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-I). 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

Box 6.3-I: 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 worldwide, 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 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 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 longer 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, N₂O, and NO; (6.1.2; 6.1.6; 6.2.4; 6.2.8). Methane (CH₄) 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 CH₄ 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 CO₂ 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 CH₄ 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.

Acknowledgements

We thank the many contributors and reviewers of Sections 5 and 6 for their dedication to the task of producing balanced and credible assessments and their patience and persistence during numerous revisions. We are particularly grateful to the John D. and Catherine T. Macarthur Foundation during the critical initial phases and, subsequently, UNEP for their support of this work through awards to the Scientific Committee on Problems of the Environment (SCOPE). We extend special recognition to Veronique Plocq-Fichelet, Executive Director of SCOPE, for her exceptional assistance and to Anne Schram for her continuing optimism and efficiency during the protracted and intense process of preparing these Sections.