

11 Global change, biodiversity and ecological complexity

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Box 11.1 Summary

Causes of change in biodiversity:

- Changes in land use and introduction of alien species are the most important causes of rapid shifts in biological diversity. Over the coming decades, the effects of land-use change may be altered by climatically induced changes in frequency and severity of disturbance. The direct effects of changes in atmospheric composition and climate will increase with time.
- Changes in land use often lead to increased habitat fragmentation, affecting species persistence, abundance and diversity at the landscape scale. Models and empirical studies confirm the existence of species-specific thresholds. When these thresholds are passed, species decline in abundance, break up into isolated populations, and ultimately may go extinct.
- The invasion of exotic species into natural systems either through accidental or purposeful introductions (e.g. in biotic control efforts) is a powerful driver of global change with increasing threats to the viability of indigenous species. Habitat fragmentation and altered disturbance regimes enhance the invasibility of alien species.
- Altered land use is affecting diversity most strongly in humid tropical and temperate regions. Changes in climate and atmospheric composition may be more important in arid and arctic/boreal ecosystems.

Consequences of changes in biodiversity:

- Species diversity affects ecosystem processes through both species traits and species numbers. Species that have largest effects on ecosystem processes include those that alter:
 - (i) frequency and intensity of disturbance;
 - (ii) water and nutrient supply;
 - (iii) trophic structure.
- There is currently no clear understanding of the relationship between species number and ecosystem processes. However, maintaining a high species number increases the probability of retaining species that:

- (i) effectively acquire resources under differing conditions;
- (ii) tolerate extreme events.

Therefore, maintaining high species number in ecosystems could result in higher productivity, nutrient retention, and buffering of ecosystems against unanticipated effects of global change.

- Genetic diversity in crops has become increasingly important to enhance resistance against new varieties of pests and diseases. High diversity of crops and associated species will increase the probability of dependable yield of low-input agriculture in unpredictable environments.
- Changes in landscape diversity may affect the spread of fire, pests, and water-borne materials.

Box 11.2 Future needs

There is a need to:

- examine diversity at scales other than species, i.e. genetic diversity, functional type diversity, and, at larger scales, landscape diversity to understand the interactions within and between these levels of organization, the effects on trophic pathways, and the consequences for ecosystem functioning;
- understand the resource requirements and population dynamics of species most responsible for ecosystem functioning, i.e. keystone and dominant species, especially in fragmented landscapes;
- intensify efforts to understand the extent, frequency, or severity of disturbance that can be tolerated by ecosystems without permanent loss of biodiversity and disruption of system-specific processes;
- undertake more observational studies of current invasion events of exotic species in natural communities and analyse past invasion events to determine (i) the effects of biological invasions on biodiversity and ecosystem functioning, (ii) the characteristics that make an ecosystem vulnerable to invasions, and (iii) the characteristics that make an organism a successful invader;
- extend local and short-term studies on biodiversity/ functioning relationships to different regions and longer time periods;
- understand the significance of species diversity within and among functional types (i.e. group of species with similar effects on ecosystem processes) with respect to the stability of ecosystem processes under global change.

11.1 Introduction

Large changes in biological diversity are occurring at a global scale simultaneously with changes in land use, composition of the atmosphere, and climate. These changes result mainly from human activity and are expected to intensify

in the near future, with both the magnitude and scope of change likely to continue to increase into the next century (see Chapter 1).

Biological diversity or biodiversity encompasses a suite of scales from species and genetic diversity to landscape diversity. Perhaps of all the changes in biodiversity currently occurring, the most widely recognized are those occurring in species diversity or species richness. However, equally important are those changes in diversity occurring within species (genetic diversity), or at larger scales such as changes in landscape diversity. In addition, changes in the trophic structure and pathways of ecosystems are occurring, and collectively all these changes are referred to as changes in ecological complexity.

Human activity influences both biodiversity and overall ecological complexity, directly and indirectly. Overexploitation of natural resources, such as overgrazing, and the conversion of natural ecosystems into croplands and urban areas results in habitat alteration, destruction, and fragmentation. These changes lead to a global reduction of species diversity and within-species diversity. Indirectly, human activity also affects biodiversity since fossil fuel combustion and land-use change affect the composition of the atmosphere and climate, which in turn result in a global reduction of species diversity.

Changes in species diversity involve not only extinctions but also invasions. Activities such as domestic livestock grazing or crop production may result, at local scales, in net increases or decreases of species diversity while at global scales they almost always result in decreases in species diversity. In summary, at a global scale the terrestrial biosphere is being impoverished and homogenized as a result of human activity.

Whereas human perturbations decrease global species diversity, they tend to increase landscape diversity as a result of the introduction of new landscape units such as croplands in a matrix of native grassland or logged patches in a forest. The intricate patterns of croplands, forests, and grasslands and their spatial distribution affect the functioning of ecosystems, such as the flow of matter, disturbance regimes, and biosphere/atmosphere interactions.

How do anthropogenic changes in land use, chemical composition of the atmosphere, and climate affect biodiversity? How do changes in biodiversity affect the ability of ecosystems to respond to the other changes that are occurring at the global scale such as deforestation, desertification, CO₂ enrichment, and climate change?

The importance of these questions has spawned a series of scientific endeavours that are described in the following pages. This chapter first reviews the causes and consequences of changes in diversity at different scales. It assesses the current understanding of the impact on diversity of changes in land use, disturbance regime, species introductions, climate, and atmospheric composition. Second, it analyses the consequences of those changes for the functioning

of ecosystems. This section is organized in a hierarchical fashion, with discussions of the consequences on ecosystem functioning of changes in genetic, species, and landscape diversity. The analyses of causes and consequences of changes in diversity are mostly retrospective and based on the interpretation of the mechanisms of phenomena that have already occurred. The last section attempts to look into the future and to develop biodiversity scenarios. Several other disciplines, from atmospheric science to human demography, provide predictions of trends and patterns of quantities as disparate as CO₂ concentrations in the atmosphere, human population density, cereal production and people at risk from hunger for the next 100–200 years. The biodiversity scenarios described here were based on simulation models of changes in land use, climate, and atmospheric composition and serve as inputs to other models.

11.2 Causes of changes in biodiversity

11.2.1 Impact of changes in land use and disturbance regime

Fragmentation

The total area of available habitat is the primary factor determining species abundance and landscape levels of biodiversity (Noss, 1996). As the habitat within a landscape becomes fragmented by natural or anthropogenic disturbances, or as the quality of ecological resources is modified by climate change, the persistence of species adapted to these landscapes may decline and invasions of exotic species increase (Hobbs, 1989). Time-delays in the response of biota to changes in the heterogeneity and availability of resources may result in several generations elapsing before the consequences of landscape change are realized (Tilman *et al.*, 1994). These interactive effects of the biota with changes in the pattern of habitat fragmentation make changes in diversity at landscape scales difficult to predict.

The degree to which fragmented habitats remain connected is an important factor affecting species abundance and diversity at landscape scales (Fahrig & Merriam, 1985; Gustafson & Gardner, 1996; Noss, 1996). A variety of theoretical models have shown that thresholds exist where incremental reductions in available habitat will result in sudden changes in connectivity (Gardner *et al.*, 1987, 1992, 1993; Lavorel *et al.*, 1995) (Fig. 11.1). Because individual species utilize landscape resources at different spatial and temporal scales, each species experiences different patterns of change depending on the 'dimensions' of their ecological neighbourhoods (Addicott *et al.*, 1987). Knowledge of the resources required by particular species, and information on their dispersal abilities, allows the value of the thresholds to be estimated for each species (O'Neill, 1988; Plotnick & Gardner, 1993). For instance, species that are capable of

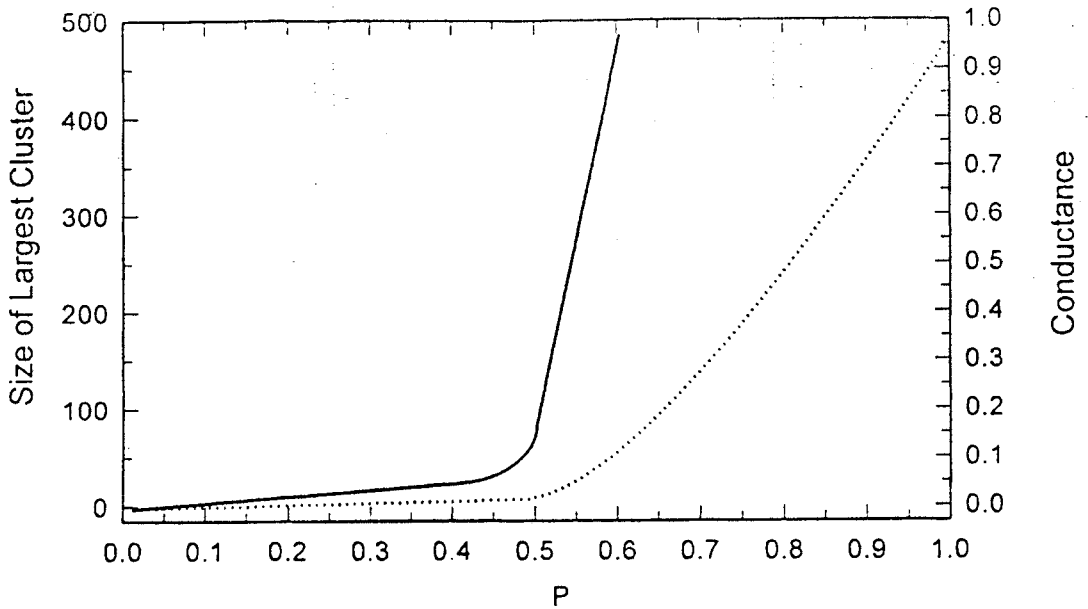


Figure 11.1 Change in conductivity (dashed line) and the average cluster size (solid line) as a function of P , the fraction of the landscape containing suitable habitat. These curves are estimated from gridded landscapes with connectivity between habitat sites established by contact along one or more edges of the four adjacent sites. A connectivity threshold exists at $P = 0.5928$ producing a sudden increase in average cluster size. Assuming that movement is restricted to adjacent habitat sites, conductance below the critical threshold is nearly zero. Above the critical threshold conductance rapidly increases as resistance to movement declines. Adapted from Plotnick & Gardner (1993).

long-distance dispersal and have small neighbourhoods may be able to locate refugia within a disturbed landscape, while species with a larger neighbourhood and poorer dispersal capabilities will be adversely affected by shifting patterns of disturbance (Baker, 1993). Typically, species that survive better in fragmented landscapes are able to either live and reproduce in the matrix of land uses surrounding remnant habitat patches, or have a sufficiently small ecological neighbourhood to persist in small remnant patches, or are mobile enough to integrate many patches into a single interbreeding population (Noss, 1996).

Two empirical studies support these results. The first effect of fragmentation on birds and mammals is the loss of habitat and subsequent reductions in overall levels of abundance (Andren, 1994). As fragmentation continues, the distribution of habitat (i.e. patch size and isolation) becomes progressively more important, with a noticeable threshold in species decline when about 30% of the suitable habitat remains. Metapopulation theory predicts that as habitats become more fragmented and patch sizes become smaller, species will be able to maintain viable populations in fewer and fewer suitable habitats, leading to

eventual extinction (Tilman *et al.*, 1994). Hanski *et al.* (1995b) have confirmed this result with observed declines of butterfly populations with diminishing fractions of suitable habitat. Although much work remains before there is a general theory that can relate metapopulation dynamics with landscape change, this confirmation of modelling results with field observation is encouraging.

The spatial arrangement of habitat types (e.g. forests, wetlands, riparian vegetation, etc.) within landscapes is a primary factor determining the rate of exchange of material, energy and organisms at scales of kilometres (Turner, 1989; Pickett & Cadenasso, 1995). The amount and spatial arrangement of different habitat types is dynamic (Romme, 1982; Baker, 1989), with disturbances (both natural and anthropogenic) and recovery from disturbance affecting the successional status of individual patches. However, over a sufficient period of time a shifting mosaic of habitat patches occurs within natural landscapes (Bormann & Likens, 1979), maintaining overall levels of habitat diversity. Because habitat patches may be temporarily or permanently lost as the result of disturbance, extinction of species within fragmented landscapes can be expected (Tilman *et al.*, 1994). Therefore, in shifting mosaics frequent exchanges of organisms among isolated habitat patches is essential for maintaining biodiversity at landscape scales (Noss, 1983).

Disturbance

Landscape disturbance is any relatively discrete event external to the system being studied that disrupts ecosystem, community, or population structure and processes (Pickett *et al.*, 1989). It includes events such as fires, storms, outbreaks of pests or pathogens, mass movement of material, and human-induced changes in land use. Rapid shifts in disturbance patterns are now occurring at global scales as humans alter land use (Turner *et al.*, 1990), replacing natural, periodic disturbances with more permanent changes in landscape pattern.

Disturbance regimes can be characterized by four parameters (Sousa, 1984): the *frequency* of disturbance (the number of occurrences within a given time period), the *intensity* of disturbance (the likelihood of spread of disturbance across the landscape), the *severity* of disturbance (the degree of ecological change caused by disturbance) and the *duration* of disturbance (the length of time the disturbance lasts). Changes in these parameters constitute a change in the disturbance regime, which ultimately affects the spatial heterogeneity of ecological resources and species that are adapted to these patterns (Franklin & Forman, 1987; Baker, 1992; Forman, 1995). For instance, if climate change produces warmer and drier conditions, more frequent fires are likely to occur (Romme & Turner, 1991). However, the relationship between changing disturbance regimes and patterns of species abundance is complex. Many species are adapted to existing disturbance regimes, with periodic disturbances provid-

ing temporary release from competitors and opportunities for increases in abundance. Disturbances may enhance the invasibility of many species, especially when the availability of a limiting resource (e.g. space or nutrients) changes (Hobbs, 1989). Severe disturbances may also eliminate seeds stored in the soil, causing declines in abundance of native species (Malanson, 1984). Climate-induced changes in the fire regime in Yellowstone National Park, USA, have probably had substantial consequences for the extent and age-class distribution of native forest communities (Romme & Turner, 1991).

The complex patterns generated by changes in landscape heterogeneity and disturbance regimes have been explored with simple probabilistic models (Gardner *et al.*, 1987; Turner *et al.*, 1989a) and have suggested that, when susceptible habitats occupy less than 50% of the landscape, disturbance effects are more related to disturbance frequency than intensity. When more than 60% of the landscape is occupied by susceptible habitat, disturbance effects are more related to increased intensity than frequency (Turner *et al.*, 1989b). Other spatially explicit models have also indicated that small changes in landscape pattern can cause dramatic shifts in the frequency, duration, and intensity of disturbance events (Franklin & Forman, 1987; O'Neill *et al.*, 1992; Turner *et al.*, 1994).

Shifts in land-use patterns and fire suppression efforts, causing fuels to accumulate, result in an increased risk of larger and more severe fires (Swetnam, 1993). The loss of large areas of forests due to fires may result in significant, long-term changes in the pattern of vegetation regrowth and succession with possible shifts to a new vegetation state (Noble & Slatyer, 1980; Starfield & Chapin, 1996). Results of a landscape-scale fire model have suggested that climate-induced changes in fire regimes produce rapid shifts in the pattern of mature forests (Gardner *et al.*, 1996). Small changes in weather produce significant shifts in the age structure and spatial arrangement of forests. A 'drier climate' results in less mature forest with a greater degree of habitat fragmentation. A 'wetter climate' produces fewer but larger fires. These results are consistent with fire records in giant sequoia stands that show that frequent small fires occurred during warm periods but more widespread fires occurred during cooler climate conditions.

Changing land-use patterns can interact with disturbances to effect changes in the frequency, severity, or extent of the disturbance. For instance, fire suppression in giant sequoia groves has shifted presettlement fire regimes from frequent low-intensity surface fires to infrequent, but increasingly numerous, large catastrophic crown fires (Swetnam, 1993). Increasingly synchronized regional fire regimes may be expected in such human-altered forest landscapes subjected to climatic extremes (Swetnam, 1993). The coexistence of some early colonizing species with more competitively dominant species depends on the

temporal phasing (or synchrony) of disturbances, even if the mean rate of disturbance remains constant (Swetnam, 1993). Therefore, it is important that the landscape management regime be formulated such that the historical variation in disturbance regime is maintained if the abundances of species adapted to these landscapes are to persist (Baker, 1992; Forman, 1995).

Many key global change-related questions remain for the study and management of disturbance-prone landscapes. What is the extent, frequency, or severity of disturbance that can be tolerated by the system without irretrievable loss of biotic elements (e.g. species) or processes? What are the ecological effects of a particular disturbance? Could a disturbance qualitatively change the system? How large should a reserve be in a disturbance-prone environment? Should management seek to alter natural disturbance dynamics? Answers to these questions are neither simple nor straightforward and will require methods that verify simulation results with direct observations of landscape change.

11.2.2 Impacts of invasive species

Invasive species pose a considerable threat to biodiversity, particularly on islands. The invasion of the brown snake into Guam has been strongly implicated in the precipitous decline in the populations of ten species of birds (Savidge, 1987). In addition, a decrease in the abundance of a native species of lizard correlated with increased abundance of an invasive lizard species, probably compounded by the effects of the brown snake on lizard predators (Rodda & Fritts, 1992).

Purposeful introductions have often resulted in species extinctions, such as the introduction of the mongoose into islands for the control of rats in sugar cane. These animals subsequently had a large impact on native populations of small rodents and birds. Other biocontrol efforts that have resulted in losses of non-targeted species include the introduction of the *Euglandia rosea*, a carnivorous mollusc from Central America, that was brought on to some Pacific Islands to control the giant African snail, *Achatina fulica*. *Euglandina* also preys on other land snails and has extirpated native snail species. Clarke *et al.* (1984) indicated that 'the number of endemic species that are endangered or already extinct as a result of the introductions must now be well over a hundred'.

Aquatic systems are particularly vulnerable to extinctions. One of the most dramatic cases of species extinctions, due to invasions, has been the introduction of the Nile perch into Lake Victoria. Following its introduction in the late 1950s, over 200 species of haplochromine fish species have been driven to extinction (Witte *et al.*, 1992). The dramatic recent invasions of the Asian clam into San Francisco Bay (Carlton *et al.*, 1990), the zebra mussel into the North American Great Lakes, and a ctenophore into the Black Sea have had enormous impacts on the populations of the native biota. Moyle (1996), in his analysis of

aquatic systems, has noted that species extinctions are most likely to occur when:

- the successful invader is a top carnivore;
- the invader carries a novel disease organism;
- the invaded ecosystem has a naturally low diversity;
- the invaded ecosystem has been highly disturbed by human or natural factors.

Even though such predictions are readily known, new introductions are continuously made into lakes.

As the biota of the world becomes increasingly homogenized, there may be rather large extinctions, even though in the short term there will be local species enrichments. The worst-case scenario is given by Wright (1987), using island biogeographic principles, that indicates the potential loss of species due to the breakdown of biogeographic barriers will be enormous. Current invasion-driven extinctions are only the tip of the iceberg of the effects of invaders on the composition and structure of biotic systems. Thus, invasive species themselves can be considered a powerful agent of global change.

11.2.3 Impacts of climate and atmospheric composition on diversity

Because of the widespread and dramatic effects of land-use change and species introductions on species diversity, it is often difficult to recognize the impacts of gradual changes in climate and atmospheric composition. Nitrogen deposition has had the most dramatic impacts – eliminating heath species from Dutch heathlands and increasing dominance by grasses in many heath, meadow, and forest ecosystems (Berendse & Elberse, 1990).

The paleo-record clearly documents changes in species composition and diversity in response to past changes in climate (Davis, 1981). Species richness of Arctic tundra declined 30% with experimental warming and 50% with warming plus nutrient addition (simulating N deposition) within a decade (Fig. 11.2) (Chapin *et al.*, 1995b). Forbs and lichens, which are critical food resources for caribou and pollinating insects, were most strongly affected, in addition to mosses, which are critical for insulation of permafrost. Thus, the species most sensitive to climatic warming have strong feedbacks to both animal diversity and biogeochemical cycling. Similarly, experimental addition of water and nitrogen greatly reduced the diversity of plant functional types in a semiarid short-grass steppe (Lauenroth *et al.*, 1978).

At a larger scale, models that predict changes in distribution of vegetation in response to climatic change (Prentice *et al.*, 1992, see also Chapter 6) suggest that there could be major changes in the relative abundance of biomes in

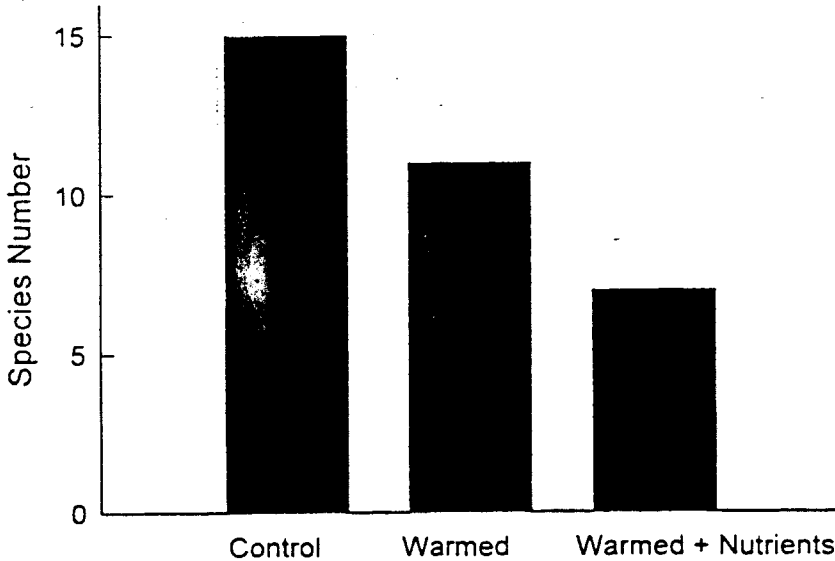


Figure 11.2 The effects of experimental warming and N addition on species richness in the arctic tundra. Adapted from Chapin *et al.* (1995b).

response to climatic warming (Chapter 8). For example, in Africa the two biomes that are currently most rare are predicted to decrease by 81% (semideserts) and 69% (broadleaved evergreen forests) in response to a doubled CO₂ climate. If these biome shifts occur, all biomes except hot deserts and tropical rainforests would decrease in abundance in national parks, particularly semideserts, warm grass/shrublands, and broadleaved evergreen forests, substantially reducing the capacity to conserve the diversity of these biomes. These predictions of biome shifts are based on the equilibrium distributions of vegetation with climate and ignore the rates and factors controlling migration of organisms in response to climatic change (Bond & Richardson, 1990). Furthermore, the developing transient dynamic global vegetation models (DGVMs) suggest that the degree of biome shifts will be less than those predicted by equilibrium models (see Chapter 8). There are increasing barriers to migration, as the land between national parks becomes more fragmented and transformed. The wise management of the land matrix between existing protected areas, to allow the movement of organisms, is thus essential to preserving species diversity of protected areas into the future. A priority for planning protected areas in the future is to conserve the connectivity among these areas and to establish new protected areas in places that are presently climatically diverse.

11.3 Consequences of changing biodiversity

11.3.1 Consequences of changes in genetic diversity

Low genetic diversity and the resulting inbreeding depression are among several processes that increase the probability of extinction in small populations. Other processes include reduced probability of interaction among individuals and vulnerability to stochastic variation in environmental and demographic processes (Hanski *et al.*, 1995a).

The reduced genetic diversity in crops is of particular concern because the world's population relies on only three species (rice, wheat, and maize) for about 60% of its carbohydrate. Approximately 95% of the protein and carbohydrate consumed comes from about 30 crops. A single variety of wheat accounted for 67% of the area planted to wheat in Bangladesh in 1983. The main crops in the United States depend on less than nine varieties (NRC, 1994). Catastrophic outbreaks of disease have occurred in the past (e.g. potato blight in Ireland) and cannot be dismissed for the future. For example, new varieties of potato blight recently discovered in Mexico and spreading to the United States are more virulent than previously known strains and are insensitive to any known fungicide. In the past, genetic diversity has been an important source of disease resistance (Holden *et al.*, 1993). Given the large increases in food production required to meet projected population growth over the next 30 years at least (see Chapter 9), the emergence of a disease capable of infesting a major wheat or rice variety could pose a major threat to production. Reductions in genetic diversity may also reduce the capacity of crops to adjust to changes in climate and atmospheric composition. Low genetic diversity is of particular concern in managed forests, where the greater longevity of individuals increases the range of conditions that each individual is likely to experience during periods of rapid environmental change.

There are several international consortia that maintain stores of genotypes of major crops, for example, the International Rice Research Institute. Maintenance of these 'genebanks' has been an important mechanism for conserving genetic diversity in these crops. Genetic engineering has the potential to increase diversity at specific loci, for example, resistance to a particular disease, although development of these varieties will always lag behind the recognition that a problem exists. Genetic engineering and breeding programmes have focused primarily on crops and varieties used in intensive agriculture, where economic and production returns are greatest.

11.3.2 Consequences of changes in species diversity

Effects of species number and relative abundance

ECOSYSTEM IMPACTS OF CHANGES IN DIVERSITY UNDER FAVOURABLE CONDITIONS. There is currently no clear understanding of the relationship between species richness (the number of species present) and ecosystem processes. For example, along natural productivity gradients, species richness can be quite high in both unproductive environments (e.g. Australian heaths) or productive environments (wet tropical forests) (Bond, 1993*a,b*; Ricklefs, 1995). Monocultures of some crop varieties are as productive as mixed-cropping systems under favourable conditions (Vandermeer & Schultz, 1990). Similarly, natural forests dominated by a single tree species do not differ consistently in productivity and nutrient cycling from more diverse forests (Rodin & Bazilevich, 1967). Depending on the taxonomic group and region, species richness can show a variety of relationships with environment and productivity (Ricklefs, 1995).

Species diversity is a function of both species richness and the relative abundance (evenness) of species (Ricklefs, 1995). This section discusses only the impacts of species number on ecosystem processes because the impacts of evenness have not yet been addressed experimentally.

Despite the lack of a clear relationship between species richness and ecosystem processes in natural ecosystems, there is concern that reductions in species diversity below naturally occurring levels might alter ecosystem processes such as productivity. A decline in species richness could reduce productivity for at least two reasons: (i) loss of species reduces the probability of there being at least one species present that is productive under a particular set of conditions; and (ii) additional species may be able to tap resources that are not captured by other species, due to differences in rooting depth, phenology, form of nitrogen utilized, etc. (Tilman, 1988; Chapin *et al.*, 1997*a*). Note that both explanations depend on traits of species and do not assume a causal link between species number *per se* and resource capture. For both hypotheses, a saturating relationship is expected between species richness and ecosystem parameters (Fig. 11.3) (Vitousek & Hooper, 1993) because the more species there are in an ecosystem, the more likely it is that a given species that is gained or lost will be ecologically similar to other species present.

Several recent experiments have shown a positive, saturating relationship between species richness and various ecosystem processes. Artificial tropical communities seeded with 0, 1, 2, or 100 species showed greater nitrogen uptake with 100 than with fewer species (Ewel *et al.*, 1991). Manipulation of diversity at four trophic levels (plants, herbivores, parasitoids, and decomposers) in experimental mesocosms also resulted in a positive correlation between

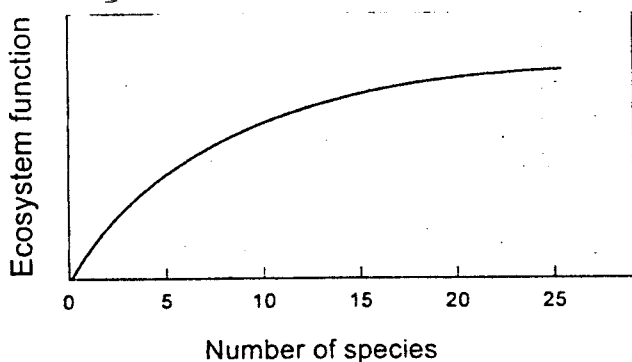


Figure 11.3 Conceptual relationship between species richness and ecosystem functioning. Adapted from Vitousek & Hooper (1993).

species richness and productivity, decomposition, and nutrient retention (Naeem *et al.*, 1994, 1995). However, since only one combination of species was used at each level of species richness in these experiments, it is difficult to separate the effects of the particular species combinations from the effect of species richness.

To minimize the possibility that diversity effects might be a simple consequence of particular species being present in high-diversity treatments, Tilman *et al.* (1996) established an experiment in which species richness was directly manipulated by sowing plots with seven levels of plant species richness (1–24 species). Each replicate was a separate random draw from a pool of 24 experimental species. This experiment also showed a positive, saturating relationship between species richness and aboveground biomass (Fig. 11.4a). Lower concentrations of inorganic nitrogen in the soil of the more diverse plots (Fig. 11.4b) suggested greater nutrient uptake by plants from these plots (Tilman *et al.*, 1996). There was a similar inverse correlation between plot-level diversity and soil nitrate in a nearby native prairie. The conclusion that there is a relationship between species richness and ecosystem processes has been questioned, because as species diversity increased, the probability of including species with large biomass increased simultaneously (Huston, 1997). Since higher diversity treatments have more large species, the reported relationship could be solely the result of higher plant biomass due to the presence of these larger species.

In other experiments plant species richness affected biogeochemical cycling without influencing plant biomass and production. In a greenhouse experiment with Mediterranean grassland species and diversity ranging from 3 to 12, plant species richness had no detectable effect on measured plant parameters but had a strong impact on soil biological activity (Chapin *et al.*, 1997b). As a result, organic matter decomposition was enhanced, and the leaching of nitrogen was reduced at high species richness.

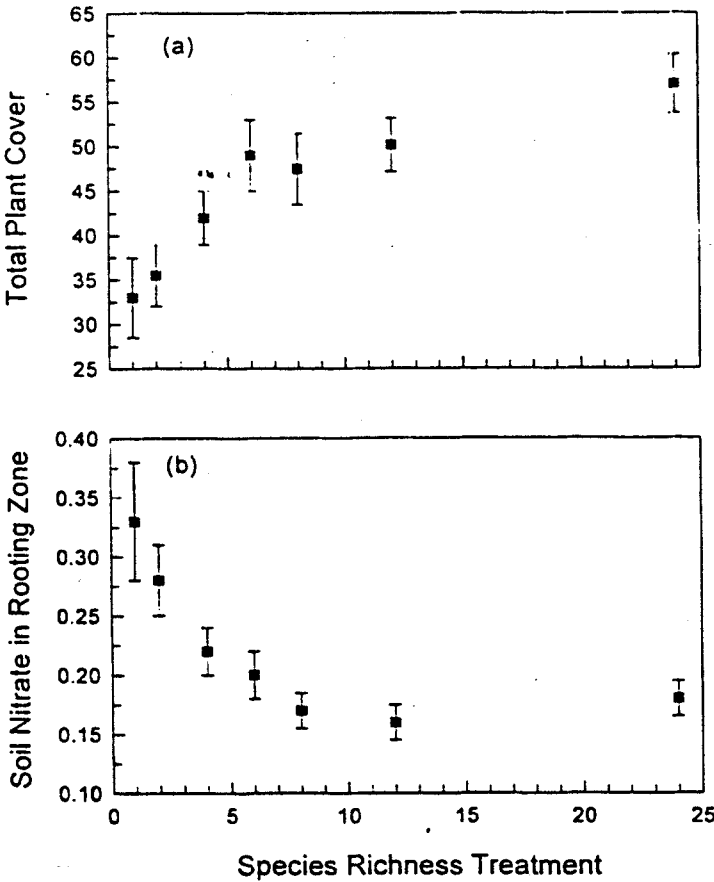


Figure 11.4 The effect of species number on (a) plant cover and (b) total nitrogen in the upper soil layer where most of the roots are concentrated. Results from a manipulative field experiment with grassland species. Adapted from Tilman *et al.* (1996).

Both Ewel’s and Tilman’s experimental results are consistent with a positive, saturating relationship between species richness and ecosystem processes, but suggest that the instantaneous effect of species richness on the measured parameters may saturate at relatively few (4–10) species. Differences in productivity and nitrogen cycling in these experiments could reflect (i) more complete spatial and/or temporal utilization of space in diverse plots (‘more niches occupied’), or (ii) that higher diversity increases the probability of having productive species in the experimental plots. Clearly, additional research is necessary to determine the mechanisms by which species richness influenced ecosystem processes in these experiments. At present, there have been too few experiments conducted to know when, how, and to what extent species richness affects ecosystem functioning. No experiments have explored the role of species richness in natural ecosystems or the role of relative abundance (evenness). As the time scale increases, plants encounter a greater variety of

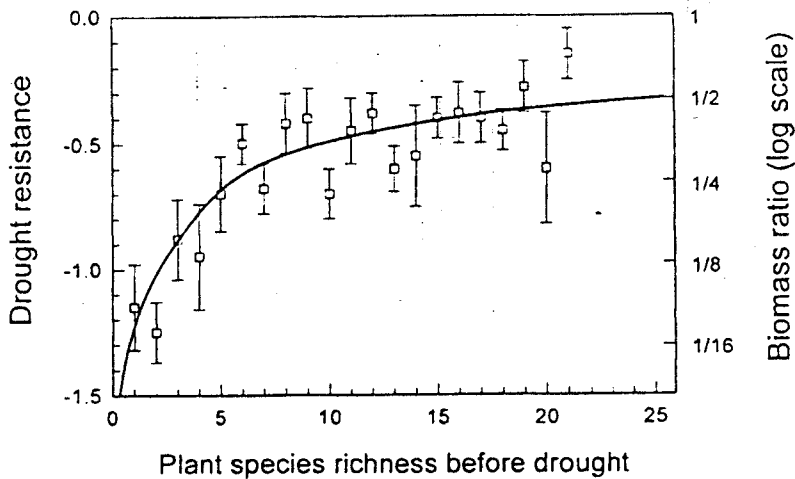


Figure 11.5 The effect of number of species on resistance to an extraordinary drought. The species richness gradient was experimentally created by adding fertilizer. Drought resistance was estimated as the biomass during the drought/long-term average biomass ratio. Results from a field manipulative experiment in a mesic grassland in tall grass prairie, North America. Adapted from Tilman & Downing (1994).

conditions, suggesting that diversity may be more important than short-term experiments would suggest. There is an urgent need for new experiments, over longer time periods, and in systems of greater diversity to see under what circumstances and by what mechanisms species diversity influences ecosystem processes.

ECOSYSTEM IMPACTS OF DIVERSITY UNDER EXTREME CONDITIONS. Species richness may buffer ecosystem processes against extreme events or unanticipated effects of global change (McNaughton, 1993). Indirect evidence for a positive relationship between species richness and ecosystem buffering comes from prairie grassland plots that differed in diversity due to long-term nutrient additions. The more diverse plots showed the least decline in aboveground biomass during a severe drought (Tilman & Downing, 1994) (Fig. 11.5) and recovered more rapidly following drought. However, the less diverse plots were those to which nitrogen fertilizer had been added, so the lower stability of these plots probably reflected a decline in abundance of drought-resistant species (Sala *et al.*, 1995). In addition, the high variability in primary production among years and the reduced primary production during drought in the low diversity-high fertility treatment could be accounted for by the fertilization treatment (Huston, 1997). This explanation is much more parsimonious than the species richness effect. The high fertility (low diversity) treatments were mostly constrained by water

availability and therefore the variability in productivity reflected the precipitation pattern. In contrast, low fertility (high diversity) treatments were highly constrained by nutrient availability, particularly when water availability was high, and showed a small response to precipitation variability.

One mechanism by which diversity might confer stability to ecosystem processes is through the contrasting responses of functionally similar species to variations in environment (McNaughton, 1977; Chapin & Shaver, 1985). For example, in response to annual variation in weather or experimental manipulation of environment, ecosystem productivity is much more stable than is that of any individual species (Lauenroth *et al.*, 1978, Chapin & Shaver, 1985). The more species there are in a functional group (group of species with similar effects on ecosystem processes), the lower is the probability that any change in climate or climatic extremes that is severe enough to cause extinction of a species will have serious ecosystem consequences. Thus, genetic diversity and diversity among ecologically similar species may provide insurance against large changes in ecosystem processes in the event of species loss. High diversity might reduce the likelihood of invasions by exotic species. For example, the smaller number of species present on islands than on mainlands may explain the vulnerability of islands to changes in ecosystem processes in response to invasion (Vitousek *et al.*, 1987; Cushman, 1995; Vitousek *et al.*, 1995). If there is greater resistance to invasions in diverse communities, it may reflect the higher probability of having a species in such a community that is ecologically similar to the invader.

Model simulations suggest that species richness could influence ecosystem response to global change. A model community consisting of nine deciduous tree species of differing CO₂ response exhibited a response to elevated CO₂ 30% greater than did a model community composed of a single species with the average CO₂ response of the more complex community (Fig. 11.6) (Bolker *et al.*, 1995). Thus, ecosystem models that neglect diversity in simulating responses to CO₂ and other environmental factors may underestimate the response of terrestrial ecosystems to global change. This modelling result contrasts with some of the conclusions of Chapter 7 where the response to elevated CO₂ decreases from leaves to individuals to ecosystems. As the hierarchical level increases and the number of factors controlling the response (from photosynthesis, to leaf growth and primary productivity) increases, the magnitude of the CO₂ effect decreases. In contrast, according to this modelling study, the increase in complexity from a single species to a community and the corresponding inclusion of mechanisms such as competition result in an amplification of the CO₂ effect.

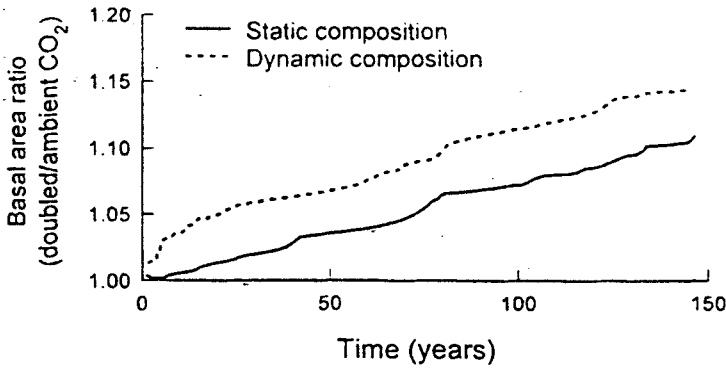


Figure 11.6 The effect of species richness on the ability of ecosystems to respond to global change. Response of a model community made up of nine species each with a different response to CO_2 (dynamic composition) or one species with the average community response to elevated CO_2 (static composition). The dynamic composition allows for competition and successional change, which results in those species with a larger CO_2 response to have a higher importance in the community than in the static composition case with a single CO_2 response. Consequently, the response to elevated CO_2 is larger in the dynamic composition model run. Adapted from Bolker *et al.* (1995).

Effects of species identity

TRAITS OF INDIVIDUAL SPECIES WITH PROFOUND ECOSYSTEM IMPACTS. Underlying the effects of species richness on ecosystem processes (Section 11.3.2) is the assumption that increased richness brings with it a greater number of 'types' of species. A predictive understanding of the consequences of changing species diversity or the introduction of exotic species would therefore benefit from knowing which traits most strongly affect ecosystem processes. Species with particularly strong impacts on ecosystem functioning include those that modify (i) resource availability, (ii) trophic structure, or (iii) disturbance regime (Vitousek, 1990; Chapin *et al.*, 1995a).

Resource Supply. The supply of soil resources is an important 'bottom-up' control that strongly influences the structure and dynamics of all terrestrial ecosystems (Jenny, 1980; Chapin *et al.*, 1996a) and consequently their role in regional and global processes. Introduction of exotic species with symbiotic N fixation in Hawaii greatly increased productivity and N cycling and altered the structure and species composition of forests (Vitousek *et al.*, 1987). As another example, Nepalese alder increases N inputs, and bamboo retains newly weathered P and K during the cropping and fallow phases in shifting agriculture in India (Ramakrishnan, 1992). Each of these species differs from other species in the community in its effects on nutrient supply, so that introduction or loss of a single species can have profound ecosystem effects. Similarly, in-

production of deep-rooted species, such as *Eucalyptus* or *Tamarix*, can tap previously inaccessible water and nutrients (van Hylekama, 1974; Robles & Chapin, 1995). These differences in rooting depth can be important at the regional scale. Model simulations suggest that conversion of the Amazon basin from forest to pasture would cause a permanent warming and drying of South America because the shallower roots of grasses would lead to less evapotranspiration and greater energy dissipation as sensible heat (Shukla *et al.*, 1990).

Plant species also affect resource supply rate through litter-quality effects on nutrient turnover in soils (Melillo *et al.*, 1982; Flanagan & Van Cleve, 1983; Berg & McLaugherty, 1989) and modification of the microenvironment (Wilson & Agnew, 1992; Hobbie, 1995). For example, Arctic mosses, with their low litter quality, low rates of evapotranspiration (leading to water-logging), and effective insulation (preventing soil warming) indirectly inhibit decomposition (Gorham, 1991).

Animals influence the resource base of the ecosystem by redistributing nutrients within an ecosystem or by importing nutrients to oligotrophic ecosystems (e.g. nutrient movement from oceans to streams by migratory salmon). Some soil processes (e.g. nitrification and denitrification) that are critical to nitrogen retention by ecosystems are controlled by relatively few species of microorganisms. Consequently, changes in their abundance could have large effects on N loss from ecosystems (Frost *et al.*, 1995; J. Schimel, 1995).

Trophic structure. Many animal species and microbial diseases (and some plant species) differ strikingly from all other species in the community in the resources that they consume and, therefore, their effects on community structure. These top-down controls are particularly well developed in aquatic systems, where addition or removal of a fish species can have large 'keystone' effects that cascade down the food chain (Carpenter *et al.*, 1992; Power, 1992). Many non-aquatic ecosystems also exhibit strong responses to changes in predator abundance (Hairston *et al.*, 1960; Strong, 1992). For example, removal of elephants or other keystone mammalian herbivores leads to encroachment of woody plants into savannas (Owen-Smith, 1988; Wilson & Agnew, 1992; Zimov *et al.*, 1995). Similarly, epidemic diseases, such as rinderpest in Africa, can act as keystone species by greatly modifying competitive interactions and community structure (Bond, 1993a,b). The top-down controls by predators have greater effect on biomass and species composition of lower trophic levels than on the flow of energy or nutrients through the ecosystem (Carpenter *et al.*, 1985) because declines in producer biomass are compensated by increased productivity and nutrient cycling rates by the remaining organisms. For example, intensely grazed grassland systems such as the southern and south-eastern Serengeti Plains (McNaughton, 1985) have a low plant biomass but

rapid cycling of carbon and nutrients due to treading and excretion by large mammals, which prevent accumulation of standing dead litter and return nutrients to soil in plant-available forms (McNaughton, 1988). Keystone predators or grazers can thus alter the pathway of energy and nutrient flow, modifying the balance between herbivore-based or detritus-based food chains, but we know less about the effects on overall energy flow and nutrient cycling by the entire ecosystem.

Disturbance regime. Disturbance is one of the most important ways in which animals affect ecosystem processes (Lawton & Jones, 1995), creating sites for seedling establishment and favouring early successional species (Hobbs & Mooney, 1991; Kotanen, 1995). At the regional scale, disturbances created by overgrazing can alter albedo of the land surface and change patterns of regional temperature and precipitation. For example, in the Middle East, overgrazing by sheep and goats reduced vegetation cover, thereby increasing the albedo and reducing energy absorption (Charney *et al.*, 1977; Schlesinger *et al.*, 1990). Consequently, there was less heating and convective uplift of the overlying air mass and less advection of moisture from the Mediterranean. This reduced precipitation and further contributed to the regional reduction in biomass and production.

Plants alter disturbance regimes through effects on soil stability and flammability. For example, introduction of grasses into forest or shrubland ecosystems can increase fire frequency and cause a replacement of forest by savanna (D'Antonio & Vitousek, 1992). Similarly, boreal conifers are more flammable than deciduous trees because of their large leaf and twig surface area, low moisture content, and high resin content (van Cleve *et al.*, 1991). In early succession, plants reduce disturbance by stabilizing soils and reducing wind and soil erosion. This allows successional development and retains the soil resources that determine the structure and productivity of late-successional stages.

GENERALIZATION OF SPECIES EFFECTS TO REGIONAL AND GLOBAL

SCALES. In contrast to species effects on resource supply, trophic interactions, and disturbance regime, which can only be predicted at present by recognizing individual species, other important effects of species on ecosystem and regional processes are shared in common by many species and their effects can often be generalized, making it possible to model the impacts of changes in species composition on ecosystem processes. Functional types are groups of species that show similar responses to, or effects on, environment (see Chapters 2 and 8). Highly generalized functional types (e.g. grasses, deciduous trees, evergreen trees), defined at the level of growth forms, are often predictable in both

their environmental responses and their effects on ecosystem and regional processes (Raunkier, 1934). However, more refined groupings of species (e.g. C₃ versus C₄ grasses) often fail to show consistent responses to climate and atmospheric composition (see Chapters 7 and 8). In this section we discuss functional types defined with respect to responses to and effects on soil resources (water and nutrients) rather than climate. These provide useful generalizations of some species effects on ecosystem processes.

Plants can be characterized by general 'adaptive strategies' that govern effects on environment (Grime, 1977; Chapin, 1993). A high relative growth rate (RGR), typical of plants from high resource environments, requires high rates (per unit tissue mass) of nutrient absorption, photosynthesis, and water loss and a large leaf area (Chapin, 1980; Lambers & Poorter, 1992). These traits result in high litter quality, which promotes decomposition and nutrient mineralization (Hobbie, 1992), and high rates of water transfer to the atmosphere. A large size, generally conferred by woodiness, allows plants to dominate light resources (Tilman, 1988) and is associated with large amounts of nutrient-absorbing, photosynthetic, and transpiring tissues. The consequences of large size include large annual fluxes of carbon and nutrients, large fluxes of water vapour to the atmosphere (and consequently reduced fluxes to lakes and streams), and a greater radiation absorption (low albedo) in snow-covered landscapes, acting as a feedback to regional climate warming (Bonan *et al.*, 1992; Foley *et al.*, 1994). Together these traits determine many ecological processes with clear ecosystem and global consequences (Chapin, 1993; Hobbie, 1995). Another general axis of plant traits is associated with responses to disturbance and relates to life-history characteristics of plants (Grime 1977; Tilman, 1988). These traits are only weakly related to RGR and size through allocation tradeoffs (Chapin, 1993).

11.3.3 Consequences of altered landscape structure for regional and global processes

Just as knowledge about the species and functional-type diversity can be important for understanding the functioning of individual ecosystems, knowledge about the diversity of ecosystems in a landscape or region can be important for understanding its biogeochemical functioning. The structure and functioning of a landscape can be described at three levels of complexity. In the simplest case, a landscape or region consists of a single homogeneous unit (one ecosystem type), which can be sampled randomly. If the area is a mosaic of different ecosystem types, each of which is biogeochemically independent from its neighbours, sampling among the different ecosystem types must be stratified and each ecosystem type weighted by its relative area. Finally, if the area consists of a mosaic of different ecosystem types that have spatially explicit interactions with

their neighbours, these neighbourhood interactions must be clearly recognized. The level of landscape complexity varies among processes. For example, the carbon capital of a region can be estimated without considering spatial interactions among ecosystems whereas spatial pattern is critical to water quality and nitrogen transport to river systems.

Each of the three cases represents a different degree of connection among ecosystems. This biogeochemical view of landscapes and regions conceptualizes diversity as being represented by the number (richness) and relative importance (evenness) of the constituent ecosystems. Examples of each case are described below.

The North American mid-latitude IGBP transect contains excellent examples of cases 1 and 2. The dominant environmental gradient along the transect is the west–east gradient in annual precipitation from 300 to 1200 mm. Regional ecosystem diversity is relatively low at the western and eastern extremes of the transect and highest in the centre. In the west, low precipitation limits land-use alternatives, and most of the area is still in native grassland. In the east, high precipitation and fertile soils have resulted in most of the area being converted to cropland that supports one or two crops. In the centre, ecosystem diversity is high because precipitation is sufficient to support crop production on the best soils and a number of crops are grown. However, on the least productive soils native grasslands still exist and, depending on site conditions, they may be similar to either the dry western types or the wet eastern types. An analysis of the potential sensitivity of the regional carbon balance to climate change and land use first assumed that the entire area was still occupied by native grassland (case 1 – no ecosystem diversity) (Burke *et al.*, 1991). The carbon balance was simulated using the CENTURY model (Parton *et al.*, 1987), and the potential effect of warming as a result of climate change was found to be small compared to the past effect of conversion of a large fraction of the area to cropland. In an ongoing effort, I.C. Burke is considering the effects of land-use diversity using a land-use map as input to CENTURY so that the effects of the various crops and management can be evaluated in terms of positive or negative effects compared to native grasslands (case 2 – regional response as the weighted average of a mosaic of biogeochemically distinct units).

An example of case 3 is given by biogeochemical questions about areas that include riparian ecosystems. These ecosystems have a specific role in landscapes, because they filter sediments and retain nutrients (Gregory *et al.*, 1991). Analysis of an experimental watershed demonstrated that while croplands released most of the nitrogen and phosphorus received during the year, a riparian forest retained most of the nutrients including those from an adjacent cropland (Peterjohn and Correll, 1984). Disturbance to riparian ecosystems may result in severe sedimentation and nutrient loading with the corresponding

landscape and regional effects (Burke & Lauenroth, 1995). In addition to being an example of the importance of the spatial arrangement of landscapes in evaluating biogeochemical response of landscapes or regions, riparian ecosystems may be one of the best examples of 'keystone' elements in landscape diversity, because their influence can be disproportionate to their areal extent.

11.4 Societal consequences of altered biodiversity

Biodiversity changes have impacts on all societies through their effect on delivery of ecosystem services, i.e. those products of ecosystems required by humans (Ehrlich & Mooney, 1983). It is not known what fraction of extant species is required to keep ecosystems functioning in a fashion that supports natural rates of carbon and trace-gas exchange with the atmosphere and water and nutrient runoff to aquatic systems. If many of the ecosystem functions of species were redundant, a less diverse world might function 'normally' under average conditions. However, species-poor ecosystems may be more vulnerable to catastrophic disease and/or be less resilient in the face of environmental change than would a natural ecosystem with its original species diversity (Section 11.3.2) (Walker, 1992; Lawton & Brown, 1993). Given the current uncertainty as to the number of species required for normal ecosystem functioning under current and future conditions, policies that conserve species and genetic diversity are a prudent course of action.

Changes in species diversity directly affect the livelihood and culture of traditional societies in the biodiversity-rich regions of the developing tropics. Inhabitants of these regions obtain a variety of resources from the forest such as food, fodder, fuelwood, medicinal plants, and timber for their own use and for cash income. Traditional societies employ a wide variety of food production systems, ranging from shifting to sedentary agriculture. These agro-ecosystem types, including traditional freshwater fishery systems, have close interconnections with natural forests and with complex village societal systems. Together they generate a landscape mosaic that includes (i) natural forests and grasslands, (ii) low-input traditional multi-species shifting agricultural systems, (iii) mid-intensity agro-ecosystems such as agroforestry, alley cropping, rotational cropping systems, etc., and (iv) high-input modern mono-cropping agriculture (Swift *et al.*, 1995). This patchwork mosaic of managed and natural ecosystems may provide a more sustainable livelihood for traditional societies in forested areas than a commitment to a single agricultural system or to a system in which natural reserves are isolated from populated areas (Ramakrishnan, 1992).

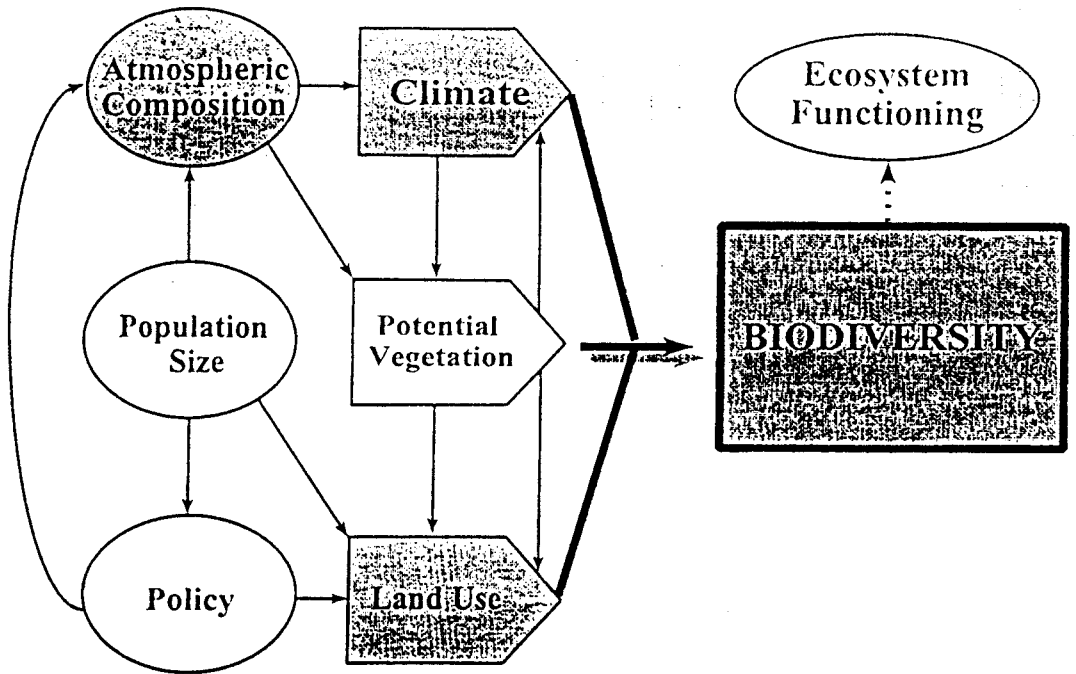


Figure 11.7 The major drivers of change in biodiversity as used in an exercise to develop biodiversity scenarios.

11.5 Implications for the future

Previous sections of this chapter described the patterns of biodiversity change that occur as a result of human activity, the mechanisms underlying the observed changes, and the consequences for ecosystem functioning. Based on this current understanding and the tools already developed, can scenarios of biodiversity change into the next century be developed? Several disciplines from atmospheric sciences to human demography have developed scenarios of such quantities as CO_2 and CH_4 emissions, climate, and population density, based on the current state of knowledge in these fields.

The development of biodiversity scenarios requires input from scenarios of changes in land use, atmospheric composition, and climate, as described in Section 11.2 (Fig. 11.7). In turn, biodiversity scenarios should serve as input to other scenarios. A GCTE project to develop biodiversity scenarios for the major biomes of the world involved scientists familiar with individual biomes and with models that simulate future patterns of the three major drivers of change in biodiversity: land use, climate, and potential natural vegetation. IMAGE 2 (Alcamo, 1994) provided scenarios of land use for the different regions of the world, which in turn were based on scenarios of change in climate and human demography. BIOME 2 (Prentice *et al.*, 1992) provided a scenario of the global distribution of potential vegetation at equilibrium with a double- CO_2 climate.

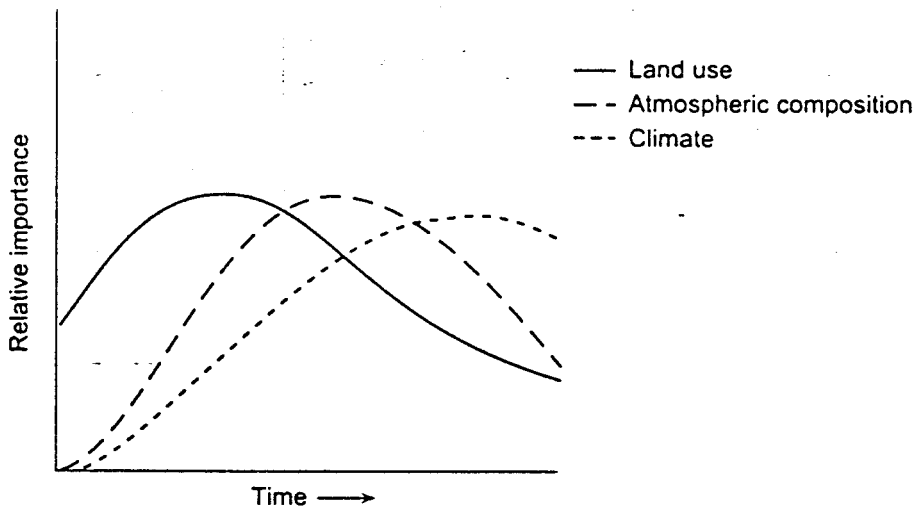


Figure 11.8 Conceptual model of the change through time in the relative importance of the different drivers of change in biodiversity. Relative importance in this conceptual model ranges from 0 to 1 and is formed by the sum of the effects of the three drivers. Consequently, decrease in the relative importance of a driver may result from either a decline of its direct effect or by an increase in the effects of other drivers.

Analysis across biomes from the present to the year 2100 suggested that the relative importance of global change drivers will change with time (Fig. 11.8). Currently, changes in land use have the largest impact on biodiversity at all levels. Conversion of natural ecosystems into croplands, fragmentation of natural ecosystems, and their over-exploitation have far larger impacts on biodiversity than do changes in climate and atmospheric CO_2 , which may result in shifts of potential natural vegetation. Changes in land use will be reduced in the short to medium term when most of the arable land is converted to cropland. The direct effect of changes in the atmospheric composition will become an increasingly important driver of biodiversity changes (see Chapter 7). Increases in the atmospheric concentration of CO_2 have already been detected, are substantial, and are expected to continue to increase (see Chapter 1). Because the climate system has considerable inertia, decades will be necessary to observe the effects of current and past changes in atmospheric composition on climate. Furthermore, because ecosystems are adapted to the existing large interannual climate variability, climate change will be the last of the drivers to affect biodiversity significantly.

Cross-biome analysis suggested important spatial patterns for the drivers and responses. The expected temperature changes increase with latitude while precipitation changes, although equally important, have more idiosyncratic patterns. Potential vegetation changes mainly reflect changes in climate since current models do not simulate migration or successional trends. Land-use change is expected to be large in savannas and forests, which are areas where

large food demand increases are expected. Therefore, IMAGE 2 predicts some of largest changes to occur in Africa (see also Section 12.4).

Assessment of expected changes in the drivers combined with the differential biome sensitivities yield the patterns of expected biodiversity change. Biomes that are characteristic of extreme environments like tundra, boreal forest, or deserts may be more sensitive to climate change than to land-use change. The difficulties of feasible commercial operations and low population densities may minimize logging of boreal forest or transformation of deserts into croplands before they are impacted by changing climate. The land-use model predicts relatively small changes in land use for these biomes. In addition, warming predictions are larger at higher latitudes.

In contrast to biomes of extreme environments, biodiversity in biomes characteristic of temperate and mesic sites is more likely to be affected more rapidly by changes in land use than by changes in climate. Not only are changes in climate predicted to be smaller but, due to their production potential, these biomes are more likely to be heavily utilized and transformed.

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