriculture and land clearance, can have major effects on biodiversity and landscape patterns. Changes in landscape patterns (e.g. edge exposure and fragmentation) may have continuing effects such as edge die-back and blow-down (Lovejoy *et al.* 1984), but the changes in landscape patterns appear to be the direct consequences of the human actions and are not moderated by changes in biodiversity directly (i.e. the chain of causality is most likely as in Figure 6.2-2*b* or *c*).

There are examples of key species affecting rain forest patches in wet–dry tropical regions. In Australia water buffalo, a recent introduction from Asia, seek out small rain forest patches where they create large wallows that are invaded by grasses and herbaceous species, many of which are also introduced. The wallows are more susceptible to fire than the rain forest itself and carry the frequent fires from the surrounding drier woodlands into the rain forest patch (Russell-Smith and Dunlop 1987). This is leading to the loss of rain forest patches within the landscape.

*6.2.5.2.5 Aquatic systems.* Water is a dense and mobile medium which readily carries material, energy and organisms between components of aquatic 'landscapes' (here interpreted as the solid substrate beneath the water rather than structures in the water column itself). Water is the dominant linkage between elements of the landscape, and organisms are most likely to affect landscapes by acting as filters or barriers to the transport process. In coral reefs the diverse biota literally create the landscape where the existence of atolls and barrier structures is dependent on the diversity of coral and planktonic organisms responsible for substrate formation and for the continued nutrition of the living landscape (see 6.1.10).

The destruction of mangrove forests can lead to a loss of the filtering process that traps soil sediments in the surface flow from the landward side (Ogden 1988). Seagrass beds perform a similar role in shallow coastal areas (Ogden and Gladfelter 1983). The loss of these species may allow large pulses of nutrients and sediment to be deposited on nearshore marine systems leading to major impacts on reef structure and diversity (D'Elia 1988). Sediments and nutrients in the outflow alter the competitive balance of the reef system by physically inhibiting coral growth and by encouraging algal growth in the higher nutrient conditions. This can lead to significant changes in landscape structure, which can be further accentuated by additional biotic interactions.

There has been concern recently about the impact on reef structure of outbreaks of the crown-of-thorns starfish (*Acanthaster planci*). Heavy grazing by this key species leads to dramatic short-term changes in the reef landscape, although it does appear that reefs eventually recover to more or less their previous condition. It has been argued that these outbreaks may be associated with the influx of additional nutrients to the reef (e.g. after shoreline clearance or heavy rains) which leads to plankton blooms, which in turn lead to increased survival of *Acanthaster* larvae (Birkland 1982). The outbreaks of crown-of-thorns starfish may be an extreme fluctuation in the complex control systems of coral reef structures where echinoid grazers control algal growth that would otherwise reduce coral recruitment and success (Mann 1982; Sammarco 1982). Any change in the populations of either the grazers or the algae (e.g. from nutrient inputs, hurricanes, overfishing or predators on the grazers) can set in chain a series of abiotic and biotic interactions leading to changes in biodiversity and landscape structure (Ogden and Lobel 1978; Wiebe 1988).

The role of sea otters (*Enhydra lutris*) in shaping the 'landscapes' of kelp communities has been well documented (see also 6.1.9). Otters feed on a range of benthic herbivores and in particular on sea urchins. In areas where otters were hunted to extinction, urchin populations exploded and overgrazing of the macroscopic algae led to a spatially heterogeneous community in which kelp was a minor component. Otters have been reintroduced into some areas and there is evidence of a shift towards a much less diverse community dominated by a single kelp species (Duggins 1980). The effect of otters on community is not only via their direct predation on herbivorous species but also via their discarded clam shells and their excavation of soft-bottom areas for clams. These activities leave more shells on the surface and these are a more favourable location for the establishment of kelp in soft-bottom environments (Kvitek *et al.* 1992). It is also possible that in the past the presence of otters led to high algal productivity which in turn supported the presence of sea-cows (*Sirenia* spp.). Sea-cows have a major effect on sea grass bed by their 'ploughing' feeding action. In the northern Pacific, Steller's sea-cow (*Hydrodamalis stelleri*) was also hunted

to extinction, so that the reintroduction of sea otters in this region may not lead to the recovery of communities or landscapes similar to those before the impact of over-exploitation (Dayton 1975; Mann 1982).

The loss of mangroves from shorelines also reduces the effectiveness of their filtering (or absorbing) the energy of wave action thus exposing coastlines to major landscape modification (see 6.1.11). There are many similar examples of where the loss of a few key filtering species from estuarine or sand-dune systems can lead to changes in landscape structure.

The water body of open oceans is patchy at various scales (Steele 1991). However, the patches tend to be associated more with physical phenomena, such as circulation cells, than with biotic phenomena. One possible exception is the effect of large floating mats of raft weed, such as *Sargassum*, which may decline due to pollution and cause changes in ocean structure (see 6.1.12).

In freshwater systems the vegetation of the riparian zone also has an energy-absorbing role. Streamside vegetation and fallen logs dissipate stream energy and trap sediment. The loss of these species either through direct human action such as clearing, or indirect action such as small changes in water flow and flooding patterns with dams or weirs causing changes in streamside and floodplain vegetation, can lead to major changes in the flow regime of the stream itself and to changes in its path (Naiman and Décamps 1990; Malanson 1993). In general, the loss of vegetative cover in mountainous topography will lead to wider, shallower valley systems with a more uniform gradient (Waring and Schlesinger 1985). The effect of the loss of large mammals on stream and wetland habitats has already been described for beavers and hippopotamuses.

### 6.2.5.3 Generalizations

It is often difficult to determine whether changes in landscapes are due to changes in biodiversity *per se* or to the processes that led to the changes in biodiversity. Even when changes in landscape structure can be linked to a biotic factor, the changes are often set in course by the gain or loss of a single key species.

Table 6.2-2 summarizes the examples presented in this review. The examples are by no means comprehensive but we suggest that they are indicative of the relative importance of the different ways in which biodiversity is linked to landscape structure across different biomes. The mechanisms are defined as 'filtering or concentrating', where organisms act primarily as physical barriers or conduits in transferring materials between landscape elements; 'disturbance regimes' where organisms are instrumental in propagating energy (or sometimes materials) between landscape elements; and 'key species' where one or a few species can directly bring about changes to landscape elements that eventually lead to changes in landscape structure.

There are a few generalizations that may be made from this review. The role of key species in triggering changes that alter landscapes is common to all biomes. Sometimes the loss or invasion of the key species is accompanied by consequential changes in biodiversity and these are the basis of changes in landscape structure and functioning (e.g. sea otters in kelp forests); in others the impacts of the key species are concentrated more directly on the landscape (e.g. elephants and hippopotamuses) which, in turn, may lead to changes in biodiversity.

Nutrient (including water) concentration and filtering effects are most important in biomes with low concentrations of nutrients. Thus, we observe changes in landscapes in arid and savannah systems as a result of the disruption of the nutrient and water concentration processes and in coral reef communities changes in communities and landscape functioning when filtering systems break down and higher concentrations of nutrients reach the reef.

In higher productivity systems changes in disturbance regimes, and particularly fire regimes, tend to be more

**Table 6.2-2:** *Summary of the examples cited in this chapter classified by the types of changes in biodiversity and by biomes. There is a question mark against the tick under tropical forests because this refers to rain forest patches embedded in a wet–dry tropical woodland.*

| | Arid | Savannah | Temperate forest and grasslands | Tropical forests | Aquatic (freshwater, estuarine and marine) |
|---|---|---|---|---|---|
| Altered material concentration or filtering | ✔ | ✔ | | | ✔ |
| Altered disturbance regimes | | ✔ | ✔ | | |
| Key species effects | ✔ | ✔ | ✔ | ✔? | ✔ |

important processes in modifying landscapes. In the most highly productive and diverse communities (i.e. tropical rain forests) changes in biodiversity appear to have little effect on landscapes. In these systems disturbances must be of large spatial or temporal scale in order to disrupt the nutrient and water cycles and thus have long-term effects on landscape structure.

## References

Birkland, C. 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata, Asteroidea). *Marine Biology* 69: 175–185.

Cumming, D.H.M. 1982. The influence of large herbivores on savannah structure in Africa. In: Huntley, B.J. and Walker, B.H. (ed.), *Ecology of Tropical Savannahs.* Ecological Studies No. 42. 217–245. Springer-Verlag, New York.

Darby, H.C. 1956. *The Draining of the Fens.* Cambridge Univesity Press, Cambridge.

Dayton, P.K. 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *Fisheries Bulletin* 73: 230–7.

D'Elia, C.F. 1988. The cycling of essential elements in coral reefs. In: Pomeroy, L.R. and Alberts, J.J. (eds), *Concepts of Ecosystem Ecology.* Ecological Studies No. 67. 195–230. Springer-Verlag, New York.

Duggins, D.O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61: 447–453.

Forman, R.T.T. and Godron, M. 1986. *Landscape Ecology.* John Wiley, New York.

Friedel, M.H., Foran, B.D. and Stafford Smith, D.M. 1990. Where the creeks run dry or ten feet high: pastoral management in arid Australia. *Proceedings of the Ecology Society of Australia* 16: 185–194.

Garcia-Moya, E. and McKell, C.M. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51: 81–88.

Garner, W. and Steinberger, Y. 1989. A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *Journal of Arid Environment* 16: 257–262.

Griffin, G.F. and Friedel, M.H. 1984. Effects of fire on central Australian rangelands. II. Changes in tree and shrub populations. *Australian Journal of Ecology* 9: 305–403.

Hammerson, G.A. 1994. Beaver (*Castor canadensis*): ecosystem alterations, management, and monitoring. *Natural Areas Journal* 14: 44–57.

Janzen, D.H. 1981. Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13: 271–282.

Jenkins, S.H. and Busher, P.E. 1979. *Castor canadensis. Mammalian Species* No. 120: 1–8.

Kvitek, R.G., Oliver, J.S., DeGange, A.R. and Anderson, B.S. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* 73: 413–428.

Laws, R.M. 1981 Experience in the study of large animals. In: Fowler, C.W. and Smith, T.D. (eds), *Dynamics of Large Mammal Populations.* 19–45. John Wiley, New York.

Lovejoy, T.E., Rankin, J.M., Bierregaard, R.O. Jr, Brown, K.S. Jr, Emmons, L.M. and Van der Voort, M.E. 1984. Ecosystem decay of Amazon forest remnants. In: Nitecki, M.H. (ed.), *Extinctions.* 295–325. University of Chicago Press, Chicago.

Malanson, G.P. 1993. *Riparian Landscapes.* Cambridge University Press, Cambridge.

Mann, K.H. 1982. *Ecology of coastal waters.* Studies in Ecology Vol. 8. University of California Press, Berkeley.

Menaut, J.-C. and Cesar, J. 1982. The structure and dynamics of a west African savannah. In: Huntley, B.J. and Walker, B.H. (eds), *Ecology of Tropical Savannahs.* Ecological Studies No. 42. 80–100. Springer-Verlag, New York.

Montaña, C. 1992. The colonisation of bare areas in two-phase mosaics of an arid ecosystem. *Journal of Ecology* 80: 315–327.

Montaña, C., Lopez-Portillo, J. and Mauchamp, A. 1990 The response of two woody species to the conditions created by a shifting ecotone in an arid ecosystem. *Journal of Ecology* 78: 789–798.

Naiman, R.J. and Décamps, H. (eds) 1990. *The Ecology and Management of Aquatic-Terrestrial Ecotones.* UNESCO, Paris and Parthenon Publishing Group, Carnforth.

Naiman, R.J., Pinay, G., Johnston, C.A. and Pastor, J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75: 905–921.

Noy-Meir, I. 1985. Desert ecosystem structure and function. In: Evenari, M., Noy-Meir, I. and Goodall, D.W. (eds), *Ecosystems of the World 12A: Hot deserts and arid shrublands.* 93–103. Elsevier, Amsterdam.

Ogden, J.C. and Lobel, P.S. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fisheries* 3: 49–63.

Ogden, J.C. and Gladfelter, E.H. (eds), 1983. *Coral Reefs, Seagrass Beds and Mangroves: Their interactions in the coastal zones of the Caribbean.* UNESCO Reprints in Marine Science No. 23.

Ogden, J.C. 1988. The influence of adjacent systems on the structure and function of coral reefs. *Proceedings, 6th International Coral Reef Symposium,* Vol. 1: 123–129.

Pickup, G. 1985. The erosion cell – a geomorphic approach to landscape classification in range assessment. *Australian Rangelands Journal* 7: 114–121.

Remillard, M.M., Gruendling, G.K. and Bogucki, D.J. 1987. Disturbance by Beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity. In: Turner, M.G. (ed.), *Landscape heterogeneity and disturbance.* Ecological Studies No. 64. 102–122. Springer-Verlag, New York.

Russell-Smith, J. and Dunlop, C. 1987. The status of monsoon vine forests in the Northern Territory: a perspective. In: *Australian Heritage Commission Special Publication Series 7(1) The Rainforest Legacy.* 227-288. Australian Government Publishing Service, Canberra.

Sammarco, P.W. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulation. *Journal of Experimental Marine Biology and Ecology* 61: 31–55.

Steele, J.H. 1991. Marine functional diversity. *Bioscience* 41: 470–474.

Tongway, D.J. and Ludwig, J.A. 1990. Vegetation and soil

patterning in semi-arid mulga lands of eastern Australia. *Australian Journal of Ecology* 15: 23–34.

Walker, B.H. 1987. A general model of savannah structure and function. In: Walker, B.H. (ed.). *Determinants of Tropical Savannahs*. IUBS Monograph Series, No 3. 1–12. International Union of Biological Sciences, Paris.

Waring, R.H. and Schlesinger, W.H. 1985. *Forest Ecosystems: Concepts and management*. Academic Press, Orlando, Fla.

Wiehe, W.J. 1988 Coral reef energetics. In: Pomeroy, L.R. and Alberts, J.J. (ed.). *Concepts of Ecosystem Ecology*. Ecological Studies No. 67. 231–246. Springer-Verlag, New York.

White, L.P. 1971 Vegetation stripes on sheet wash surfaces. *Journal of Ecology* 59: 615–622.

## 6.2.6 Biotic linkages and ecosystem functioning

### 6.2.6.1 Introduction

In this essay, biotic linkages are considered as an ecosystem functional property in their own right. Thus a major emphasis will be placed on discussing the roles of biodiversity in biotic linkages and community structure, specifically exploring how these are disrupted by human activities. In addition, an attempt will be made to discuss further how biotic linkages may in turn influence some of the other more conventional ecosystem properties (e.g. nutrient cycling, primary production, microbial activities) reviewed in Section 5 of the GBA. In this analysis, however, it is important to bear in mind the following caveat. The roles of biodiversity in biotic linkages and species interactions are difficult to assess since changes in species richness (i.e. deletions/additions) imply consequent changes in linkages and therefore it is difficult to assign causality for the observed effects unequivocally. An appropriate assessment, for the future, would require different approaches, such as assessing effects as a result of changes in the strength of interactions without changing species richness.

Occasionally, biological interactions may have discernible direct benefits to humans, as described in Box 6.2-1.

The biological activities of one individual invariably impinge upon the activities of other individuals of the same or different trophic levels, and the magnitude and direction of these effects are commonly referred to as biotic linkages or species interactions. Though activities occur at the level of the individual, typically the individual interactions are grouped according to their species designation (i.e. intra- or interspecific). According to their sign, these interactions can be classified into two broad groups – antagonistic and mutualistic — and can be further classified into many kinds of more specific interactions, most of which are described and treated in text books of ecology (e.g., Begon *et al.* 1993; Ricklefs 1993).

Most species are involved in several interactions with other species and each interaction can differ in its sign (antagonistic, mutualistic), magnitude (strong, weak),

specificity (ranging from complete specialism to generalism), and degree of dependence on interacting organisms (obligate, facultative). The multiple interactions of species imply that most communities consist of a pattern of interactions among their member species that we refer to as a community web (this differs from a food web, which focuses on trophic links among species). This implies that besides direct interactions there are complex indirect or non-linear interactions among species (e.g. a top predator that feeds on a polyphagous herbivore which in turn determines relative competitive interactions among plants). Effects, consequently, are usually non-linear. The impact of a single species on a community is therefore a complex function of the number of interactions, the signs and magnitudes of those interactions, and the number of indirect links with other species in the community. This complex function can be referred to as the average strength of a species interaction with its community, and this strength can range from strong in keystone species (see Terborgh 1986) to weak in relatively independent species. A more detailed discussion of the contrasts between direct and indirect interactions and non-linearities is given by Menge (1995) and in Box 5.2-1. Although there is still an ongoing debate about the relative importance of types of interactions, or of keystone species, and about the role of compensations among species within functional groups, particularly in terrestrial biomes (see reviews in Ricklefs and Schluter 1993), there is a consensus that biotic interactions play a crucial role in structuring communities. This is particularly highlighted in studies of coastal benthic communities, where experimental manipulation has been actively applied, leading to a mechanistic understanding of such details and to a clarification of the importance of biotic linkages and species interactions for community structure and composition (see a recent review in Menge 1995). However, there is still a major gap in the knowledge needed to assess to what extent community structure in turn affects ecosystem functioning. Here we attempt to review (1) how changes in biodiversity (largely due to human activities) in different biomes affect biotic linkages or species interactions and, to the extent that the scant information permits, (2) how this scales up to alterations of ecosystem functioning.

### 6.2.6.2 Human impacts

Human activities produce alterations of biodiversity that directly or indirectly affect the patterns of interactions and linkages of species to one another in communities. In Arctic and subalpine systems, overhunting and overharvesting of marine and terrestrial mammals is leading to population declines (6.1.1). When these animals are keystone or top predators (e.g. sea otters), the effects seem to alter dramatically the pattern of interactions and may propagate to the entire ecosystem. Likewise, herding

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### Box 6.2-1: Potential human benefits of the *Urania/Omphalea* coevolution.

The day-flying moth *Urania fulgens* and its host plants *Omphalea* spp. provide a remarkable example of the complex and fascinating ways in which elements of biodiversity (viewed at the species level in this case) operate in their natural settings, as well as the potential implications these seemingly obscure organisms may have for human society.

The adult moths migrate northwards and southwards between several localities in northern South America and southeastern Mexico. In many of these localities, with a certain periodicity, they undergo dramatic local population explosions. The caterpillars of this moth feed exclusively on the foliage of plants of the genus *Omphalea*, such as the vine *O. diandra* in Panama, or the 25 m tall tree *O. oleifera* in Mexico. During years of the moths' population explosions, these plants are heavily defoliated. If fed with the leaves of other plants, the caterpillars will not eat, and starve to death. In the Mexican populations this was found to be the case, consistently, even if the moths were fed with all the local species of the same family as *Omphalea* (Euphorbiaceae). The *Omphalea* plants, in turn, are rarely eaten by herbivores (either invertebrates or vertebrates in the Mexican situation) other than *Urania*. This high degree of mutual specialization indicates a long joint evolutionary history, of the type usually referred to as coevolution. In addition, it has been noted that the moths' migrations and the magnitude of the their population explosions appear to occur with a certain periodicity – but the underlying mechanisms for this are not fully understood.

Such tight biotic interaction appears to be mediated by some peculiar metabolites (apparently toxic to many animals) that were unknown until very recently, and which are present in the plants' tissues and can be sequestered by the caterpillars without them, in turn, being affected. Specifically, it has been found that *O. diandra* produces and *U. fulgens* concentrates dihydroxymethyldihydroxypyrrolidine (DMDP). These remarkable compounds have been found to be quite promising in three aspects of relevance to humans. The first of them has to do with AIDS, due to their role in blocking the activity of the HIV virus. Secondly, DMDP suppresses enzymatic activity in *Callosobruchus* beetles. The beetles attack stores of beans in the tropics; and as a result of the differential effect of the chemical, humans can eat beans treated with DMDP (which the beetles would not have been able to eat). Thirdly, it has been found that DMDP also has some activity against cancer and diabetes. Such remarkable activities of these metabolites and the moths' ability to deal with them constitute promising avenues not only for the prospecting and development of new drugs, but also for the understanding and possible application of novel detoxifying mechanisms.

On the other hand, based on the understanding of the activity of the plants' toxic metabolites, some evidence suggests that the periodicity of the migrations and the magnitude of the moths' population explosions might be governed by the time it takes for the heavily defoliated plants to induce and relax the production and build-up of their toxic compounds.

Given the migratory habits of the moth and the great specialization of their ecological interaction with the *Omphalea* plants, this system highlights two points pertinent to biodiversity conservation: that conservation efforts should not be directed only to biodiversity components (e.g. species) *per se*, but also to their underlying ecological and evolutionary processes (such as biotic linkages) and to the global nature of the conservation/disruption of biodiversity. In this system, for example, perturbations in a given locality (say Mexico) may dramatically disrupt the ecological interactions and destroy a complex ecological process in another distant locality (say Panama) and vice versa.

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practices or changes in reindeer abundance change lichen cover and vegetation structure (Andreev 1978). In tropical forests, habitat destruction (deforestation, forest fragmentation) and contemporary hunting (6.1.2) produce dramatic alterations of biodiversity components which are beginning to show consequences in biotic interactions such as pollination (Aizen and Feinsinger 1994) and herbivory (Dirzo and Miranda 1991). Temperate forest systems show a marked vulnerability to species introductions of pathogenic pests such as the ones causing Dutch-elm disease and chestnut blight, or insects such as the gypsy moth (6.1.3). In arid lands, both importation of non-native plants and removal of native ones are occurring actively in association with forage improvement plans (6.1.4). Human activities are also leading to the decline of bat populations, which in turn affects the pollination pattern of *Agave* plants in North American deserts (Howell and Roth 1981). Introduction of mammals and other changes in grazing

regime cause marked alterations of the vegetation structure and composition and plant-plant interactions in savannahs (6.1.5), boreal forests (6.1.6) and temperate grasslands (6.1.7). Species introductions and habitat modification are argued potentially to disrupt biotic interactions such as pollination and dispersal (6.1.8). In aquatic biomes the removal or partial displacement of predators by overfishing, overcollecting or pollution, as well as the introduction of new species can produce considerable effects (particularly well documented in coastal systems – see 6.1.9) which can propagate to the rest of the ecosystem by means of the disruptions of biotic interactions.

From the point of view of the relevance of biodiversity with regards to biotic linkages, the effects of human activities can be assessed more simply in terms of species deletions or species additions.

### 6.2.6.3 Effects of removal of species on biotic linkages

The removal of a species from a community may cause further losses and therefore profoundly affect biotic linkages, or it may cause no further losses (although all the other persisting species may do so at different densities) thus leading, at least theoretically, to what Pimm (1986) calls the species deletion stability of systems. Within a web, species deletion stability may vary considerably, depending, among other things, on the species richness of the system, the trophic level from which the species are removed, and the degree of connectance of the species removed (connectance being the actual number of species interactions in a food web divided by the number of possible interactions (Pimm 1986). Studies of model communities suggest that species-rich communities (i.e. those with high connectance) are more sensitive to the loss of top predators while the loss of primary producers and consumers has less of an effect on community dynamics (Pimm 1986).

Field data show that most natural systems, regardless of species richness, appear to be changed after the removal of top predators or herbivores. This conclusion appears to hold for a wide variety of biomes including marine and freshwater systems (Pimm 1980), East African savannahs (McNaughton 1985), desert communities in North America (Brown 1985), and tropical forests (Terborgh 1988). In an excellent experimental study McNaughton (1977) found that the consequences of the removal of herbivores depended upon species richness: plant species composition changed more when a grazing herbivore, the African buffalo, was excluded from a species-rich grassland, than when the same herbivore was excluded from a species-poor one. No explicit experiments seem to be available to assess the consequences of the removal of plant species from species-poor and species-rich systems. Although species-rich systems might be expected to be more resistant to the loss of plant species, the occurrence of keystone plant

species such as *Ficus* spp. in highly diverse tropical forests (see Terborgh 1986), suggests that removal of certain plant species can indeed have profound effects on species composition and linkages in the rest of the web. In summary, the outcome of alterations in the web of interactions is very much dependent on the complexity of the web and the identity (e.g. keystone status) of the species.

### 6.2.6.3.1 Empirical evidence of the effects on ecosystem functioning.
Apart from the alteration of biotic linkages and community structure due to species removals, consequences can be seen at the level of ecosystem processes. For example, the native moose, *Alces alces*, on Isle Royale, Lake Superiot, Canada, feeds preferentially on early successional species, avoiding those of late successional stages (Pastor *et al.*, 1993). Thus herbivory determines the structure and composition of these forests. By comparing browsed and unbrowsed plots, it has been shown that this herbivore significantly reduces nutrient availability and microbial activity and, in the longer term, primary production and successional trends.

A 12-year study by Brown and Heske (1990) showed that the removal of three seed-eating kangaroo rat species caused habitats to shift from desert to scrub to arid grassland. While not documented by the authors, such dramatic alterations in plant species composition should lead to considerable changes in the amount and chemistry of leaf litter, decomposition rates and nutrient cycling. Thus, seed predation appears largely responsible for determining the type of community in this system and therefore may control a wide range of ecosystem-level processes.

### 6.2.6.4 Effects of addition of species on biotic linkages

Food web theory argues that, on average, communities seem to be highly resistant to species introductions (Pimm 1986). Nevertheless, there seems to be good evidence to suggest that species richness affects the susceptibility of a community web to ecological invasion (introduction of non-native species). In general, it appears that species-rich tropical forests are very resistant to invasions (see 6.1.2). Diamond (1985) found that the rate of success of bird introductions on tropical and subtropical islands declines steeply with the species richness of the extant native avifauna. An extrapolation of these findings would suggest that temperate biomes (with lower species richness) should be more susceptible to species invasions. Data for insect introductions suggest a similar pattern (see a review in Pimm 1986), but prediction of the success of insect introductions from a knowledge of the community structure and diversity is still somewhat debatable. Other noticeable patterns involve the apparent susceptibility of islands to invasions (related in some instances to species diversity) and the

subsequent (in some cases devastating) effects of such invasions on the rest of the biotic linkages.

*6.2.6.4.1 Empirical evidence of the effects on ecosystem functioning.* Aside from the question of the role of species diversity in susceptibility to invasion, there remains the issue of the possible consequences of such additions to some ecosystem functions or properties. The following examples indicate such potential ecosystem consequences. The Argentine ant (*Iridomyrmex humilis*) has invaded extensive areas of the world causing considerable changes in the species interactions of the invaded systems. In the South African Cape Region it has radically altered the composition of the native ant fauna by replacing dominant species. Bond and Slingsby (1984) documented the consequences of this invasion for the mutualistic interactions between plants and seed-dispersing ants. They found that, compared to the native ant species, the Argentine ant was much slower to discover the seeds of an exclusively ant-dispersed plant, dispersed these seeds shorter distances, and failed to store them below ground where they would have gained protection from seed predators. Given the importance of ant seed dispersal in this system, the invasion of such an influential ant species has the potential substantially to alter community composition and ecosystem-level processes.

The inadvertent introduction of the house mouse to Marion Island in 1818 resulted in substantial alterations in decomposition and nutrient cycling on the island (Crafford 1990). This introduction was found to be particularly influential because the mice preferentially feed on the island's dominant detritus-feeding invertebrate, the endemic moth *Pringleophaga marioni*. Larvae of this moth are estimated to consume up to 50% of the primary production on the island. Such processing considerably enhances microbial activity and subsequent release of essential nutrients. Some experiments (Crafford 1990; Smith and Steenkamp 1990) have shown that the addition of just two moth larvae into litter stimulated mineralization of nitrogen ten-fold and phosphorus three-fold. Thus, these moth larvae appear to be the primary mediators of nutrient mineralization and introduction of an exotic predator has greatly altered ecosystem processes on this island.

## 6.2.6.5 Cross-biome comparison and ecosystem services

In an attempt to summarize the available information in a way that permits us to highlight the effects of human activities on biodiversity components, and the consequences of this on biotic linkages, we present a cross-biome comparison based on a distillation of several published accounts that provide information on (1) the kinds of biomes that are likely to be affected by the modification documented; (2) the interaction type; (3) the biotic hierarchical level at which it operates (e.g. gene, individual, population, species, community, ecosystem,

landscape, region, global); (4) the human activity responsible for the change; (5) the ecological effect, and (6) the human consequences. The working set consisted of 11 examples of mutualistic and antagonistic interactions which included cases applicable to specific biomes and cases applicable to all biomes (Table 6.2-3).

*6.2.6.5.1 Pollination linkages.* This review indicates that landscape modification in the form of partial deforestation and habitat fragmentation affects pollination linkages in a variety of terrestrial biomes, from temperate sandy meadows (Jennersten 1988) to tropical forests (Karr 1982). Thus it appears that pollination disruptions occur across most biomes except in aquatic ones, where biotic pollination *per se* is poorly represented. The alteration of this type of biotic interaction occurs largely due to the reduction of species or abundance of pollinators. The consequences of this disruption range from potential local extinction of plant species to reduced genetic variation in partly self-compatible outcrossers which thus depend to a larger extent on self-pollination (Jennersten 1988). The consequences of reduced genetic variation can in some cases scale up to ecosystem functions and affect a given service. For example, in agroecosystems, where single hybrids are planted over large areas, pests and pathogens can be devastating. The outbreak of *Helminthosporium maydis* on the CMS hybrid corn (Williams and Levings 1992) is an outstanding example of the consequences of reduction in biodiversity (genetic variance in this case) which affects biotic linkages and in turn affects an ecosystem function and service (the regulation of production).

*6.2.6.5.2 Seed dispersal linkages.* Deforestation and fragmentation lead to the loss/decline in abundance of some species of frugivores in tropical forests, which in turn have the potential to reduce biotic seed dispersal (Kattan 1992). The greater occurrence of plant modifications for biotic dispersal in terrestrial tropical and temperate deciduous forests (Howe and Smallwood 1982) suggests an expected trend of greater importance of this biotic linkage in such biomes than in more dry and aquatic ones. A similar trend could be expected in the case of defensive mutualisms, though appropriate information for cross-biome comparison is very limited. The expected consequences of reductions in such mutualisms as frugivory may include reductions in the reproductive capacity of highly dependent (specialized) plants, or reductions in genetic variability (similar to the case of pollination described above) though no information seems to exist regarding the ecosystem-functioning consequences.

*6.2.6.5.3 Grazing linkages.* Modifications of grazing regimes dramatically affect several ecosystem processes in a variety of both terrestrial and aquatic biomes (Table 6.2-3). Additions or deletions of top predators alter the abundance or occurrence of herbivores and this in turn may

Table 6.2-3: Effects of human activities on biodiversity components.

| Interaction | Species | Human Activity | Effect | Potential consequence | Biodiversity hierarchy | Applicable biome | Source |
|---|---|---|---|---|---|---|---|
| Pollination | Several | Landscape modification (habitat fragmentation) | Reduction of pollinator efficiency | Inbreeding local extinction | Gene-landscape | Terrestrial | 1, 2 |
| Grazing | Ungulates | Simplification of herbivore guild, overgrazing | Change in vegetation structure and composition | Desertification | Spp.-landscape | all | 3 |
| Predation-grazing | Otters | Eliminate top predator | Overgrazing by urchins | Local extinction of algae | Gene-landscape | all | 4 |
| Predation-grazing | Nile perch | Addition of top predator | Loss of grazers | Spp. extinction collapse of fisheries | Spp.-landscape | all | 5 |
| Predation-grazing | Beaver | Deletion of keystone sp. | Loss or disturbance | Homogenization of habitat | Landscape | all | 6 |
| Predation-grazing | " | Addition of keystone sp. (Chile, Argentina) | Increased disturbance | Disruption of habitat | Landscape | all | 7 |
| Predation-grazing | Fish | Deletion of zooplankton grazers | Phytoplankton bloom | Ecosystem collapse | Gene-landscape | all | 8 |
| Dispersal | Birds | Deforestation fragmentation | Reduction of dispersal agents | Reduced reproductive potential of plants | Gene-spp. | Moist-wet >dry forests | 9 |
| Dispersal | Argentine ant | Introduction of exotic sp. | Excluded native ants | Reduced reproductive potential of plants | Extinction | Terrestrial | 10 |
| Predation | Mouse/moth | Addition of top predator | Extinction of prey (keystone detritivore) | Potential disruption of detritus pathway | Gene-ecosystem | all | 11 |
| Predation | Cats | Deletion of top predators in tropical rainforest | Mammalian herbivores increase | Overgrazing, excessive seed predation, change in vegetation structure and composition | Gene-spp. | all | 12 |
| Predation | Lamprey | Addition of top predator (building of dams) | Locks bring predator and prey together which results in extinction of prey (fish) | Collapse of fisheries | Gene-spp. | all | 13 |

Sources: 1. Jennersten (1988); 2. Karr (1982); 3. B. Huntley (pers. comm.); 4. Estates and Palmisano (1974); 5. Keenlyside (1991) 6. Nieman et al. (1988); 7. Lizarralde (1993); 8. D. Soto (pers. comm.) 9. Brooks and Dodsan (1965); 10. Bond and Slingby (1984); 11. Crafford (1990); Smith and Steenkamp (1990); 12. Terborgh (1988); 13. O. Solbrig (pers. comm).

have a range of effects from modifications of vegetation structure to disruptions of detritus pathways. This type of ecosystem function consequence occurs in several forest biomes from boreal to tropical ones, as well as in aquatic ones. The introduction of exotic species affects trophic relationships and a number of biotic linkages (predation, herbivory, hierarchical competitive relationships) in non-linear ways and this type of effect is known for both aquatic and terrestrial biomes of several types Some of the best-known examples are referred to in Table 6.2-3.

### 6.2.6.6  Conclusions

Although there is little specific documentation about the importance of biodiversity components affecting biotic linkages and then ecosystem processes, our review of the available information indicates that a common outcome of human impacts on biotic linkages is alteration of the stability of community structure (pattern of interactions) and composition (distribution and abundance of species). From our analysis, it appears that in low-diversity systems, the full set of species within functional groups is important. This is the case in boreal forests (Pastor *et al.* 1993) and temperate rocky intertidal shores (6.1.9), while it appears that in high-diversity systems (e.g. tropical forests, tropical rocky shores) the deletion of species can be compensated for by the other species in the available pool. However, compensation does not seem to occur when deletion of a whole functional group takes place, even in high-diversity systems (e.g. the deletion of the guild of understorey herbivorous mammals in tropical forests; Dirzo and Miranda 1991).

The present assessment allowed us to consider the certainties and uncertainties of how changes in biotic interactions affect community stability (cf. Orians 1982). We conclude that stability changes occur when biotic interactions and linkages are altered through deletions, additions or other alterations of structure — and that the effects can range from reductions of genetic variability to landscape-level effects and from moderate to catastrophic. Effects are generally confined to within ecosystems or biomes and there is little evidence of them scaling up to geographically distant biomes. However, an example of the potential of the latter can be drawn from the case of across-biome migratory organisms such as birds or insects. Deforestation and habitat fragmentation in tropical forests affect several species of migratory birds, which in turn may affect biotic interactions involving these birds in temperate forests. The alterations of temperate forests may have similar effects in tropical forests.

Much of the available evidence demonstrates that changing biodiversity changes biotic interactions and links in communities, but this is evidence that is generally gathered *after* alterations have occurred. Effective prediction and management modelling is dependent upon further research involving the experimental manipulation of species, through natural and planned experiments.

### References

Aizen, M.A. and Feinsinger, P. 1994. Forest fragmentation, pollination and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75: 330–341.

Andreev, V.N. (ed.) 1978. *Seasonal and Weather-related Dynamics of Phytomass in the Subarctic Tundra.* Nauka, Siberian Section, Novosibirsk.

Begon, M., Harper, J.L. and Townsend, C.R. *Ecology: Individuals, populations and communities.* Sinauer Associates, Sunderland, Mass.

Bond, W.J. and Slingsby, P. 1984. Collapse of an ant–plant mutualism: the Argentine ant (*Iridomyrmex humilus*) and myrmechorous Proteaceae. *Ecology* 65: 1031–1037.

Brooks, J.L. and Dodson, S. 1. 1965. Predation, body size, and composition of plankton. *Science* 150: 28–35.

Brown, J.H. 1985. Experiments on desert rodents. In: Case, T.J. and Diamond, J.H. (eds), *Community Ecology.* Harper and Row, New York.

Brown, J. and Heske 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705–1707.

Crafford, J.E. 1990. The role of feral house mice in ecosystem functioning on Marion Island. In: Kerry, K.L. and Hempel, G. (eds,. *Antarctic Ecosystems: Ecological change and conservation.* 359–364. Springer-Verlag, Berlin.

Diamond, J.H. 1985. Introductions, extinctions exterminations and invasions. In: Case, T.J., and Diamond, J.H. (eds), *Community Ecology.* 65–79. Harper and Row, New York.

Dirzo, R. 1987. Estudios sobre interacciones planta-herbívoro en Los Tuxtlas, Veracruz. *Revista de Biología Tropical* 37: 119–131.

Dirzo, R. and Miranda, A. 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. In Price, P.W., Lewinsohn, T.M., Fernandes, W. and Benson, W.W. (eds), *Plant–Animal Interactions.* 273–287. John Wiley, New York.

Estetes, J.A. and Palmisano, J.F. 1974. Sea otters: their role in structuring seashore communities. *Science* 185: 1058–1060.

Fellows, L.E. 1989. Botany breaks into the candy store. *New Scientist* 26: 45–48.

Fellows, L. E. and Nash, R. J. 1990. Sugar-shaped alkaloids. *Science Progress*, Oxford 74: 245–255.

Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Howell, D.J. and Roth, B.S. 1981. Sexual reproduction in Agaves: the benefits of bats, the cost of semelparous advertising. *Ecology* 62: 1–7.

Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2: 359–366.

Karr, J.R. 1982. Avian extinction in Barro Colorado Island, Panama: a reassessment. *American Naturalist* 119: 220–239.

Kattan, G.H. 1992. Rarity and vulnerability: the birds of the Cordillera Central in Colombia. *Conservation Biology* 6: 64–70.

Keenleyside, H.A. (ed.) 1991. *Cyclid Fishes: Behaviour, ecology and evolution*. Chapman and Hall, London.

Kite, G.C., Hom, J. M., Romeo, J.T., Fellows, L.E., Lees, D.C., Scofield, A.M. and Smith, N.G. 1990. A homonojirimycin and 2,5-dihydroxymethyl-3,4-dihydroxypyrrolidine: alkaloidal glucosidase inhibitors in the moth *Urania fulgens*. *Phytochemistry* **29**: 103–105.

Lizarralde, M.S. 1993. Current status of introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. *Ambio* **22**: 351–358.

McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**: 515–525.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* **55**: 259–294.

Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**: 21–74.

Nieman, R.J. 1988. Animal influences on ecosystem dynamics. *BioScience* **38**: 750–752.

Pastor, R.M., Dewey, B., Naiman, R.J., McInnes, P.F. and Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forest of Isle Royale National Park. *Ecology* **74**: 467–480.

Pimm, S.L. 1986. Community stability and structure. In: Soulé, M.E. (ed.). *Conservation Biology*. 309–329. Sinauer Associates, Sunderland, Mass.

Pimm, S.L. 1980. Food web design and the effects of species deletions. *Oikos* **35**: 139–149.

Ricklefs, R.F. 1993. *The Economy of Nature*, 3rd edn. 319–357. W.H. Freeman, New York.

Ricklefs, R.F. and Schluter, D. 1993. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.

Smith, N.G. 1983. Host plant toxicity and migration in the day-flying moth *Urania*. Florida *Entomologist* **66**: 76–84.

Smith, V.R. and Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**: 14–24.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. In: Soulé, M.E. (ed.). *Conservation Biology*. 330–344. Sinauer Associates, Sunderland, Mass.

Terborgh, J. 1988. The big things that run the world – a sequel to E.O. Wilson. *Conservation Biology* **2**: 402–403.

Tyms, A.S., Berrie, E.M., Ryder, T.A., Nash, R.J., Hegarty, M.P., Taylor, M.A., Mobberly, Davies, J.M., Bell, E.A., Jefferies, D.J., Taylor-Robinson, D. and Fellows, L.E. 1987. Castanospermine and other plant alkaloid inhibitors of glucosidase activity block the growth of HIV. *Lancet* **20**: 1025–1026.

Williams, M.E. and Levings, C.S. 1992. Molecular biology of cytoplasmic male sterility. *Plant Breeding Reviews* **10**: 23–51.

indispensable activities in the circulation of matter, on which all larger organisms, including humans, depend (Hawksworth and Colwell 1992; Guerreo and Pedros-Alio 1993; Allsopp *et al*. 1995). Primary production, decomposition, nutrient recycling, trace gas production and the other processes considered in the preceding chapters either have a microbial component or are carried out only by microorganisms.

Microorganisms occupy a greater range of ecological niches than macroorganisms (Price 1988) and some groups were diverse as long ago as 3.5 billion years (Schopf 1993). They occur in all niches where life is thermodynamically possible, including many extreme environments in which no other life is found: high temperatures (80–110°C), high salinity (e.g. the Dead Sea, >320 g salt/litre), high pressure (deep ocean hydrothermal vents, >600 atm), very acid (below pH 2), low water activity (under 0.65 aw) and extreme cold (e.g. cryptoendoliths in Antarctica, with photosynthesis at −8°C) (Vestal and Hobbie 1988; Edwards 1990).

Microbial diversity does not represent a monophyletic group, but includes archaea, eubacteria, fungi, algae, protozoans and viruses. In practice, microorganisms are species either belonging to a phylum many members of which cannot be seen by the unaided eye, or where microscopic examination, and in many cases growth in culture, is essential for identification. Culturing, however, reveals only a biased subset of the species present in natural systems and may not accurately reflect either the actual composition or the activity of microbial communities (Hobbie and Ford 1993). New techniques (White *et al*. 1991) are beginning to rectify this problem in many ecosystems, including oceans (Giovannoni *et al*. 1990), coral reefs (Rowan and Powers 1991, 1992), hot springs (Ward *et al*. 1990; Barns *et al*. 1994) and hydrothermal vents (Hedrick *et al*. 1992). However, they are also uncovering whole groups of previously unknown organisms (DeLong *et al*. 1994, Olsen 1994: oceanic archaebacteria; Sherr and Sherr 1991: ultraplankton). Perhaps fewer than 5% of microbial species have been discovered and named (Hawksworth 1991; Hawksworth and Ritchie 1993; Trüper 1992; see Section 3.1) and in many cases their precise ecological and biogeochemical roles are unclear (Hobbie and Ford 1993).

Our task is to describe how this dramatic and relatively unknown diversity influences a huge range of ecosystem processes and to elucidate how it might be threatened by anthropogenic activities.

### 6.2.7 Microbial diversity and ecosystem processes

#### 6.2.7.1 Background

Microorganisms are crucial to the functioning of every ecosystem on Earth. They perform unique and

#### 6.2.7.2 Important aspects of microbial diversity

Due to a limited set of morphological traits identifiable in microorganisms, microbiologists have commonly classified organisms according to detectable metabolic substrates and end products, by trophic categories, or by size. In some

ways, such functional groupings put us closer to an understanding of the roles of microbial diversity in ecosystem processes than for other groups of organisms. To say that functional group diversity is important to ecosystem processes is circular – known groups are classified as such *because* of their importance to the process at hand (Vitousek and Hooper 1993). The task is to discern what the important groups are and how they interact with each other and with abiotic controls.

*6.2.7.2.1 Substrate-based groups.* The functional diversity of microbes, particularly as defined by the substrates used for energy metabolism (both electron donors and -acceptors), is integral to our understanding of biogeochemistry. Substrate linkages between microbial functional groups form the basis of element cycling (e.g. N-fixers, heterotrophs, nitrifiers, denitrifiers: Meyer 1993; sulphate/sulphur reduction and sulphur/sulphide oxidation: Howarth and Stewart 1992; Meyer 1993). In some cases, as in oxic/anoxic sediment interfaces (Schlesinger 1991; Andreae and Jaeschke 1992), microbial mats, and hydrothermal vents (Hedrick *et al.* 1992), multi-organism redox cycles can be relatively localized and major transitions between groups take place over very short (millimetre) distances. At the other end of the scale, through trace gas production frequently due to metabolic redox reactions, microbes shaped the composition of the atmosphere and currently play a significant role in its maintenance (Hedrick *et al.* 1992; 6.2.4).

Vast complexity exists within the broadly defined redox groups. Within the wide range of aerobic heterotrophic microbes, the importance of further substrate specialization is frequently cited for carbon metabolism during degradation of plant material (e.g. specialists on lignin, cellulose, pectins; Garland and Mills 1991; Meyer 1993; Schimel 1994; Zak *et al.* 1994). Even within the group that decomposes lignin, however, metabolism of this recalcitrant plant compound is carried out by hundreds of species of fungi (even at a single site) and by bacteria of several genera (Meyer 1993). These can occur in succession and may be attacking different ligno-cellulose bonds, so we cannot necessarily assume 'redundancy'. Some transformations, such as nitrification and sulphate reduction, require multiple groups to complete the process (ammonium oxidizers and nitrite oxidizers, sulphate reducers and sulphur reducers, respectively). Some functional groups form consistent taxonomic groups (e.g. the nitroso-bacteria in ammonium oxidation) or at least share common metabolic constraints (sulphur-oxidizing bacteria). Others, such as denitrifiers, are very diverse with different substrate specificities and share only the use of either nitrate or nitrite as electron acceptors in a facultative anaerobic metabolism (Cook and Kelly 1992; Meyer 1993). Again, the importance of these functional groups is widely acknowledged in that loss of an entire group would lead to

loss of a process and potential disruption of the entire cycle. We know almost nothing, however, about whether or how diversity within groups might contribute to process rates, process stability, or the types of processes that are active. Though it is a common assumption (used in this assessment as well) that more diverse groups are less sensitive to disruption, this warrants empirical verification.

*6.2.7.2.2 Size-based groups.* Functional group classifications based on size are important particularly in aquatic food webs. The relatively recent discovery of nano-(2-20 $\mu$m), pico- (0.2–2.0 $\mu$m) , and even femtoplankton (0.02–0.2 $\mu$m) has changed our understanding of energetics and nutrient cycling in both marine and freshwater systems (Sherr and Sherr 1991; Steinberg and Geller 1993). The classical aquatic food chain from diatoms to metazoans to small fish to large fish holds only for pieces of a more complex web. The size-class microbial groups are both taxonomically and trophically diverse, including photoautotrophic and heterotrophic prokaryotes and eukaryotes. Mixotrophs abound and feeding is based as much on the relative sizes of predator and prey as on classical trophic categories of primary producers, herbivores and predators (Sherr and Sherr 1991). Consequently, large fractions (20–60%) of primary production are cycled through 'microbial loops' with no link to macrofauna due to the energetic losses at trophic stages too small to be consumed by metazoans (Pomeroy and Wiebe 1988; Pomeroy 1991; Sherr and Sherr 1991).

In these loops, not unlike terrestrial ecosystems (e.g. Clarholm 1985; Jackson *et al.* 1989; Schimel *et al.* 1989), bacteria compete with primary producers (larger phytoplankton) for nutrients, rather than just serving as nutrient regenerators themselves, and grazing on bacteria is responsible for large amounts of nutrient regeneration (Pomeroy and Wiebe 1988; Pomeroy 1991; Goldman and Dennett 1992). The rapid nutrient recycling provided by the aquatic microbial loop leads to relatively stable primary production in oligotrophic systems. In such systems, the microbial pathway is favoured because low nutrient concentrations give a competitive advantage to smaller individuals (i.e. higher surface to volume ratios; Pomeroy 1991). As nutrient concentrations increase, as in seasonal lake turnovers or areas of oceanic upwelling, larger phytoplankton are favoured. These in turn are fed on by metazoans and those are subsequently eaten by fish. Due to the life-cycle constraints of metazoans, however, their growth frequently lags behind that of the blooming algae, whose populations become nutrient-limited and crash (Pomeroy 1991; Sherr and Sherr 1991). Thus, trophic diversity within the size-based groups leads to alternative pathways for nutrient and energy flow, and diversity among size-based groups results in different patterns of primary production (stable vs boom and bust) in response to the bottom-up controls of nutrient availability. Nutrients may

regulate the total productivity of some systems, but species characteristics (size, competitive abilities) regulate the relative amounts that flow to larger metazoans and fish. As with the redox functional groups, knowledge of the roles of individual microbial species is rare at best.

*6.2.7.2.3 Species-specific interactions.* When a single species has a strong effect on ecosystem processes, that species may be looked upon as a functional group with only one member. For example, for an exotic species to alter ecosystem processes, Vitousek (1986) lists the following criteria: that it must acquire or use resources differently from native species, that it must alter trophic structure, or that it must alter disturbance regime. The clearest cases of such effects for microbial species (whether invaders or not) are in species-specific interactions. The importance of individual microbial species is much better known for effects on economically important organisms, as for both mutualists and pathogens in agroecosystems, than for carbon and nutrient cycling in natural systems, particularly given the problems of identification discussed above. Microbial mutualists and pathogens, however, can have important ramifications in structuring natural ecosystems as well (e.g. N-fixing in primary succession and mycorrhizal associations: Vitousek and Walker 1989; Galloway 1992; Dhillion and Zak 1993; Read 1993; Schimel 1994; Chestnut blight (*Cryphonectria parasitica*), *Myxoma* virus, *Phytophthora cinnamomi*: Burdon 1993; Dobson and Crawley 1994; Castello *et al.* 1995). In cases with dramatic ecosystem level effects, both novel characteristics of the organisms involved and the specificity of the biotic interactions are relevant aspects of biodiversity.

*6.2.7.2.4 Qualitative and stabilizing effects of diversity.* Two important ways in which microbial diversity (and biodiversity in general) can affect ecosystem functioning are (1) qualitative effects, as with different functional groups (Chapin *et al.* 1994); and (2) stabilizing effects (cf. McNaughton 1977; Tilman and Downing 1994), as with diversity within functional groups. The sensitivity of ecosystem functioning to environmental change (anthropogenic or otherwise) becomes a question of the presence/absence of basic functional groups, the strength of control exerted on a given process or interaction, and the plasticity of organisms within groups to operate over a range of conditions. While many soil and aquatic bacteria are widespread, it is a myth that all microorganisms are distributed ubiquitously. Those that are restricted to special environments (e.g. isolated hot springs) or lack broad dispersal (many fungi, especially lichen-forming species) may not recolonize easily if they are lost from an ecosystem. Some of these, such as mycorrhizas, play key roles in the re-establishment of systems following disturbance (Perry *et al.* 1987, 1989; Dhillion and Zak 1993). At the same time, we have only very limited knowledge of the identity and functional attributes of the myriad microbes found in even one gram of soil (see 6.2.2). Predictions of the strength of control are most easily and frequently based on abundances, though 'keystone' organisms/groups are often not recognizable on this basis. Predictability is a major problem, especially in microbial communities, as we often are not aware of species' roles as keystones until they are either lost from systems or introduced as invaders (Sherr and Sherr 1991; Bond 1993). For microbial groups whose members are cosmopolitan and whose activity depends on environmental conditions, ecosystem-level processes carried out by more diverse groups will probably continue as conditions change, but may be carried out by different organisms (Hobbie and Ford 1993). Of course, when conditions cross certain critical boundaries (as in going from aerobic to anaerobic), different organisms and processes may become active while others become inactive. The problem is the identification of the boundary conditions and rate changes through that spectrum of conditions and microbes. Thus, microbial diversity (and biodiversity in general) could be important in the sense that either (a) process rates are stabilized through a variety of environmental perturbations because of compensatory changes in community composition (cf. McNaughton 1977; Tilman and Downing 1994), or (b) process rates change as the species performing them change, due to differences in the functional properties of the organisms. In the first case, diversity is thought to be important for maintaining consistency (stability and/or resilience) in ecosystem properties/process; in the second case, it is seen as important for helping to create or maintain ecosystem heterogeneity through functional differences. (cf. Chapin *et al.* 1994; Schimel 1994). These seemingly contradictory statements point out the need to be precise about the expected ecosystem-level effects of diversity when addressing hypotheses on this topic.

The predictions may, in fact, not be contradictory, but just opposite ends of the perturbation spectrum. Shifts in dominance within a diverse extant community may stabilize processes over a relatively narrow range of environmental conditions; if changes are long enough or strong enough, however, and if appropriate organisms are present or can colonize, entirely different communities with different functional properties may become established (e.g. shifts in phytoplankton dominance with changes in nutrient availability).

*6.2.7.3 Changes in biodiversity and microbial activity*
Using the criteria of specificity of interactions, sensitivity to disturbance/change, and diversity within functional groups, we can recognize microbially mediated ecosystem processes sensitive to changes in biodiversity and those in which, in addition, anthropogenic forces have affected or may affect microbial diversity (Table 6.2-4). The biome

types (Chapter 6.1) in which occur both the anthropogenic forces and the microbial processes that are sensitive to those forces are also identified. In many cases, the reason for the biome listing is the prevalence of a particular type of disturbance; absence of a biome from the listing should not be taken to imply that it is necessarily resistant to that threat.

*6.2.7.3.1 Biotic interactions.* Species-specific biotic interactions, both mutualistic and pathogenic, are the most vulnerable to changes in microbial composition and diversity. The gain or loss of a microorganism involved in a mutualistic or pathogenic interaction can have consequences that range from subtle changes in competitive ability of the host species to the loss of populations or whole communities of macro-organisms. What makes an ecosystem process particularly susceptible to change, however, is difficult to predict. If only one or a few species of microorganisms are responsible for a mutualistic or pathogenic interaction of importance to an ecosystem process, the risk of changing that process given a loss of diversity is very high. If that species is widespread and disperses and colonizes easily, however, then the risk of actually losing it may be low. The most sensitive processes may be those controlled by highly specific interactions that are themselves sensitive to disturbance.

Nutrient-based mutualisms, especially those of mycorrhizas and nitrogen-fixers, are susceptible to eutrophication, acid precipitation and nutrient deposition, with major implications for forest health (Perry *et al.* 1989; Arnolds 1991; Vitousek 1994). Lichenized fungi are sensitive to a variety of chemical stresses (Galloway 1992) independent of biome type. These and other listed mutualisms are sensitive to physical disturbance (Pilz and Perry 1984; Perry *et al.* 1987) and to pollutants, such as acid and alkaline deposition (Adamson and Seppelt 1990; Lovett and Kinsman 1990; Richardson 1992), heavy metals (Zabowski *et al.* 1990; Richardson 1992), pesticides and radioisotopes (Haselwanter *et al.* 1988; Wood *et al.* 1990) in any system in which such anthropogenic stresses occur. In many systems (e.g. island and Mediterranean-type systems; D'Antonio and Dudley 1994; see 6.1.8), exotic species are frequently a problem, and these systems may suffer from addition of N-fixing species (e.g. Vitousek and Walker 1989; Table 6.2-4).

The zooxanthellae mutualists in corals and other marine organisms are sensitive to both natural and anthropogenic disturbances, including storm waves, freshwater pulses from flooding, nutrient loading, sedimentation and over-fishing (Holthus *et al.* 1989; Smith and Buddemeier 1992; Dollar and Tribble 1993; Richmond 1993; Hughes 1994). An important difference between these categories may be that many natural disturbances are episodic and allow recolonization, whereas many human disturbances are chronic and, while perhaps initially more subtle, can result

in long-term changes in viability of the mutualism and the health of the reef (Dollar and Tribble 1993; Hughes 1994; Richmond 1993). The role played by the zooxanthellae in ecosystem nutrient cycling and productivity is relatively well characterized compared to our understanding of how different microbial mutualists affect these processes (Cook and D'Elia 1987; Muscatine and Weis 1992; Falkowski *et al.* 1993). Indeed, it has only recently been discovered that the genetic diversity of algal symbionts, mostly classified within the genus *Symbiodinium*, is equivalent to the diversity between different orders of other microbes (Rowan and Powers 1991, 1992).

Arthropod gut microbiotas, while potentially sensitive due to the restricted number of microbes involved, may be less vulnerable because of lower degrees of host specificity (Martin 1991) than more closely allied mutualisms, such as the fungi of gall midges (Bisset and Borkent 1988) and algae in lichen thalli (Honegger 1992). This may be true in the case of trees able to form ectomycorrhizas with more than a single fungus, though variable environmental conditions and successional relationships could make this diversity important (Perry *et al.* 1989). Mycophagy is widespread in insects but the degree of specificity is frequently unclear (Hammond and Lawrence 1989). Disruption of a microorganism–arthropod mutualism or the sole food source of a fungus-feeding insect would be of particular significance if the arthropod was, for example, the pollinator of a predominant tree, i.e. held a keystone role.

Sensitive pathogenic interactions may be positive (e.g. biocontrol agents; Batra 1982) or negative (e.g. crop pathogens) from a human perspective, with exotic species introductions generally having the greatest visible impact (Dobson and Crawley 1994; Castello *et al.* 1995). Extreme cases can include destruction of dominant native trees by pathogens, with subsequent losses in macro-, meso- and microbiota (Podger and Brown 1989; Wills 1992). In agroecosystems, the genetic simplification of crop plants, rather than loss of microbial diversity itself, can result in adverse microbial outbreaks (Vanderplank 1982; Leonard and Fry 1989). Pathogenic interactions in natural communities may be equally important in determining ecosystem structure and functioning, but are often overlooked because of their subtlety and are much less extensively researched (Burdon and Leather 1990; Burdon 1993; Dobson and Crawley 1994).

*6.2.7.3.2 Trace gas production.* Microbial trace gas production can be sensitive to species interactions and is particularly important regionally and globally when land-use changes result in changes in rates of release to the atmosphere (Table 6.2-4). The oceanic production of dimethylsulphide (DMS) from relatively few species of phytoplankton plays an important role in atmospheric dynamics as the dominant natural source of sulphate

aerosols (6.2.4). Zooplankton grazing can dramatically increase rates of DMS release (Dacey and Wakeham 1986; Turner *et al.* 1988). The broad distribution of the species involved (Andreae and Jaeschke 1992), however, leads to controversy over whether or not disruption of this process due to species loss is likely in practice (6.2.4). Coastal systems have higher flux rates than pelagic systems and often suffer more intense disturbance from humans, both directly and indirectly through land-use transformations in adjacent terrestrial systems. While they have potential for greater changes in sulphur gas fluxes because of this, the relatively small area of these regions may make the inputs minor on a global scale (6.1.9; but see also 6.2.4).

Land-use transformations leading to increased methane release, such as livestock grazing and rice paddy management, are already responsible for part of the change in Earth's radiative balance (Watson *et al.* 1990). Methane production in temperate and tropical grasslands and agroecosystems is affected by management practices, while climate warming may affect methane production in saturated areas, particularly in northern ecosystems (Table 6.2-4). Changes in methane flux are due to impacts both on the microbial environment (e.g. inducing anoxic conditions necessary for the methanogen functional group, or increasing temperature) and on microbial interactions (e.g. by the bypassing, via plant aerenchyma, of diffusional and microbial (methane oxidizers) boundaries which normally impede transfer of methane to the atmosphere (see 6.2.4). While changes become globally significant only when extended over large areas, the extent to which landscape diversity *per se* contributes has not yet been fully explored.

*6.2.7.3.3 Carbon and nutrient cycling.* While microbial functional diversity is clearly important in the major nutrient and carbon transformations, the risk from biodiversity loss is scored as 'low' because many micro-organisms appear to be able to undertake these functions (Table 6.2-4). Successional relationships may, however, decrease some of the apparent redundancy. The extent to which this within-group diversity results in process heterogeneity (Schimel 1994) and/or the buffering of systems against changing environmental conditions or species loss, has yet to be determined for most of the processes involved in both terrestrial and aquatic systems. While nitrification is particularly susceptible to pH (Meyer 1993) and may be affected in certain areas by acid deposition, does this mean that the limits of a functional group have been exceeded or merely that pH exerts a direct control on the process? Changes in plant species composition, and thus litter quality, may occur in many biomes for a variety of reasons (e.g. climate change in Arctic, alpine and boreal systems: 6.1.1, 6.1.6; increased disturbance and therefore prevalence of more secondary successional species in tropical forests: 6.1.2; management regimes in grasslands: 6.1.7). This may change microbial

communities (Garland and Mills 1991; Zak *et al.* 1994), but it will probably not interrupt carbon and nutrient cycling. Extreme environments in which a minimal number of species fulfils each functional role could prove to be an important exception (e.g. Friedman *et al.* 1988; Table 6.2-4).

In one subcategory of carbon cycling — the microbial decomposition of hazardous wastes — microbial diversity is clearly important in dealing with the myriad toxic contaminants we have put into our natural and managed ecosystems (Aelion and Bradley 1991). Furthermore, diversity within communities, through co-metabolism, gene transfer via plasmids, provision of necessary co-factors and other mechanisms, is frequently necessary to degrade recalcitrant compounds (Weightman and Slater 1988). We do not know of threats to this diversity other than the inputs of xenobiotics themselves, which is happening in all biomes (Table 6.2-4). Community interactions such as those just listed may be important in other close microbial associations such as biofilms and microbial mats, but their potential for disruption, and the ecosystem consequences thereof, remain largely unexplored. The intentional release of genetically engineered micro-organisms poses yet another set of questions about the potential ecosystem-level effects of microbial diversity (Smit *et al.* 1992). See Section 10 for a further discussion of many of these issues.

In aquatic systems, microbes form the base of the food web leading to macrofauna. As previously described, microbial loops offer alternative pathways for primary production and nutrient transformations. In this case, trophic diversity within size-based functional groups (both plankton and metazoans) influences pathways of nutrient regeneration and carbon/energy flow, and has implications for fisheries (Pomeroy 1991; O'Brien *et al.* 1992; Steinberg and Geller 1993). Loss of phytoplankton productivity itself may not be currently under major threat from changes in microbial diversity (the major exception being cases of severe pollution which push environmental conditions beyond the bounds of most primary producers). However, both directly and through species interactions, nutrient loading can alter pathways of carbon cycling (e.g. Peterson *et al.* 1985, 1993), can result in plankton blooms leading to anoxia in extreme cases, and can also result in changes in species composition leading to outbreaks of noxious species such as red tide (6.1.9). Coastal and freshwater systems are particularly susceptible to such disturbances due to their proximity to terrestrial sediment, toxics and nutrient sources.

### 6.2.7.4 Conclusions

Despite our relative lack of knowledge in the face of the staggering diversity of microbes, we do know something about the importance of many microbial functional groups. We can begin to look at how microbial diversity affects

Table 6.2-4: Microbially mediated ecosystem processes and their sensitivity to the loss of biodiversity. See text for references.

| Sensitivity[1] | Ecosystem functions | Interface[2] and biome[3] | Organisms | Ecosystem processes affected | Ecosystem processes involved | Human threats |
|---|---|---|---|---|---|---|
| High | Biotic interactions 1. Mutualisms | 1,2,3 TeF, TrF, TrS | Mycorrhizas | Nutrient cycling, primary production physical disturbance | Nutrient and water uptake | Eutrophication, acid deposition, |
| | | 2,3,4 CoR, CoS, L&R, Med, TeF | N-fixers (nodule formers, cyanobacteria) | Nutrient cycling primary production | N-fixation | Eutrophication, physical disturbance, species introductions |
| | | 2,3,4 TeF, ArL | Lichens | Primary colonization, biogeochemical weathering | Photosynthesis, N-fixation | Acid deposition |
| | | 2,3,4 ArL | Cryptogamic crusts | Primary production, soil stabilization | N-fixation | Acid deposition, physical disturbances |
| | | 4 CoR | Corals | Primary and secondary production | Photosynthesis | Eutrophication, physical disturbances, sedimentation, over-fishing |
| | | 2 all | Arthropods/bacteria | Decomposition | Cellulose digestion | No known immediate threats |
| | 2. Pathogens | 2,3,4 AgE | Myriad | Primary and secondary production | Natural biocontrol and population control | Genetic simplification species introductions species losses |
| High | Trace gas production | 1,3 AA, AgE, BoF, TeF, TeG, TrS | Methanogens/ methanotrophs | Radiative balance | Methane production and consumption | Land-use transformations e.g. grazing, rice paddies, N fertilization |

| Sensitivity | Process | Interfaces | Biomes | Component | Key processes | | Comments |
|---|---|---|---|---|---|---|---|
| High | Xenobiotic degradation | 1,3 | all | Myriad | Carbon cycling | Metabolism of recalcitrant/toxic substrates | Xenobiotics may both threaten diversity and select for novel organisms |
| Low/High | C and nutrient cycling | 1,2,3,4,5 | | Microbes in extreme environments | Primary production, nutrient cycling, decomposition, soil structure | | Physical and chemical disturbance – extent not known |
| Low/High | C and nutrient cycling | 1,2,4 CoS, CoR, L&R, TrE | | Phytoplankton | Primary production, secondary production, decomposition | Primary production | Severe pollution, eutrophication |
| Low | All other | 1,2,3,4,5 AA, BoF, TeF, TeG, TrE, TrF | | Myriad | Nutrient cycling, carbon cycling, soil formation | Decomposition, mineralization, nitrification, denitrification, immobilization primary production, ecosystem respiration. Soil organic matter synthesis and breakdown, etc. | Changes in plant species composition |

1. 'Sensitivity' refers to potential for change/disruption of ecosystem processes due to change/loss of biodiversity; High = dependence on either a few species or very specific species interactions, or particularly subject to disruption. Low/High = in general assumed not to be sensitive but may be highly vulnerable in extreme environments or near-shore aquatic systems; Low = due to the lack of adequate information, generally assumed not to be sensitive.

2. Interfaces: 1 = atmosphere/biotic; 2 = biotic/biotic; 3 = biotic/soil; 4 = biotic/hydrologic; 5 = soil/hydrologic.

3. Biomes: AA = Arctic and Alpine; AgE = Agroecosystems; ArL = Arid Lands; BoF = Boreal Forests; CoR = Coral Reefs; CoS = Coastal systems; L&R = Lakes and Rivers; Med = Mediterranean-type; OpO = Open Oceans; TeF = Temperate Forests; TeG = Temperate Grasslands; TrE = Tropical Estuaries; TrF = Tropical Forests; TrS = Tropical Savannahs.

ecosystem-level processes, and how this may be threatened by human impacts, by using the criteria of specificity of interactions, sensitivity to disturbance, and diversity within functional groups. Some or all of the assumptions underlying these criteria may need further testing.

For carbon and nutrient transformations, the importance of microbial functional diversity is well known. However, these processes do not seem to be immediately threatened unless anthropogenic changes cross process-level thresholds by pushing the range of environmental conditions beyond either the ability of particularly sensitive and specific micro-organisms to operate (e.g. pH with nitrifiers; Meyer 1993) or the abilities of the microbial assemblages in that group to respond. This assumes that the species diversity within most functional groups related to carbon and nutrient cycling substantially buffers processes in changing conditions (Hobbie and Ford 1993). For this reason, we conjecture that microbial communities in extreme environments, in which a restricted number of species carry out each process step, are particularly susceptible to these changes. The role of diversity within functional groups, however, has barely been explored, not only for microbes but for most organisms and processes.

Biotic interactions, both mutualistic and pathogenic, belong to another category of microbial diversity that may substantially affect ecosystem-level processes and which is probably the one currently most threatened by anthropogenic activities. The sensitivity of mutualisms to disruption may be a function of both their specificity and the number of different species involved (again, within-functional group diversity), though ecosystem level impacts would be expected only where the interactions are widespread or in some sense 'keystone' in nature. Pathogenic interactions have the most dramatic effects on natural systems when either the host or the pathogen (or both) are introduced (Dobson and Crawley 1994).

For diverse functional groups, we need to look more closely at how changes in diversity affect the boundaries of processes (i.e. determine thresholds of functional change) as well as how such changes modulate the rates of those processes. For very specific biotic interactions or important element transfers carried out by few species, we need more information on their susceptibility to both physical or chemical disturbance. As McNaughton (1988) has previously observed, microcosm experiments which manipulate both species composition and diversity (e.g. Hairston *et al.* 1968) could provide useful insights both for microbial communities and for general principles on how diversity affects ecosystem properties.

## References

Adamson, E. and Seppelt, R.D. 1990. A comparison of airborne alkaline pollution damage in selected lichens and mosses at Casey Station, Wilkes Land, Antarctica. In: Kerry, K.R. and Hempel, G. (eds), *Antarctic Ecosystems*. 347–353. Springer-Verlag, New York.

Aelion, C.M. and Bradley, P.M. 1991. Aerobic biodegradation potential of surface micro-organisms from a jet fuel-contaminated aquifer. *Applied and Environmental Microbiology* 57: 57–63.

Allsopp, D., Colwell, R.R. and Hawksworth, D.L. (eds) 1995. *Microbial Diversity and Ecosystem Function*. CAB International, Wallingford.

Andreae, M.O. and Jaeschke, W.A. 1992. Exchange of sulphur between biosphere and atmosphere over temperate and tropical regions. In: Howarth, R.W., Stewart, J.W.B. and Ivanov, M.V. (eds.) *Sulfur Cycling on the Continents: Wetlands, terrestrial ecosystems, and associated water bodies*. 27–61. John Wiley, Chichester, UK.

Arnolds, E. 1991. Decline of ectomycorrhizal fungi in Europe. *Agriculture, Ecosystems and Environment* 35: 209–244.

Barns, S.M., Fundyga, R.E., Jeffries, M.W. and Pace, N.R. 1994. Remarkable archaeal diversity detected in a Yellowstone National Park hot spring environment. *Proceedings of the National Academy of Sciences USA* 91: 1609–1613.

Batra, S.W.T. 1982. Biological control in agroecosystems. *Science* 215: 134–139.

Bisset, J. and Borkent, A. 1988. Ambrosia galls: the significance of fungal nutrition in the evolution of the Cecidomyiidae (Diptera). In: Pirozynski, K.A. and Hawksworth, D.L. (eds), *Coevolution of Fungi with Plants and Animals*. 203–225. Academic Press, London.

Bond, 1993. Keystone species. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 237–253. Springer-Verlag, Berlin.

Burdon, J.J. 1993. The role of parasites in plant populations and communities. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 165–179. Springer-Verlag, Berlin.

Burdon, J.J. and Leather, S.R. (eds) 1990. *Pests, Pathogens and Plant Communities*. Blackwell Scientific Publications, Oxford.

Castello, J.D., Leopold, D.J. and Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. *BioScience* 45: 16–24.

Chapin, F.S., III, Reynolds, H., D'Antonio, C. and Eckhart, V. 1994. The functional role of species in terrestrial ecosystems. In: Walker, B. (ed), *Global Change in Terrestrial Ecosystems*. Cambridge University Press, Cambridge.

Clarholm, M. 1985. Possible roles for roots, bacteria, protozoa and fungi in supplying nitrogen to plants. In: Fitter, A.H., Atkinson, D., Read, D.J. and Usher, M.B. (eds), *Ecology and Interactions in Soil: Plants, microbes and animals*. 355–365. Blackwell Scientific Publications, Oxford.

Cook, C.B. and D'Elia, C.F. 1987. Are natural populations of zooxanthellae ever nutrient-limited? *Symbiosis* 4: 199–212.

Cook, R.B. and Kelly, C.A. 1992. Sulphur cycling and fluxes in temperate dimictic lakes. In: Howarth, R.W., Stewart, J.W.B. and Ivanov, M.V. (eds), *Sulfur Cycling on the Continents: Wetlands, terrestrial ecosystems, and associated water bodies*. 145–188. John Wiley, Chichester, UK.

D'Antonio, C.M. and Dudley, T.L. 1994. Biological invasions as

agents of change on islands versus mainlands. In: Vitousek, P.M., Adsersen, H. and Loope, L.L. (eds), *Islands: Biodiversity and ecosystem function*. Springer-Verlag, Berlin.

Dacey, J.W.H. and Wakeham, S.G. 1986. Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. *Science* 233: 1314–1316.

DeLong, E.F., Wu, K.Y., Prézelin, B.B. and Jovine, R.V.M. 1994. High abundance of Archaea in Antarctic marine picoplankton. *Nature* 371: 695–697.

Dhillon, S.S. and Zak, J.C. 1993. Microbial dynamics in arid ecosystems: desertification and the potential role of mycorrhizas. *Revista Chilena de Historia Natural* 66: 253–270.

Dobson, A. and Crawley, M. 1994. Pathogens and the structure of plant communities. *Trends in Ecology Evolution* 9: 393–398.

Dollar, S.J. and Tribble, G.W. 1993. Recurrent storm disturbance and recovery: a long-term study of coral communities in Hawaii. *Coral Reefs* 12: 223–233.

Edwards, C. (ed.) 1990. *Microbiology of Extreme Environments*. Open University Press, Milton Keynes, UK.

Falkowski, P.G., Dubinsky, Z., Muscatine, L. and McCloskey, L. 1993. Population control in symbiotic corals. *BioScience* 43: 606–611.

Friedman, E.I., Hua, M. and Ooamp-Friedman, R. 1988. Cryptoendolithic lichen and cyanobacterial communities of the Ross Desert, Antarctica. *Polarforschung* 58: 251–259.

Galloway, D.J. 1992. Biodiversity: a lichenological perspective. *Biodiversity and Conservation* 1: 312–323.

Garland, J.L. and Mills, A.L. 1991. Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. *Applied and Environmental Microbiology* 57: 2351–2359.

Giovannoni, S.J., Britschgi, T.B., Moyer, C.L. and Field, K.G. 1990. Genetic diversity in Sargasso Sea bacterioplankton. *Nature* 345: 60–63.

Goldman, J.C. and Dennett, M.R. 1992. Phagotrophy and $NH_4^+$ regeneration in a three-member microbial food loop. *Journal of Plankton Research* 14: 649–663.

Guerreo, R. and Pedros-Alio, C. (eds) 1993. *Trends in Microbial Ecology*. Spanish Society for Microbiology, Barcelona.

Hairston, N.G., Allan, J.D., Colwell, R.K., Futuymn, D.J., Howell, J., Lubin, M.D., Mathias, J. and Vandermeer, J.H. 1968. The relationship between species diversity and stability: an experimental approach with protozoa and bacteria. *Ecology* 49: 1091–1101.

Hammond, P.M. and Lawrence, J.F. 1989. Mycophagy in insects. In: Wilding, N., Collins, N.M., Hammond, P.M. and Webber, J.F. (eds), *Insect–Fungus Interactions*. 275–324. Academic Press, London.

Haselwanter, K.M., Berreck, M. and Brunner, P. 1988. Fungi as bioindicators of radiocesium contamination: Pre- and Post-Chernobyl activities. *Transactions of the British Mycological Society* 90: 171–174.

Hawksworth, D.L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Research* 95: 641–655.

Hawksworth, D.L. and Colwell, R.R. 1992. Microbial Diversity 21: biodiversity amongst micro-organisms and its relevance. *Biodiversity and Conservation* 1: 221–226.

Hawksworth, D.L. and Ritchie, J.M. 1993. *Biodiversity and Biosystematic Priorities: Micro-organisms and invertebrates*. CAB International, Wallingford.

Hedrick, D.B., Pledger, R.D., White, D.D. and Baross, J.A. 1992. *In situ* microbial ecology of hydrothermal vent sediments. *FEMS Microbiology Ecology* 101: 1–10.

Hobbie, J.E. and Ford, T.E. 1993. A perspective on the ecology of aquatic microbes. In: Ford, T.E. (ed.), *Aquatic Microbiology: an Ecological Approach*. 1–14. Blackwell Scientific Publishers, Oxford.

Holthus, P.F., Maragos, J.E. and Evans, C.W. 1989. Coral reef recovery subsequent to the freshwater kill of 1965 in Kaneohe Bay, Oahu, Hawaii. *Pacific Science* 43: 122–134.

Honegger, R. 1992. Lichens: mycobiont–photobiont relationships. In: Reisser, W. (ed.), *Algae and Symbioses*. 255–275. Biopress, Bristol.

Howarth, R.W. and Stewart, J.W.B. 1992. The interactions of sulphur with other element cycles in ecosystems. In: Howarth, R.W., Stewart, J.W.B. and Ivanov, M.V. (eds), *Sulfur Cycling on the Continents: Wetlands, terrestrial ecosystems, and associated water bodies*. 67–84. John Wiley, Chichester.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:

Jackson, L.E., Schimel, J.P. and Firestone, M.K. 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. *Soil Biology and Biochemistry*. 21: 409–416.

Leonard, K.J. and Fry, W.E. (eds), 1989. *Plant Disease Epidemiology: Genetics, resistance, and management*. Vol. 2. McGraw-Hill, New York.

Lovett, G.M. and Kinsman, J.D. 1990. Atmospheric pollution deposition to high elevation ecosystems. *Atmosphere and Environment* 24A: 2767–2786.

Martin, M.M. 1991. The evolution of cellulose digestion in insects. *Transactions of the Royal Society of London, B* 333: 281–288.

McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* 111: 515–525.

McNaughton, S.J. 1988. Diversity and stability. *Nature* 333: 204–205.

Meyer, O. 1993. Functional groups of micro-organisms. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 67–96. Springer-Verlag, Berlin.

Muscatine, L. and Weis, V, 1992. Productivity of zooxanthellae and biogeochemical cycles. In: Falkowski, P.G. and Woodhead, A.D. (eds), *Primary Productivity and Biogeochemical Cycles in the Sea*. 257–271. Plenum Press, New York.

O'Brien, W.J., Hershey, A.E., Hobbie, J.E., Hullar, M.A., Kipphut, G.W., Miller, M.C., Moller, B. and Vestal, J.R. 1992. Control mechanisms of arctic lake ecosystems: a limnocorral experiment. *Hydrobiologia* 240: 143–188.

Olsen, G.J. 1994. Archaea, Archaea, everywhere. *Nature* 371: 657–658.

Perry, A.D.M., Amaranthus, M.P., Borchers, J.G., Borchers, S.L. and Brainerd, R.E. 1989. Bootstrapping in ecosystems. *BioScience* 39: 230–237.

Perry, D.A., Molina, R. and Amaranthus, M.P. 1987.

Mycorrhizae, mycorrhizospheres and reforestation: current knowledge and research needs. *Canadian Journal of Forest Research* 17: 929–940.

Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M.A.J., Moller, B., Ford, T.E., Hershey, A.E., Hiltner, A., Kipphut, G., Lock, M.A., Fiebig, D.M., McKinley, V., Miller, M.C., Vestal, J.R., Ventullo, R.M. and Volk, G. 1993. Biological responses of a tundra river to fertilization. *Ecology* 74: 653–672.

Peterson, B.J., Hobbie, J.E., Hershey, A.E., Lock, M.A., Ford, T.E., Vestal, J.R., McKinley, V.L., Hullar, M.A.J., Miller, M.C., Ventullo, R.M. and Volk, G.S. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. *Science* 229: 1383–1385.

Pilz, P.D. and Perry, D.A. 1984. Impact of clearcutting and slash burning on ECM associations of Douglas-fir seedlings. *Canadian Journal of Forest Research* 14: 94–100.

Podger, F.D. and Brown, M.J. 1989. Vegetation damage caused by *Phytophthora cinnamomi* on disturbed sites in temperate rainforest in western Tasmania. *Australian Journal of Botany* 37: 443–480.

Pomeroy, L.R. 1991. Relationships of primary and secondary production in lakes and marine ecosystems. In: Cole, J., Lovett, G. and Findlay, S. (eds), *Comparative Analyses of Ecosystems: Patterns, mechanisms and theories*. 97–119. Springer-Verlag, New York.

Pomeroy, L.R. and Wiebe, W.J. 1988. Energetics of microbial food webs. *Hydrobiologia* 159: 7–18.

Price, D. 1988. An overview of organismal interactions in ecosystems in evolutionary and ecological time. *Agriculture, Ecosystems and Environment* 24: 369–377.

Read, D.J. 1993. Plant–microbe mutualisms and community structure. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 181–209. Springer-Verlag, Berlin.

Richardson, D.H.S. 1992. *Pollution Monitoring with Lichens*. Naturalists' Handbook No.19. Richmond Publishing, Slough, UK.

Richmond, R.H. 1993. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *American Zoologist* 33: 524–536.

Rowan, R. and Powers, D. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal–algal symbioses. *Science* 251: 1348–1351.

Rowan, R. and Powers, D.A. 1992. Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proceedings of the National Academy of Sciences, USA* 89: 3639–3643.

Schimel, J.P. 1994. Ecosystem consequences of microbial diversity and community structure. In: Chapin, F.S., III and Korner, C. (eds), *Arctic and Alpine Biodiversity: Patterns, causes, and ecosystem consequences*. Springer-Verlag, Berlin.

Schimel, J.P., Jackson, L.E. and Firestone, M.K. 1989. Spatial and temporal effects on plant-microbial competition for inorganic nitrogen in a California annual grassland. *Soil Biology and Biochemistry* 21: 1059–1066.

Schlesinger, W.H. 1991. *Biogeochemistry: An analysis of global change*. Academic Press, San Diego.

Schopf, J.W. 1993. Microfossils of the Early Archean apex chert: new evidence of the antiquity of life. *Science* 260: 640–646.

Sherr, E.B. and Sherr, B.F. 1991. Planktonic microbes: tiny cells at the base of the ocean's food webs. *Trends in Ecology and Evolution* 6: 50–54.

Smit, E., Van Elsas, J.D. and Van Veen, J.A. 1992. Risks associated with the application of genetically modified micro-organisms in terrestrial ecosystems. *FEMS Microbiology Reviews* 88: 263–278.

Smith, S.V. and Buddemeier, R.W. 1992. Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* 23: 89–118.

Steinberg, C.E.W. and Geller, W. 1993. Biodiversity and interactions within pelagic nutrient cycling and productivity. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 43–64. Springer-Verlag, Berlin.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.

Trüper, H.G. 1992. Prokaryotes: an overview with respect to biodiversity and environmental importance. *Biodiversity and Conservation* 1: 227–236.

Turner, S.M., Malin, G., Liss, P.S., Harbour, D.S. and Holligan, P.M. 1988. The seasonal variation of dimethyl sulfide and dimethylsulfoniopropionate concentrations in nearshore waters. *Limnology and Oceanography* 33: 364–375.

Vanderplank, J.E. 1982. *Host-Pathogen Interactions in Plant Disease*. Academic Press, New York.

Vestal, J.R. and Hobbie, J.E. 1988. Microbial adaptations to extreme environments. In: Lynch, J.M. and Hobbie, J.E. (eds), *Micro-organisms in Action: Concepts and applications in microbial ecology*. 193–206. Blackwell Scientific, Oxford.

Vitousek, P.M. 1986. Biological invasions and ecosystem properties: can species make a difference? In: Mooney, H.A. and Drake, J.A. (eds), *Ecology of Biological Invasions of North America and Hawaii*. 163–176. Springer-Verlag, New York.

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861–1876.

Vitousek, P.M. and Hooper, D.U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 3–14. Springer-Verlag, Berlin.

Vitousek, P.M. and Walker, L.R. 1989. Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59: 247–265.

Ward, D.M., Weller, R. and Bateson, M.M. 1990. 16S rRNA sequences reveal numerous uncultured micro-organisms in a natural community. *Nature* 345: 63–65.

Watson, R.T., Rodhe, H., Oeschger, H. and Siegenthaler, U. 1990. Greenhouse gases and aerosols. In: Houghton, J.T., Jenkins, G.J. and Ephraums, J.J. (eds), *Climate Change: The IPCC Scientific Assessment*. 1–40. Cambridge University Press, Cambridge.

Weightman, A.J. and Slater, J.H. 1988. The problem of xenobiotics and recalcitrance. In: Lynch, J.M. and Hobbie, J.E. (eds), *Micro-organisms in Action: Concepts and applications in microbial ecology*. 322–347. Blackwell Scientific, Oxford.

White, D.C., Ringel, D.B., Gucket, J.B. and Phelps, T.J. 1991. Biochemical markers for *in situ* microbial community structure. In: Flierman, C.B. and Hazen, T.C. (eds), *Proceedings of the*

*First International Symposium on Microbiology of the Deep Subsurface.* 4-45 to 4-56. WSRC Information Services, Aiken, South Carolina.

Wills, R.T. 1992. The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* **17**: 145-159.

Wood, W.F., Marsh, K.V., Buddemeier, R.W. and Smith, C. 1990. Marine biota as detection agents for low-level radionuclide contamination in Antarctica and the southern hemisphere oceans. In: Kerry, K.R. and Hempel, G. (eds). *Antarctic Ecosystems.* 372. Springer-Verlag, New York.

Zabowski, D., Zasoske, R.J., Little, W. and Ammirati, J. 1990. Metal content of fungal sporocarps from urban, rural and sludge-treated sites. *Journal of Environmental Quality* **19**: 372-377.

Zak, J.C., Willig, M.R., Moorhead, D.L. and Wildman, H.G. 1994. Functional diversity of microbial communities: a quantitative approach. *Soil Biology and Biochemistry* **26**: 1101-1108.

### 6.2.8 Agroecosystems

#### 6.2.8.1 Introduction

Agroecosystems are ecosystems in which people have deliberately selected crop plants and livestock animals to replace the natural flora and fauna. These artificial systems vary enormously in the intensity of human intervention (Harwood 1979), from those with only low-intensity management (e.g. shifting cultivation, home gardens, nomadic pastoralism, traditional compound farms, rotational fallows and savannah mixed farming) to those of middle-intensity management (including multiple cropping, horticulture, improved pasture mixed farming and alley farming), and high-intensity management (intensive cereal cropping and crop rotations, orchards and plantations, and intensive livestock raising). Intensive cropping systems are often monospecific and usually composed of genetically uniform plant stands. Functioning in agroecosystems is determined by the production goals of the farmer which include economic, cultural and often aesthetic values as well as those of biological production. Dependent on the circumstances of the farmer, preference may be given to short-term maximization of specialized productivity or to the diversity, persistence and stability of production. These factors influence the way in which biodiversity is managed.

#### 6.2.8.2 *Impact of agricultural intensification on relevant biodiversity components*

There is no simple quantitative index of agricultural intensification but increasing human intervention results in a deliberate reduction of the diversity of plant and vertebrate animal species. Continuing harvesting and the practices of plant, soil and pest management lower the diversity of associated plants, invertebrates and microbes (Swift *et al.* 1995). Many of the changes in ecosystem diversity and complexity associated with intensification affect a variety of ecosystem functions. Modern intensive agriculture utilizes a narrow range of crop species and genetic varieties which have been bred for high yield, including response to inorganic fertilizers and resistance to selected pests and diseases (Vanderplank 1984; Fageria 1992). Less intensive systems commonly incorporate a wider range of species and genotypes which serve a variety of production goals and/or are used for differential exploitation of microhabitats, and for their resistance to diseases and pests (Ramakrishnan 1992). Decreased plant diversity often reduces the overall biomass and almost invariably the structural complexity of the ecosystem. Multi-strata high-biomass vegetation is replaced by single-canopy monocrops often incorporating varieties with a reduced proportion of non-grain biomass. Complex horizontal patterns of intercropping are succeeded by monocultural row cropping (Wolman and Fournier 1987). Decreases in the diversity of plant species lead to increased pest and disease problems. This is accompanied by a drop in the diversity of invertebrate consumers, predators and parasites (Altieri and Liebmann 1986) a feature further exacerbated by the use of pesticides. Substitution of annual for perennial vegetation reduces the extent of soil cover and produces periods when the soil is left bare. These selective influences produce decreases in the quantity and diversity of organic matter inputs and residues, the mineral nutrient content of which may be substituted by inorganic fertilizers. Decreases in organic inputs and removal or burning of residues also reduce soil cover. Above-ground changes are reflected below ground by decreased biomass, diversity and complexity of rooting systems, and particularly the absence of deep rooting which comes from exclusion of trees from the systems (Persson and McMichael 1991).

At the landscape scale, intensification of agriculture commonly includes an increase in the size of fields and progressive specialization in production goals leading to homogenization of the landscape both within farms and across substantial areas or even regions (Wolman and Fournier 1987). This entails a move away from farming systems with a diversity of different production systems, e.g. home gardens (gardens for fruit, vegetables, spices and medicines), a variety of specialized or species-diverse crop fields, including systems related to specific micro-environments (e.g. wetlands used for rice cultivation) and associated livestock production areas (including aquaculture in wetlands) (Okigbo and Greenland 1976). This homogenization reduces the complexity of the interface between units on the landscape and leads to reduced biological migration, habitat diversity (particularly of ecotones) and disruption of nutrient flows.

#### 6.2.8.3 *Ecosystem consequences of impacts*

6.2.8.3.1 *Productivity capacity, biomass and decomposition.* The utilization of high-yielding varieties

has enabled farmers to exploit the full range of yield potential for many crops in many environments (Fageria 1992). Monocultures also can increase the efficiency of management by facilitating harvesting and simplifying marketing of the product. The narrowing of the genetic base for host resistance (particularly by dependence on a few 'major genes') produces an increased risk of yield loss through epidemic outbreaks in contrast to the 'chronic' status of disease in systems with a range of genotypes including those incorporating 'tolerance' characteristics and multiple-gene resistance (Vanderplank 1984). In some environments intercrops, tree–crop combinations and rotations show significant yield advantages over monocrops (Francis 1989; Vandermeer 1989). A component of this yield advantage is attributed to reduced pest and weed infestation due to enhanced natural biological control by natural predators (Altieri 1987). Reduced amounts and diversity of organic residues result in a reduced range of decomposition rates in intensive systems (Tian *et al.* 1992).

*6.2.8.3.2 Soil structure and nutrients.* The practices employed in clearing land for cultivation, subsequent tillage, the lowered diversity and complexity of rooting systems, and the decreased biomass and diversity of organic inputs to the soil, all act to reduce the diversity of soil organisms (Hendrix *et al.* 1990; Swift and Anderson 1992). These changes in below-ground diversity may extend to the elimination of keystone species or even entire functional groups. Some of the groups are general in distribution e.g. nitrogen-fixing bacteria, mycorrhizal fungi and predators of soil-borne pests, whilst others such as earthworms and termites are more environmentally restricted in their distribution. Clearing of vegetation and subsequent tillage leads to a decline in soil organic matter and the consequent loss of associated properties of nutrient storage, cation exchange and moisture-holding capacities (Greenland 1981). Decline in SOM is most rapid in tropical environments and also has more serious effects in the highly weathered soils of these areas which have low activity clays and thus little capacity to compensate for loss of the functions associated with SOM. Increased use of inorganic N, together with enhanced decomposition and nitrification rates, results in increased loss of N as $NO_3$ leachate or by volatilization or denitrification and soil acidification (Lowrance *et al.* 1983). The availability of high levels of inorganic N may also increase the nitrate to protein ratio in above-ground vegetation leading to enhanced susceptibility to pests and pathogens (Altieri 1987). Reduced vegetation and litter cover increases the risk of erosion (Boarden *et al.* 1990) and recorded rates of erosion in many environments now indicate losses of topsoil much in excess of the rates of renewal (Pimentel 1993). Increased biomass of livestock can result in soil compaction and changes in soil water regimes (Bochet 1983).

*6.2.8.3.3 Water distribution, balance and quality.* Decreased soil cover from canopy and litter together with a lack of contour barriers and deep-rooting plants results in decreased infiltration and increased water runoff (Hamilton and King 1983). Increased use of inorganic fertilizers across the landscape, associated with decreased capacity of the soil community to immobilize nutrients, and the absence of deep-rooting systems, leads to eutrophication of ground water (Lowrance *et al.* 1983). The same effects may be felt from disposal of high-N manures from intensive livestock production.

*6.2.8.3.4 Atmospheric properties.* Enlargement of the net area of agricultural land gives rise to increased $CO_2$, $CH_4$ and $NO_2$ when the primary productivity of the subsequent cropping system is lower than that of the vegetation it replaces. This difference is most marked in agriculture based on annual cropping, but it may be significant even in fallow rotation systems where the biomass and persistence of vegetation is low due to shortening of the fallow period. Similarly continued burning of residues may or may not lead to net emission balances dependent on whether or not this is balanced by subsequent fixation of C and N. Additional changes in carbon equilibrium come from oxidation of soil organic matter in the absence of a sufficient input of organic matter to balance this loss (Bouwman and Sombroek 1990). Agroecosystems with higher plant biomass (e.g. those incorporating trees or with fallow biomass periods in the cropping cycle) can help to compensate for these imbalances. Clearing of natural vegetation, and drainage of wetlands for cultivation, may be a major source of $CO_2$ emission from oxidation of the large stocks of organic matter. Methane is generated from anaerobic decomposition in wetlands, and increases in the area of permanently or near-permanently flooded rice cultivation are thought to account for a significant proportion of the increase in net $CH_4$ emission (Schutz *et al.* 1990). Intermittently wet and dry systems produce less $CH_4$ but more $CO_2$. Methane is also produced by anaerobic digestion in animal guts and increased specialization of ruminant production has contributed significantly to global $CH_4$ emission (Schutz *et al.* 1990). Increases in $N_2O$ emissions have been linked to the stimulation of denitrification following intensified use of inorganic-N fertilizers (Bouwman and Sombroek 1990) and from expansion of the area of flooded cultivation.

*6.2.8.3.5 Landscape and waterscape structure.* Complex agroecosystems have substantial linkages between production units in the form of natural migrations of biota (e.g. of pest predators from fallow vegetation refuges to crop areas; livestock feeding in crop fields in the dry season) or of materials (e.g. transfer of nutrients and organic matter from livestock pens as

Ramakrishnan, P.S. 1992. *Shifting Agricultural and Sustainable Development: An interdisciplinary study from North-Eastern India.* UNESCO-MAB Series, Paris, and Parthenon Publ., Carnforth.

Read, D.J., Lewis, D.H., Fitter, A.H. and Alexander, I.J. (eds) 1992. *Mycorrhizas in Ecosystems.* CAB International, Wallingford.

Schutz, H., Seiler, W. and Rennenberg, H. 1990. Soils and land use related sources and sinks of methane ($CH_4$) in the context of the global methane budget. In: Bouwman, A.F. (ed.), *Soils and the Greenhouse Effect.* 269–288. John Wiley, Chichester.

Swift, M.J. 1993. Maintaining the biological status of soil : a key to sustainable land management? In: Greenland, D.J., Knowland, J. and Szaboks, I. (eds) *Soil Resilience and Sustainable Land Use.* 235–248. CAB International, Wallingford.

Swift, M.J. and Anderson, J.M. 1992. Biodiversity and ecosystem function in agricultural systems. In: Schulze, E.D. and Mooney, H. (eds), *Biodiversity and Ecosystem Function.* 15–42, Springer-Verlag, Berlin.

Swift, M.J., Frost, P.G.H., Campbell, B.M., Hatton, J.C. 1989. Nitrogen cycling in farming systems derived from savannah: perspectives and challenges. In: Clarholm, M. and Bergstrom, L. (eds), *Ecology of Arable Land.* 63–76, Kluwer Academic Publishers, Dordrecht.

Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Ong, C.K., Anderson, J.M. and Hawkins, B. 1995. Biodiversity and agroecosystem function. In: Mooney, H.A. *et al.* (eds), *Biodiversity and Ecosystem Function.* SCOPE. John Wiley, Chichester (in press).

Tian, G., Kang, B.T. and Brussaard, L. 1992a. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions – decomposition and nutrient release. *Soil Biology and Biochemistry* 24: 1051–1060.

Vandermeer, J. 1989. *The Ecology of Intercropping.* Cambridge University Press, Cambridge.

Vanderplank, J.E. 1984. *Disease Resistance in Plants.* Academic Press, Orlando, Fla.

Wolman, M.G. and Fournier, F.G.A. 1987. *Land Transformation in Agriculture.* SCOPE 32. John Wiley, Chichester.

## 6.3 Conclusions

### 6.3.1 Background

Understanding the role of biodiversity's elements in the functioning of ecosystems is a relatively new field of research endeavour. This science is crucial in its own right for learning about the evolution of biotic interactions, the structural and functional properties of ecosystems, and the degree of sensitivity of these properties to changes in underlying diversity. Understanding the functional role of biodiversity is also important in management applications. Valuable scientific principles and guidelines for making ecosystem management decisions are beginning to emerge in spite of the field's youth and the relatively small number of experimental studies from which we can draw. We can

expect much more to follow in the near future as these research areas gather momentum.

### 6.3.2 *The importance of ecosystem approach*

The ecosystem integrates both the physical and the biological environment, and thus changes in any of the elements of the ecosystem affect the quantity and quality of its functioning. These changes in functioning may themselves then affect the biological composition of the ecosystem, its physical characteristics, and its dynamics. From a very practical standpoint, it is the ecosystem, and the array of ecosystems over entire landscapes and regions, that provides a broad diversity of goods and services to human society. The ecosystem is the level of ecological organization that most closely corresponds to the primary targets of most management decisions. Therefore, understanding the functional consequences of changes in the underlying biodiversity assumes tremendous importance for managers and scientists alike.

### 6.3.3 *Ecological goods and services*

Of particular importance in understanding the role of changes in biodiversity in ecosystem functioning is the concept of ecological goods and services. Ecosystems obviously provide marketable commodities, e.g. food from fisheries and agroecosystems and timber from forests (Box 6.3-1). Ecosystems also provide a wealth of products from which marketable goods are made, e.g. taxol from the North American yew (*Taxus brevifolia*), or from which they can ultimately be synthesized, such as the precursor to taxol found in the commonly occurring European Yew (*Taxus baccata*) or the original sources of aspirin and

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**Box 6.3-1: Biodiversity's influence on yield.**

Yield is one of the most important parameters to understand and manage sustainably in managed ecological systems. In agricultural systems, genetic diversity is very important for determining yield (Section 5.2.1). Although the highest known yields in terrestrial systems occur in species monocultures (6.2.1), substantial amounts of energy, fertilizer and pesticide are required to maintain these levels, and their long-term sustainability is difficult to ascertain. Moderate yields can be achieved without energy subsidies in managed mixed crops (6.2.8), suggesting that increased diversity at the species level can reduce the overall subsidies needed to maintain adequate, although not maximum, yields. Management that decreases animal diversity in pastures is correlated with increased yield of animal products (6.1.7). Loss of coastal habitat diversity can lead to lessening of production in unmanaged fisheries (6.1.9).

digitalis. Ecosystems further provide services for which there are obvious economic returns: ecotourism, whose popularity is growing world-wide, is one example, but the same principles hold for sport fishing and hunting, where the economic activities range from the purchase of licences to expenditures for travel and lodging.

Ecosystems also provide services that are more difficult to measure in economic terms, but which are nevertheless fundamentally important to our quality of life. For example, wetlands provide substantial capabilities to assimilate wastes and to purify the water that flows through them; microbial diversity can be important for the degradation of hazardous wastes; adequate functioning of the soil microbiota is partially responsible for the maintenance of soil fertility, while the contribution of intact forests in controlling soil erosion, particularly in mountainous regions, is well known. Although diminutions in these services can be shown to have social and economic costs, markets do not capture their full worth. They have thus been labelled 'free' services (Box 6.3-2). Our understanding of ecosystem functioning must be improved so as to enable society to maintain these 'free' services, as well as providing marketable goods and services. Building this understanding is an increasing challenge for managers and scientists.

### 6.3.4 Drivers of change

Human activities are now the dominant force in causing the alteration, redistribution and loss of biodiversity. The rate at which humans are altering the environment, the extent of that alteration, and the consequences of these changes for biological diversity are unprecedented in human history, and are now beginning to pose substantial threats to economic and cultural aspects of many societies. Depending on the circumstances, human activities may increase, maintain or diminish the diversity of species, genes or ecological communities in a given region and at a given time, but the general trend is an increasing loss of biodiversity at the global scale. Some of these changes, such as the erosion of genetic variability and the extinction of species, are truly irreversible; others are not, but the challenge of managing natural resources while maintaining adequate levels of biodiversity has increased markedly. Moreover, pressures on biological diversity are likely to increase still further as a consequence of human-induced climate change.

### 6.3.5 Factors affecting the functional sensitivities of ecosystems

Reductions in species diversity can reduce the ability of ecosystems either to resist stress from environmental factors or to recover from disturbance. For example, coral reefs, mangroves and kelp forests can buffer adjacent terrestrial systems from ocean waves, and thus the presence of coastal landscape diversity can mitigate the effects of

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**Box 6.3-2: Water quality and flood control: provision of 'free' services by ecosystems.**

Biodiversity at both landscape level and species level influences water quality and quantity. For example, conversion of vegetation within a watershed from forest or shrubland to grassland increases stream-flow out of the watershed. Loss of the woody overstorey in riparian systems greatly increases water temperature, and reductions in the diversity and productivity of the herbaceous layer increase the velocity and erosive capacity of the stream-flow (6.1.7). Thus, landscape-level conversions, particularly those involving hydrological changes associated with clearing forested watersheds, can increase flows and the variance of flows, making flood control more difficult and expensive.

In aquatic ecosystems, even the addition of a single species can greatly affect water quality. For example, the accidental introduction of the zebra mussel into the Great Lakes greatly increased water clarity due to its tremendous filtering capacity and rapid population growth (Ludyanski *et al.* 1993). This increase in clarity, unfortunately, comes at the expense of many natural plankton communities, and thus affects fish populations.

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storms that would otherwise produce substantial erosion (6.1.9; 6.1.10; 6.1.11). Experimental studies have shown that species-rich temperate grasslands exhibit smaller changes in plant biomass after drought than less rich areas (6.1.7). The existence of relatively undisturbed communities within a mosaic of different land uses can serve as sources of propagules, seeds and dispersing animals to recolonize areas that have been adversely affected by other stresses (6.1.1).

The sensitivity of ecosystem functioning to changes in biodiversity appears to be influenced in part by the number of species that contribute to processes in similar ways (6.2.2). For example, the functional consequences of species losses should be greatest for those systems that have few species – such as boreal forests, deserts and islands, because there are few species that can substitute for the deleted taxa, and thus the chance of adversely affecting an ecosystem process from even a single deletion is high (6.1.4; 6.1.6; 6.2.6; 6.2.7). For example, emissions of methane, nitrous oxide, dimethyl sulphide and volatile organic chemicals, each seem to depend on a limited number of taxonomic groups with functionally similar properties. It is not understood why this is the case, but it seems reasonable to presume that the marginal effect of losing any one of them would be high.

Conversely, ecosystems or processes with many functionally similar species should be better protected from such disruptions in the long term, because there are more species that respond differently to environmental stress. For example, a wide variety of organisms comprise the functional group of primary producers, and there is no good evidence that primary productivity in ecosystems depends strongly on the number of species, within reasonable limits (Box 6.3.3).

On short time scales, some degree of substitutability can be documented in particular cases (6.1.1). In a temperate grassland system, dominant species fully compensated for the removal of subordinate species, while the subordinate species only partially compensated for the removal of dominant species (6.1.7). Substitutability has some limitations, however. At the genetic level, populations may not be completely substitutable because of local adaptations. Thus, even for small areas, when a longer timescale is considered, our best understanding is that functional substitutability among species is limited, and it is unwise to assume that species are functionally redundant.

Ecosystems can vary tremendously in the number of functionally similar species they contain, and there is no consensus on what determines the number of functionally similar species in particular biomes. For example, marine ecosystems (open ocean, near coastal, estuarine) tend to have greater phyletic diversity among functionally similar species than do terrestrial ecosystems, due at least in part to their greater overall phyletic richness. Many tropical terrestrial ecosystems have large numbers of apparently

functionally similar species, especially when compared to their temperate analogues. Even within a climatic zone, historical factors can result in substantial variation in the number of functionally similar species, as is seen in the wide variation in numbers of flowering plant species in different zones of temperate deciduous forest and different Mediterranean ecosystems.

Each individual species may play many different functional roles, which are rarely fully understood. It is possible for an organism to have a suite of biological traits that confer on it a dynamic importance out of proportion to its abundance, i.e. it plays a keystone role in organizing structure and processes throughout an ecosystem. The effects of moose and reindeer on boreal and Arctic ecosystems; sea otters in northern California kelp forests; many parasitoids and parasites in biological control programmes; and the major grazers on grassland ecosystems, all provide well-documented examples. The full influence of such species is generally only seen and understood when it has been lost from the system. Our ability to predict *a priori* which species will have such effects is very poor, and they may occur in either species-poor or species-rich systems.

When changes in ecosystem composition and functioning do occur, they are often gradual. However, some systems, especially islands, lakes and agroecosystems, exhibit dynamic thresholds in their response to a major stress or disturbance that affects diversity. Others seem to be susceptible to chronic stress, and these tend to have very few species with functional similarities: e.g. boreal, Arctic and alpine systems.

### Box 6.3-3: How does biodiversity influence productivity?

The relationship between biodiversity and primary productivity needs to be considered over both short and long time scales. On relatively short time scales and small spatial scales, the most important issue is whether reductions in species diversity will adversely impact productivity. Over longer time scales, the role of diversity in the maintenance of productivity in systems undergoing a variety of stresses becomes paramount.

In most biomes, primary productivity appears to be only weakly related to the number of plant species, as it usually peaks at relatively low species-richness levels (6.2.1; 6.1.2; 6.1.7). Diversity may play a role in the maintenance of productivity in the face of natural and human-induced change (e.g. disturbance, drought, climate change, toxins) (see 6.2.1; 6.1.2), and changes in landscape configuration can have large and long-lasting effects on regional productivity (e.g. banded vegetation systems, 6.2.5).

### 6.3.6 Invasions, introductions and species losses

International travel and trade, in addition to climatic variation, provide opportunities for the deliberate introduction or accidental invasion of species into new ecosystems. When a species enters an ecosystem in which it previously did not occur, it can either adversely disrupt ecosystem processes or have positive effects — such as providing biocontrol of pests or pathogens in agroecosystems. Microbial species introductions, particularly of plant pathogens, have had a large effect on ecosystem composition in both natural and managed systems, but these effects do not always have large observable effects on ecosystem processes (6.2.7). For example, the loss of chestnut from eastern deciduous forests in North America, due to the introduction of chestnut blight from Europe, was both rapid and dramatic, but there have been no discernible consequences for ecosystem functioning as other tree species seem to have fulfilled its original functional roles. On the other hand, introductions of new capabilities such as nitrogen fixation into ecosystems whose component species previously did not have this ability, typically have dramatic changes in

both composition and ecosystem functioning. The introduction of nitrogen-fixing trees into sites in Hawaii has led to a complete restructuring of the plant communities, with consequent changes in nutrient supply, fire frequency and water availability. Biotically impoverished systems whose major species have only limited genetic diversity, such as many production agroecosystems, are often very susceptible to the effects of introductions and invasions (5.2.1; 6.2.1; 6.2.6), with the introduction of pathogens being of primary concern.

Islands and ecosystems with relatively few component species, such as boreal forests, seem to be more susceptible to species invasions than species-rich biomes such as tropical forests, so it would be expected that invasion of species leading to disruption of ecosystem processes is more likely to occur in the former than in the latter (6.2.6). Freshwater ecosystems in all climatic zones also seem to be especially sensitive to invasions and introductions (6.1.13). In general, areas of ecosystems that have been subjected to disturbance or stress from other environmental factors, such as fire, drought, overgrazing or extensive clearing, can provide open habitat and resources that allow invaders to become established. Whether or not introduced species will spread from their original entrance depends on the particulars of their biology, and the biology of the native species they encounter. Apart from these generalizations, there is very little ability to predict a *priori* the effects of accidental or deliberate introductions, suggesting that considerable prudence be exercised.

### 6.3.7 Transformation and fragmentation of populations and ecosystems

The net effect of human activities may possibly be an increase in the overall diversity of ecosystem types around the world, some of which are extremely important to societal well-being. Human activities are, for example, directly responsible for creating agroecosystems. However, these increases in the diversity of ecosystem types have come at the expense of impoverishment of a great number of natural communities, and the reduction of at least some ecosystem services.

Some fragmentation of existing ecological communities is inevitable, except in areas that have been specifically protected. In nearly all cases, the fragmentation of existing communities reduces the diversity of native species in their natural habitats. Human impacts, in particular habitat loss, fragmentation and over-exploitation, tend to reduce severely the size of many biological populations, and this increases the risk that a population will be lost, ultimately leading to species' extinction. Even when the species does not become extinct, its loss from a local region or a major reduction in its population can have significant consequences for human livelihoods and ecological services. The species most likely to be lost are large predators and other species with large body sizes and area requirements. Also likely to be lost are species with less ability to disperse among and colonize habitat patches. Species likely to survive fragmentation will be those best adapted to patchy and frequently disturbed environments, especially early successional and easily dispersed species. Fragmentation is thus expected to result in ecosystems dominated by such 'weedy' species. Such systems have characteristically higher losses of nutrients, nitrogen and carbon; higher litter quality and therefore faster decomposition rates; simpler spatial structure; and less overall protection from herbivory than the original communities that preceded them.

No biome is functionally resistant to landscape-scale changes in diversity, particularly those changes due to anthropogenic alterations. The large-scale conversion of ecosystems in landscapes tends to have long-lasting effects on system processes independently of whether the particular ecosystems were originally of high or low diversity. For example, the large-scale transformation of forested ecosystems to pastureland, grasslands and agriculture has been an important contributor to the increase in atmospheric carbon dioxide over the last several hundred years. The first phase of this transformation occurred in the developed countries of the Northern Hemisphere, but in recent decades tropical conversion of forested ecosystems to grassland has become the main contributor. During the 1980s, conversion of tropical forest to grassland contributed approximately 1.6 gigatons of carbon per year to the atmosphere, in addition to the 5.5 gigatons of carbon per year released by fossil fuel combustion. This was slightly offset by regrowth of temperate and boreal forests, which sequestered about 0.5 gigatons per year during the same time period. Improved management of forested ecosystems and reforestation in both the temperate and tropical regions can continue to sequester carbon from the atmosphere and move it to longer-lived soil pools, thus reducing the rate at which greenhouse gases are added to the atmosphere.

The interactions among different ecosystems determine a landscape's functional sensitivity to changes in diversity. Landscape-scale functions are affected by changes in diversity at lower hierarchical levels either when the changes in diversity affect the strength of the spatial interaction, or when the changes in diversity affect the strength of sources or sinks of the materials being transferred. There are characteristic differences in these aspects of ecosystem 'connectedness': e.g. ocean systems have high connectedness compared to terrestrial systems, therefore changes in one place may ultimately have effects far away. In many terrestrial systems, the connectedness of landscape components is determined by water flow, and thus both topography and vegetation play major roles in determining landscape-level functional responses. However,

even in terrestrial systems, atmospheric or climatic stress or disturbance, or processes that produce feedbacks to the atmosphere, operate through a medium that provides high connectedness. The acidification of soil and surface water in forested landscapes; changes in soil microflora; and loss of nitrogen from previously nitrogen-limited forests as a consequence of acid precipitation in North America and Europe, demonstrate that landscape-level functional changes can occur in terrestrial systems because of atmospheric stress.

Within reasonable bounds, we cannot consider transformations of ecological communities to have only local effects. In marine systems, changes in geographically distant ecosystems may greatly affect one another through, for example, larval transport or the transport of pollutants by currents (6.1.12). Even in terrestrial ecosystems, migratory animals and the atmosphere provide similar linkages between distant ecosystems. Fragmentation of temperate forests in North America can, for example, affect the survivorship of tropical-temperate migratory birds, which are important seed dispersal and biological control agents in neotropical areas. Changes in forested watersheds can have obvious effects on water flow and quality far downstream. Current rates of forest conversion will also reduce potential or actual sustainable economic benefits due to soil and water conservation services, recreation and tourism, and non-timber products.

### 6.3.8 Goods and services at risk

The transformation, fragmentation and loss of habitats has had many different effects on the provision of ecological goods and services. The massive creation of new agroecosystems has obviously resulted in the ability to increase food production dramatically. At the same time, it has led to the impoverishment of natural communities and can reduce the ability of ecosystems to maintain productivity in the face of environmental fluctuation. Substantial alteration in soil fertility can be driven by changes in plant species composition and microbial functional groups which are required for the cycling of important plant nutrients. The loss of particular plant species and loss of critical communities, such as forested watersheds, can reduce the ability of ecosystems to control soil erosion and retain water. Conversion from forest or shrubland to grassland dramatically increases stream-flow, and if this occurs in the upper reaches of watersheds, can increase the need for additional water control measures through dams. Thus, degradation and conversion of forested watersheds can result in significant economic costs due to increased flooding and sedimentation.

The rapid transformation of forested ecosystems without regard for appropriate management of water resources, has had serious consequences for human health (Box 6.3-4). Deforestation led to major malaria outbreaks in the western Amazon, due to the creation of new habitats for mosquito

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**Box 6.3-4: How do disruptions in biodiversity influence human health?**

Disruptions in biodiversity can affect disease transmission either through their influence on vectors of disease, or more directly on their influence on the disease-causing organisms themselves. Changes in landscape diversity, due to agriculture, have resulted in the the spread of human diseases. For example, the introduction of slash-and-burn agriculture into wet tropical Africa resulted in an increase in malaria which in turn increased the occurrence of sickle-cell anaemia (5.2.1). Physically damaged reefs are often invaded by the dinoflagellate *Gambierdiscus toxicus*, which is responsible for ciguatera in humans (6.1.10). Unidentified precursors in the dinoflagellate are transformed into toxins which accumulate in food chains leading to table fish.

Other direct or indirect effects on health can come from biodiversity's influence on particular ecosystem processes. Changes in plant species composition can result in changes in the emissions of volatile organic compounds by plants which can lead, along with industrial pollutants, to increases in tropospheric ozone that can indirectly affect human health (6.2.4). Rooting depth changes as a result of replacing species when forests are converted to agricultural systems. These changes in rooting depth affect the amount of water percolating through the soil and may increase the levels of nitrate in ground water (6.1.4; 6.1.7).

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vectors, and also to the increased colonization of the region by susceptible human populations. However, management of vector habitats, when coupled with other public health measures, dramatically reduced the incidence of the same disease in the southern United States.

Increases in the extent and yield of rice agroecosystems have provided food for vast numbers of people. At the same time, the increases in rice cultivation and livestock husbandry have been major contributors to the increased methane concentrations in the atmosphere, and thus to concerns over greenhouse warming. It is likely, although less certain, that increases in the use of nitrogenous fertilizer in the tropics in order to enhance agricultural productivity are also contributing to rising atmospheric concentrations of nitrous oxide, a very powerful greenhouse gas, in the atmosphere (Box 6.3-5).

Transformation of parts of ecosystems that then acquire substantial economic value often requires intensive management in other parts of the ecosystem. Fire control in forest ecosystems provides one example. Fire control in

many forests provides substantial benefits for adjacent property owners, and for hunting and recreation. However, because fire control completely alters the frequency of naturally occurring fires, it also can have the unintended side-effect of contributing to the buildup of fuel, possibly leading to more intense fires which have adverse effects on plant regeneration and wildlife habitat, and threaten human habitation. Prescribed burning can partially mitigate these potential adverse consequences, but can itself be expensive. Fire control thus illustrates the need to balance carefully the costs and benefits of maintaining diversity in ecological communities.

Over-exploitation in extracting materials and goods from converted or degraded ecosystems, such as poorly managed cropping and timber harvesting, while providing food and wood, also tends to disrupt some ecosystem services by decreasing the ability of the ecosystems to retain nutrients, water and topsoil. These effects are due directly to the mechanical effects of extracting the desired materials, along with the longer-term biogeochemical effects of removing carbon, nitrogen and nutrients from the systems. Over the long term, reductions in soil carbon and soil fertility, and increases in overland flow and sedimentation rates, are often the result (Box 6.3-6). Increased fertilizer and pesticide subsidies are then often required to maintain adequate agricultural yields, resulting in increased direct costs.

The introduction of non-native species, and over-exploitation of resources, has been especially problematic in grassland ecosystems. In arid and semi-arid regions, the introduction of cattle, sheep and other non-native grazers, subsequent overgrazing, over-use of fire, and the introduction and spread of alien plant species, can result in desertification because the new species lack the adaptations of the natural communities for using water efficiently in the face of the original herbivores.

### 6.3.9 Implications

Understanding the functional role of biological diversity is important scientifically, but as our analysis makes clear, it also is important from a managerial and policy perspective. Changes in biodiversity will, to the best of our current knowledge, have important implications for sustainable resource management, and for the continued provision of ecological goods and services. Our analyses suggest that these implications may be particularly important for longer time scales, especially for those ecosystem processes and goods such as primary productivity and crop yields that do not depend strongly on diversity over short time scales. As the need for sustainable management of ecological goods and services increases, the maintenance of these processes becomes more important over long time scales, and the importance of considering biodiversity as a component to be managed also increases. Ecosystems can be managed so as to maintain goods and services that might otherwise be lost, if

### Box 6.3-5: How does biodiversity influence atmospheric composition and climate?

The influence of biodiversity on air quality is not generally thought to be strong in comparison with direct anthropogenic effects. However, there is some relationship between the actual composition of ecosystems and landscapes and air quality. Because different plant species emit different volatile organic compounds, species composition can affect the concentration of tropospheric ozone, in conjunction with industrial pollutants (6.2.4). Certain ecosystems within a landscape serve as particularly efficient sinks for pollutants (6.1.3).

Biodiversity at a species or ecosystem level plays a stronger role in the relative strength of sources and sinks of trace gases. Some species and systems are particularly high sources of trace-gas emissions, such as DMS, CH4, $N_2O$, and NO; (6.1.2; 6.1.6; 6.2.4; 6.2.8). Methane ($CH_4$) is one of the most important greenhouse gases and its production is restricted to a single group of bacteria species that require anaerobic conditions, they are found especially in wetlands and in the digestive tracts of ruminants and termites (6.1.2; 6.1.7; 6.2.4). For DMS, microbial species interactions such as grazing can have a strong influence on emission rates (6.2.4; 6.2.7), but the sensitivity to anthropogenic disturbance is not known. Other microbial species provide important sinks for $CH_4$ and NO.

The changes in atmospheric concentrations of some trace gases can be related in part to alterations in landscape-level diversity and human activities. One of the sources of the net addition of $CO_2$ to the atmosphere is land-cover conversion (i.e. change in landscape diversity) notably in the direction of tropical evergreen > tropical deciduous > temperate forests (6.1.2). Net additions of $CH_4$ can largely be attributed to human activities enhancing the extent of rice paddy soils, livestock, and other sources rather than one particular change in landscape diversity.

In temperate forests, changes in species composition can affect atmospheric interactions and local weather through changes in evapotranspiration and albedo (6.1.3). In desert and grassland systems, the amount of water transpired — and hence the local climate — depends very strongly on the particular complement of species present and the way in which they partition water (6.2.3). In marine systems, planktonic algae emit considerable amounts of dimethylsulphide (DMS), which subsequently have a strong influence on cloud formation (6.1.9; 6.1.12; 6.2.4).

**Box 6.3-6: How is biodiversity related to soil fertility, soil erosion and the control of hazardous waste?**

Soil fertility is related to soil parent material, litter type and the presence of basic microbial species richness. Therefore, within an ecosystem, species composition certainly matters, and changes in species diversity can therefore lead to changes in soil fertility. Substantial alterations in soil fertility can be driven by changes in plant species composition (6.1.6), both within and among ecosystems. Unfortunately, few data are available on microbial richness in soils, or the interactions among plant species richness per se, litter quality, soil biota and soil fertility. We know that different microbial functional groups are required for the cycling of important plant nutrients. However, at present we have little knowledge of the comparative roles of microbes within functional groups (6.2.7).

Biodiversity can affect rates of soil erosion in a variety of ways. At the species level, individual plant species, due to their growth form and canopy architecture, can play a crucial role in controlling soil erosion (6.2.5). Particularly in arid and semi-arid regions, then, reducing the diversity of plant species can accentuate soil losses through erosion. Landscape diversity resulting mainly from land-use patterns can also affect erosion rate directly (6.1.2; 6.1.4; 6.1.7). These changes largely come about through land-cover conversion, especially the transformation of forested systems to agricultural uses or pastures, but they can also come about through the intensification of agricultural management. Both changes generally have the effect of lowering the water and soil retention capabilities of the landscape, leading to increased soil erosion. Coastal forested wetlands play an important role in controlling shoreline erosion (6.1.11).

Microbial diversity can be very important for the degradation of xenobiotic compounds (i.e. hazardous wastes). It is important both for dealing with the myriad toxic compounds entering the environment in all biomes and also in cases in which microbial community interactions, such as co-metabolism, are necessary to break down a single compound (6.2.7). These phenomena can be exploited to identify specific organisms, or groups of organisms, that possess traits that could be harnessed on larger scales either to mitigate the effects of accidental contamination, or to reduce hazardous waste production in industrial processes

the appropriate components of biodiversity are maintained (Box 6.3-7). Changes in biodiversity can have direct and indirect effects on atmospheric composition, management of water, and human health. Thus, management caution in reducing diversity is indicated for both species-rich and species-poor systems, when it is important to sustain the provision of goods and services over long time scales.

**Box 6.3-7: Appropriate management can enhance ecosystem services**

Carbon sequestration can be enhanced by managing landscape diversity. Conversion to grassland, the most common type of forest conversion in the tropics, contributes the largest amounts of carbon emissions in those areas. Returning agricultural land to forest, or managing agricultural land more effectively to enhance soil carbon sequestration, can lead to lower emissions of trace gases, and can slow the rate at which excess carbon dioxide is added to the atmosphere.

Forest fragmentation profoundly affects biotic interactions which constitute important ecosystem services. A clear example of this is biotic pollination (6.2.6). Reducing the degree of fragmentation, perhaps by providing sufficient corridors for dispersal, might be able to maintain an acceptable level of pollination while allowing some harvesting of resources.