

Biodiversity and Ecosystem Functioning: Basic Principles

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EXECUTIVE SUMMARY

The chapters in this section explore the ways in which diversity, at various levels, influences the functioning of ecosystems and how this, in turn, relates to human needs.

1. Ecosystems are composed of all the individuals of all the species in a given area, and their physical environment. Ecosystems provide free services to society including clean water, pure air, soil formation and protection, pest control, foods, fuel, fibres and drugs.
 2. The loss of genetic variability within the populations of a species in a given area reduces the flexibility of those species to adjust to environmental changes (such as climate changes, for example) and narrows the options available for the rehabilitation of specific habitats.
 3. The addition or deletion of a species can have profound effects on the capacity of an ecosystem to provide ecosystem services.
 4. We are beginning to develop the capacity to predict which species will cause the greatest system impacts, and hence the greatest ecosystem service changes, when added or deleted.
 - (a) Species with unique traits for fixing nitrogen, capturing water, emitting trace gases, and so forth, when added or deleted will have profound effects on the functioning of an ecosystem. These effects can be predicted *a priori*.
 - (b) Certain other species, without readily recognized specialized traits, when added or deleted may also have profound effects on the capacity of ecosystems to provide services. These are so-called 'keystone' species. With our current state
 - of knowledge, their potential effects can only be assessed by direct experimentation.
 5. Based on the latest evidence, the capacity of ecosystems to resist changing environmental conditions, and to rebound from unusual climatic or biotic events, is related positively to species numbers.
 6. Fragmentation and disturbance of ecosystems and of landscapes will have profound effects on the services provided, since these impacts shift the balance of the kinds of species present - from large, long-lived species to small, short-lived ones. These shifts reduce the capacity of the systems to store nutrients, sequester carbon and provide pest protection, among other things.
 7. The simplification of ecosystems to obtain higher yields of individual products comes at the cost of the loss of ecosystem stability and of free services such as controlled nutrient delivery and pest control, which thus need to be subsidized by the use of fertilizers and pesticides.
 8. Modification of ecosystems by the introduction of alien species, either deliberately or accidentally, has positive and negative ecosystem effects - but too often the latter because of the reduced biotic controls on the invading species.
 9. We have been more successful in simplifying than in reconstructing complex ecosystems. Our lack of success in ecosystem restoration suggests that great caution should be exercised in reducing biodiversity through management practices because of the potential loss of goods and services in the long term.
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5.0 Introduction

5.0.1 Background

Does it make any difference to the functioning of an ecological system if there are many species or only a few? Are species that perform similar functions within an ecosystem interchangeable, or do they differ in ways that matter to the workings of the system? Does the genetic diversity of species affect the sustainability of ecosystem-level functions? How does diversity among ecosystems affect the flow of energy, water or chemicals across the landscape? What are the ecosystem-level ramifications of human-driven changes in biodiversity?

Addressing these questions requires an understanding of the relationships between biological diversity and ecosystem functioning, and thus the functional consequences of changes in biological diversity. The importance of this topic is underscored by the realization that the provision of marketable goods and free ecological services are essential features of humankind's interest in and benefit from the biosphere's diversity. The explosive growth of the human population and its use of resources, energy and land are resulting in massive changes in diversity at a variety of levels throughout the world. Some of these changes, such as extinction of species, are truly irreversible; while others are not, but the challenge of managing natural resources in a sustainable manner has clearly increased. Increases in our understanding of the relationships between changes in biological diversity and the functioning of ecosystems can help improve a wide range of policies involving agriculture, forestry, fisheries and land use, transcending traditional conservation-based policies. Assessing our knowledge of the general principles of the relationships between diversity and the functioning of ecological systems is the focus of this Section.

Understanding the functional implications of biodiversity requires that issues addressed in population and community ecology be merged with those in ecosystems ecology. Each of these areas of ecology has developed research traditions largely without interaction with the other. However, in the past decade, there have been a number of attempts to bridge these two approaches (Vitousek *et al.* 1987; Vitousek 1990; Schulze and Mooney 1993; Naeem *et al.* 1994; Tilman and Downing 1994; Jones and Lawton 1995). International scientific reviews by SCOPE (Mooney *et al.* 1995) aimed at understanding the relationship between biodiversity and ecosystem functioning, and the broader approach by the Diversitas programme of IUBS and UNESCO (Solbrig 1991) designed to also analyse the origins, maintenance and monitoring of diversity, have played a critical role in the preparation of Sections 5 and 6 of the GBA.

5.0.2 Important concepts

The term biodiversity has frequently been equated with diversity of species. The strength of the term is its

simplicity. However, understanding the functional significance of biodiversity necessitates teasing apart the rich and multiple dimensions of the concepts underlying the term (see Section 1). There are four key concepts to consider: (1) the levels of biological and ecological organization and their interactions, (2) the numbers of different biological units within each level, (3) the influence and degree of similarity in the traits or roles that biological and ecological units within each level play, and (4) the spatial configuration of the units within any level. For example, at the species level we need to consider whether there are functional consequences of the total numbers of different species, whether the degree of similarity in their functional roles or traits has ecosystem-level consequences, and whether the spatial configuration of the species influences ecosystem functioning.

Ecological systems can be viewed at increasing levels of organization: genetic, population, species, community, ecosystem and landscape. Patterns and processes at any particular level affect not only the target level, but also the levels above and below. Because ecosystems provide ecological goods and services to humanity, the assessment in the following chapters is focused generally on the ecosystem level, but includes relevant functioning at lower and higher levels.

We use the term 'ecosystem' to refer to all the individuals, species and populations in a spatially defined area, the interactions among them, and those between the organisms and the abiotic environment (Likens 1993; see Section 2.3). 'Ecosystem functioning' denotes the sum total of processes operating at the ecosystem level, such as the cycling of matter, energy and nutrients, as well as those processes operating at lower ecological levels which impact on patterns or processes at the ecosystem level. Interactions among species or the transfer of genetic material are examples of some of the lower level processes that are immediately relevant to the ecosystem consequences of biodiversity. Thus, in the following sections, patterns of diversity at the genetic, species, community and ecosystem levels are related to key functional properties of ecosystems.

Following other syntheses (Lubchenco *et al.* 1991), we use the term 'ecological system' to refer to the characteristics or functioning of organisms, populations, communities or ecosystems at a level that is appropriate to the particular questions being asked. Thus, it is analogous to the use of the word 'taxon' by systematists.

The roles of different species and the extent to which they overlap in function have been a common theme in community ecology. The concepts of 'keystone species', 'redundancy', 'compensation', 'functional groups' and 'rivets' all deal with the extent to which individuals or species overlap in function, and the consequences of this overlap to the system. An understanding of unique species'

traits, overlap among species, and the possible functional significance of low or high numbers of species, apart from how they differ in traits, is clearly immediately relevant to understanding the conditions under which 'species matter'. Historically less attention has been paid to the equivalent questions dealing with functional overlap among genes or ecosystems. Nonetheless, comparable information is now recognized as immediately relevant to conservation and management.

The third important topic of interest to the relation between diversity and the functioning of ecological systems is that of the spatial configuration of the units within the system. For example, knowing the consequences of different habitat or ecosystem configurations to the functional properties of landscapes would enhance the design of reserves as well as the management of resources. Knowing how the populations within an ecosystem are distributed in space would enhance our ability to predict its functional resilience to stress from pathogens and environmental variability.

5.0.3 Section organization

Chapter 5.1 begins with an exploration of the social and political context within which the study of biodiversity and ecosystem functioning occurs. Why should society care? In particular, it considers the notion that one of the very important aspects of ecosystem functioning that depends on diversity is the provision of goods and services, and the provision of insurance against adverse changes due to stress or environmental variability.

Chapter 5.2 then considers how the diversity of the natural world is organized, and how diversity at each level of organization affects ecosystem functioning. Subsection 5.2.1 addresses the question of the extent to which intraspecific genetic variation is important in understanding the relationship between biodiversity and ecosystem functioning; 5.2.2 addresses the degree to which we can predict the ecosystem-level consequences of species additions, deletions and replacements, and synthesizes the state of knowledge with respect to the processes that determine the importance of species and communities in ecosystem-level functioning; 5.2.3 addresses the spatial structure of populations, its effect on abundance, species interactions and life-history characteristics, and the subsequent consequences for ecosystem functioning and 5.2.4 analyses the larger spatial scales of landscapes and regions, in which human activities exert large influences, and considers how the relationships of diversity and functioning at these scales are similar to, or different from the relationships at other levels of organization.

Chapter 5.3 considers the drivers and dynamics of changes in biodiversity, and their subsequent consequences for ecosystem functioning. Subsection 5.3.1 assesses our knowledge of disturbance as a factor that

strongly affects the structure and function of ecological systems, and examines closely the role that different intensities and frequencies of disturbance have in determining species diversity within ecosystems, while 5.3.2 reviews the influence of human-driven changes in diversity due to changes in land use and resource use, atmospheric composition and climate change, and the potential or realized consequences for ecosystem and landscape/regional-scale functioning.

The Conclusion to Section 5 summarizes key findings and provides a synthesis of the general patterns and principles relating biodiversity and ecosystem functioning.

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5.1 Context: biodiversity and ecosystem services

The conditions and processes characterizing natural ecosystems supply humanity with an array of free services upon which society depends. These include: maintenance of the gaseous quality of the atmosphere (which in turn helps to regulate climate); amelioration of the weather;

control of the hydrological cycle (including reduction of the probability of serious floods and droughts); protection of coastal zones by generating and conserving coral reef and sand dune systems; generation and conservation of fertile soils, which are essential to agriculture and forestry; dispersal and breakdown of wastes and cycling of nutrients; control of the vast majority of potential crop pests and vectors of disease; pollination of many crops, and direct provision of food from sea and land; and the maintenance of a vast 'genetic library' from which *Homo sapiens* has already extracted the very basis of civilization in the form of crops, domestic animals, medicines and industrial products (Ehrlich and Ehrlich 1981, 1992).

One of the most important questions in ecology – indeed, one of the most important ones facing humanity – is the degree to which some overall level of biodiversity is required for the delivery of ecosystem services (Ehrlich 1993). This question is ordinarily interpreted to mean 'what is the minimum fraction, of the estimated 13.5 million species now extant, required to keep ecosystems functioning so that they can continue to supply these services?' In other words, how much of the world's species diversity is redundant? Would a 'weedy' world (see 5.2.3) from which most species diversity had been lost remain hospitable to humanity? If not, where on the continuum between today's species richness and a species-poor planet would one expect a serious deterioration of services? It is clear that many ecosystem services are already faltering: maintenance of the mix of gases in the atmosphere is an obvious example. Deforestation is partially responsible, and is associated with major losses of species diversity. In this case, however, as in most others, it is not possible to determine the degree to which species loss will impair the services in the long term. One can imagine polycultures substituted for natural forests that would sequester carbon, reduce nitrous oxide fluxes and otherwise help stabilize atmospheric composition. Similarly, ice plant (*Mesembryanthemum crystallinum*) and Bermuda grass (*Cynodon dactylon*) might hold soils in place in many parts of the world as thoroughly as species-rich mixes of native plants. Eucalyptus trees transpire, break the force of rain, protect soils, and thus contribute to regular flows of fresh water in California – possibly just as well as native live oaks. They also can provide the shade and wind-screening functions of a diversity of indigenous trees. It may be that most species are redundant from the viewpoint of ecosystem services, as suggested by Walker (1992) and developed further by Lawton and Brown (1993) – the so-called 'redundant species hypothesis' (see further discussion in 5.2.2). Even looking at the short term, it seems unlikely, however, that this is the case (e.g. Naeem *et al.* 1994).

The ability of a monoculture to maintain services becomes more problematical if the longer term is considered. A monoculture of a tree species may provide

many ecosystem services for decades or even a few centuries, but it may be more vulnerable to catastrophic disease and/or be less resilient in the face of environmental change than would a natural forest with its original tree species diversity. The presence of many species would generally increase the chance that, if rapid change exterminated some species, there would be ecological equivalents present, more tolerant to the particular change and able to take over their roles. Furthermore, a drastic reduction in species diversity in an ecosystem may lead to sequences of community development whose direction and consequences for ecosystem services may be very difficult to predict (e.g. Drake *et al.* 1993; Hughes 1994; Luh and Pimm 1993).

If the tree monoculture were genetically uniform, the ecosystem services it supplied would be even more vulnerable to disruption. A natural forest often contains a diversity of populations of component tree species – populations adapted to different environmental regimes (say, north- and south-facing slopes). They would contain interpopulation genetic variation which could be crucial to the ability of species to evolve in response to rapid changes in environmental conditions, such as climatic shifts due to global warming.

From a very broad perspective, the redundant species hypothesis seems even less likely to be correct. While a 'weedy' ecosystem might satisfactorily maintain the gaseous mix of the atmosphere, control erosion, conserve water flows, and so on, other services seem almost certain to be less secure than in a diverse natural system. A tree farm might not shelter the diversity of natural enemies of crop pests that would be found in a natural forest. For example, avian diversity is correlated with structural diversity in forests, and many bird species have habitat requirements not met in even aged stands of monocultures. In addition, a tree farm may be less effective than a mix of native species at recycling nutrients and maintaining a fertile soil (Aber and Melillo 1991).

Of course, it is difficult to predict the need for pest control services in a highly biologically depauperate world, although simple food-chain considerations would suggest that herbivorous pests would be more likely than their predacious enemies to persist in such an environment. Ecologists know that extinction of species will not necessarily cause deterioration of certain ecosystem services – that there is some redundancy at least in the short term since observed extinctions do not always cause detectable impacts on services. However, ecologists cannot determine the actual degree of redundancy present, nor whether short-term redundancy holds for the long term.

There are, of course, some ecosystem services that automatically would be compromised by losses of species, populations and genetic diversity. Direct provision of food and maintenance of the genetic library are the best

examples. Loss of fisheries or game species can more or less permanently remove a substantial source of human food – as did the extermination of the passenger pigeon (Blockstein and Tordoff 1985). The extinction of one species often leads to the extinction of others, which often are directly (as in the case of monophagous herbivores and parasites) or indirectly (e.g. Paine 1966; Gilbert 1980; Daily *et al.* 1993) dependent on the organism that has disappeared. Thus, while loss of any species or genetically distinct population by definition depletes the genetic library (and thus its potential for supplying direct economic benefits to society), each extinction also has the potential for generating cascades of further losses. Therefore, conservation efforts should focus not only on species, but also on ecological and evolutionary processes which occur in the matrix of the community and ecosystem (see also Section 4.5).

Given such examples, it would be prudent to assume that ecosystem services depend significantly on species diversity, and more heavily on population diversity (Ehrlich and Daily 1993; Daily and Ehrlich 1994), since on local, regional and global scales, ecosystem services are delivered by populations. Multitudinous populations of plants, animals and microorganisms, each usually genetically adapted to a relatively narrow range of environmental conditions, are necessary to maintain ecosystem functioning. After all, very few organisms of any functional group can thrive under a wide variety of physical and biotic conditions: adaptation to local circumstance is nearly ubiquitous. Much too little attention has been paid to the connection between the diversity of populations (both Mendelian populations and demographic units) and the delivery of ecosystem services.

The uncertainties of the relationship between species diversity and ecosystem services led more than a decade ago to the formulation of the 'rivet hypothesis' (Ehrlich and Ehrlich 1981). It says, in essence, that given the complexity of ecosystems and our lack of detailed knowledge of their functioning (especially in the long term), it is foolish to remove species randomly just as it would be foolish to pop rivets from an airplane's wing. There are more rivets in an airplane's wing than are necessary for its integrity, but removing too many can cause a structural disaster. At some point, removing one more rivet will cause others to pop out and the wing to fail. While there is at least some redundancy in the role of species in delivering services, there may also be extinction thresholds. For instance, if a 'keystone' species (see 5.2.2) is extirpated, it could lead to an extinction cascade that would eliminate a series of functionally related species and lead to unacceptable deterioration of an ecosystem service. Or, the removal of one or a few predatory species can lead to serious outbreaks of pest species. This is demonstrated by a well-

documented set of examples of the problem of 'promotion' of previously harmless organisms to the status of agricultural pests when natural predators have been reduced or eliminated from a system by misuse of pesticides (e.g. Barducci 1972).

There are, of course, costs involved in making an airplane wing safer. Strengthening the structure usually means adding more weight, which in turn means that less fuel or fewer passengers can be carried. A 747 that carried only one passenger could be made very safe indeed, but would be totally uneconomical. There are both costs and benefits of safety in airliners, and where the balance is struck is largely a social and economic decision.

The same is true for the preservation of biodiversity. About 11% of Earth's land surface is now covered by crops, rather than more diverse ecosystems, and attempts to provide food for a human population that may more than double in the next century is likely to lead to further conversion to agriculture of relatively natural ecosystems. Diverse systems seem doomed to diminish as a result of increasing urbanization, grazing pressure, and other consequences of the expanding scale of the human enterprise. Because of human needs (and greed), the costs of preserving diversity seem bound to increase rapidly, but simultaneously the costs to civilization of destroying it may escalate as well.

It remains a major challenge to ecologists to improve their understanding of the relationship between biodiversity and ecosystem functioning so they can better predict where the increasing risks of destroying biodiversity become greater than the increasing costs of preserving it. At the moment, about all that can be said is that until and unless it can be definitively shown that the rivet hypothesis is over-conservative, it would be folly for humanity to continue to wipe out species diversity indiscriminately. Further deliberate destruction of biodiversity at the genetic, population, species or ecosystem level should be permitted only as a last resort, when crucial human needs can be met in no other way. The burden of proof of need must rest on those proposing the destruction, and societies must guard against short-term financial gain at the expense of the majority.

On the basis of present knowledge, we cannot safely assume that a 'weedy world' will support the human enterprise as effectively or for as long as one rich in organisms that are not human inquilines. Until and unless further research clearly shows how diversity can safely be reduced, we must act as if all levels of diversity will be essential if ecosystems are to respond to the rapid and unprecedented environmental changes that now face human society. And even if ecologists show that 'weedy' species are all we need to supply basic services to humanity, they cannot show that the ethical and aesthetic arguments for

maximizing the preservation of biodiversity are incorrect. They lie outside realm of science, but contain some of the most powerful reasons for saving our only known living companions in the universe.

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5.2 Functional properties of biodiversity: a hierarchical perspective

5.2.1 Genetic diversity and ecosystem functioning

In order to evaluate the significance of genetic diversity in ecosystem functioning, the role of the individual must first be appreciated. Individuals – not species – eat or are eaten, live or die, capture energy and transfer energy. Species do not interact: individuals of different species interact. Communities are not assemblages of species: they are assemblages of individuals of the same and different species. All too often in the ecological literature, species are treated as monolithic, static entities that are the basic building blocks of communities and ecosystems. Fortunately, a new, individual-based ecology is emerging (Hogeweg and Hesper 1990; Rose *et al.* 1993), and as it matures and develops, the role of individuals in ecological processes will undoubtedly gain a deeper appreciation. Much of the individual variation observed at the intraspecific level is due for example to the individual's sex, age or past interactions with the environment. However, one class of intraspecific variation – genetic variation – plays a particularly important role in processes above the individual level and this subsection will deal only with this genetic component of individual variation.

Genetic variation ties together the biological properties of the individual and the biological properties of the species. DNA, the material basis of genetic variation, can replicate and be passed on to future generations and to more than one individual. Accordingly, genetic variation has an existence in space and time that transcends the individual. This temporal and spatial existence of genetic variation provides both the raw material and the physical continuity for the process of evolution at the species level. This capacity to evolve provides insurance against future environmental changes. Therefore, the emergent population property of evolution augments – not diminishes – the importance of genetic diversity among individuals.

The above does not imply that species are not important in ecology or that they are not real biological units (Templeton 1989). Adaptation is one of the most important evolutionary processes that emerge at the population level. Through adaptation, individuals within a species come to have traits that help in their survival and reproduction with regard to both their physical and biotic environments. These adaptations result in an ecological distinctiveness that emerges at the species level that has been described as the 'keystone of evolution' because it serves as the basis of diversification of the organic world, adaptive radiation and evolutionary progress (Mayr 1970). Ecosystems function by a variety of processes that are shaped by adaptive evolution. They first require that energy be captured from the physical environment and be transferred into the biological realm in the form of biomass. The amount of physical energy that is converted into biomass is influenced

by the genotype of the individual, as evidenced by the fact that genetic variation among individuals is the basis of much of the improvement in biomass productivity of modern crop plants (Oldfield 1984). The genetic improvement of domesticated animal stocks also shows that the efficiency of energy transfer from one trophic level to the next is another genetically variable trait (Oldfield 1984), and indeed genetic variation of the proportion of ingested energy that is converted into biomass exists within our own species (Reilly *et al.* 1992).

The transfer of energy from one trophic level to the next is mediated by interactions among individuals, including individuals of different species. Many other types of inter-specific interactions are critical for ecosystem functioning, including competitive and mutualistic interactions. These interactions are shaped by adaptive processes working upon intraspecific genetic variability, as illustrated by the extensive literature on coevolution (Pirozynski and Hawksworth 1988; Thompson 1988; Mitter *et al.* 1991; Fritz and Simms 1992; Jolivet 1992; see Section 4.5), the evolution of human diseases (Ewald 1994), and the human evolutionary responses to these diseases (Weiss 1993). These biotic interactions shape the structure and the functioning of the biological community component of ecosystems. Although described as 'interspecific', these interactions are sometimes best understood at the level of intraspecific genetic variation. For example, in *Heliconius* butterflies the genetic system controlling adult wing pattern evolves as an intra- and interspecific mutualism (to provide a common inter/intraspecific signal of distastefulness to potential predators), while the genetic system controlling adult foraging behaviour evolves through intra- and interspecific competition for scarce pollen resources (Templeton and Gilbert 1985). Thus, species and even individuals cannot be said to have an interaction in this example. Rather, the community structure in this case can only be understood at the level of genetic traits within individuals (Templeton and Gilbert 1985).

Finally, ecosystem functioning requires interactions of individuals with the physical environment, and as with biotic interactions, these are shaped by adaptive evolution operating upon individual genetic variation. This includes adaptation to the geological/chemical environment (Ware 1990; Ware and Pinion 1990) and to physical stresses such as desiccation (Templeton *et al.* 1989) or flooding (Schwartz 1969).

As discussed above, genetic diversity as shaped by adaptive evolution underlies ecological processes at the population, species, community and ecosystem levels. Genetic diversity itself has a variety of meanings and levels of measurement (Templeton 1994; see also Section 2.2), the most basic being allelic diversity (alternative forms of genes at the same locus). Allelic diversity is created by the

process of mutation and can subsequently be lost during the evolutionary process, either at random (genetic drift in the species as a whole), or due to natural selection (elimination of deleterious alleles and fixation of favourable alleles). The amount of allelic diversity in a species represents a dynamic balance between these processes.

Species exist in both space and time, and so does intraspecific allelic diversity. In some species, the allelic diversity is widely and nearly uniformly distributed across a species' geographical range (Barrowclough 1983). At the other extreme are species in which local populations have little or no allelic diversity, although different local populations can be fixed for alternative alleles (Templeton *et al.* 1990). The forces that partition and create genetic hierarchies within a species include such factors as the system of mating, genetic drift, population subdivision, dispersal and gene flow (see Section 4.2). The partitioning of allelic diversity within and among local breeding populations is primarily due to the dynamic balance between local genetic drift (which causes the local breeding population to lose allelic diversity but causes an increase in among-population genetic differentiation) versus gene flow or dispersal (which brings new allelic diversity into the local population and reduces genetic differentiation among populations). In sexually reproducing populations, the allelic diversity within a local population is amplified into vast numbers of combinations of genotypic diversity through the mechanisms of gamete formation and union (system of mating). This determines the extent to which diploid individuals will themselves carry allelic diversity in the form of heterozygosity (an individual carrying two different alleles at a locus).

What is the significance of genetic diversity at these various intraspecific levels? Starting at the individual level in sexual populations, attention has focused on the importance of heterozygosity (see also Section 4.2). Several studies have concluded that as heterozygosity increases, individual fitness or fitness correlates also increase (Clarke 1993). Unfortunately, due to confounding factors, there is little convincing evidence for heterozygote superiority as a general phenomenon (Clarke 1993) or as a quantitatively important explanation of inbreeding depression (a loss of fitness in the offspring of matings between close biological relatives) (Templeton 1987). This is not to say that heterozygote superiority does not occur (for an example, see Templeton 1982): only that it is not universal. Plants and animals adapt to their system of mating, and if they have a system of mating that favours homozygosity, alleles with high fitness under homozygosity are favoured by natural selection (Templeton 1982). Because there is much diversity in systems of mating across species (from panmixia to selfing), heterozygosity may be important in some species and irrelevant in others. Heterozygosity is certainly irrelevant in

the vast numbers of haploid individuals that dominate the microbial world and commonly represent critical components of ecosystem functioning.

Studies on fitness and heterozygosity, and on inbreeding depression, do reveal one common theme – the importance of multilocus combinations in individual fitness (Templeton and Read 1984, 1994; Clarke 1993). Despite the fact that there is more consistent evidence for epistasis (multilocus interactions) leading to co-adapted gene complexes being more important than heterozygosity in determining individual fitness (Clarke 1993) and that epistasis is important for individual fitness in the haploid, microbial world as well (Lenski 1988a, b), combinatorial genetic diversity has been explicitly incorporated into only a handful of conservation programmes (e.g. Templeton and Read 1984, 1994; Emlen 1991).

At the level of a local population, genetic variation exists in the form of allelic and combinatorial diversity in the local population's gene pool. Concern about variation within local populations has focused on two issues: (1) the fear that genetic uniformity makes populations more susceptible to pests or disease pathogens (O'Brien *et al.* 1985; Potts and Wakeland 1993), and (2) the fear that loss of genetic diversity at this level will reduce a population's ability to respond to environmental change (both biotic and abiotic) through the process of adaptation via natural selection. Recently, Caro and Laurenson (1994) questioned the importance of genetic variation with respect to evidence for increased risk to short-term population extinction. The cases of increased susceptibility to pathogens in natural populations that are low in genetic variation are not definite proofs of the importance of genetic variation but are consistent with this conclusion (O'Brien *et al.* 1985; Moritz *et al.* 1991). Moreover, there is a rich agricultural literature on the dangers of genetic monocultures with respect to pathogens (Bishop and Cook 1981; Oldfield 1984; Browning 1991). Accordingly, it would be foolish to dismiss this role of genetic variation in mediating the intensity and ecological consequences of host/pathogen interactions. The necessity of genetic diversity for adaptive evolution is well established both theoretically (Templeton 1982) and experimentally (e.g. Carson 1961). There are also abundant natural examples of organisms utilizing their genetic diversity to adapt to environmental change, including human-induced environmental change (Bishop and Cook 1981). These adaptations can directly affect an organism's niche and biotic interactions in the community (Singer *et al.* 1993). For example Sork *et al.* (1993) have found that the northern red oaks in the Ozarks adapt very finely to variations in interactions with herbivores and to the physical environment. These examples illustrate the importance of genetic diversity as a component of adaptive evolution. Because adaptive flexibility is only realized in evolutionary time, the criterion of short-term extinction risk

(Caro and Laurenson 1994) is inherently inappropriate for assessing the importance of genetic diversity with respect to adaptation. The real danger from loss of genetic variation is the concomitant loss of adaptive flexibility in the face of changing environments, which reduces the long-term probability of persistence of the population.

Finally, genetic diversity exists as differences among local populations, with among-population differentiation tending to increase with decreasing gene flow in sexual populations and decreasing dispersal in asexual populations (see Section 3.1). This spatial component of genetic diversity augments the likelihood and accuracy of adaptation to local environments (Bishop *et al.* 1978; Templeton *et al.* 1989) and response to environmental change (Lynch and Lande 1993). As a result of local adaptation, different local populations of a species cannot be regarded as interchangeable (Powers *et al.* 1991; Watt 1991). One consequence of local adaptation is the expectation that reintroduction programmes will have increasing chances of success with increasing geographical proximity of the site of origin of the propagules to the site of release, as indeed has been repeatedly observed (Greig 1979; Griffith *et al.* 1989). In addition, genetic diversity has several direct implications for the relationship between biodiversity (at the intraspecific level in this case) and ecosystem services. Two representative examples are: (1) the maintenance of adaptive flexibility – an important component in recovery from disturbance and (2) the introduction of slash-and-burn agriculture which increased malaria in tropical Africa which in turn affected the incidence of sickle cell anaemia there (see Templeton 1982).

In summary, genetic diversity has many manifestations and plays many biologically significant roles within a species. This significance does not stop at the species boundary; rather, primarily through the intraspecific genetic process of adaptation, genetic diversity influences the emergence and functioning of higher order, ecological, systems.

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5.2.2 Biodiversity effects on patterns and processes of communities and ecosystems

5.2.2.1 Introduction

The loss of species through changes in land-use has occurred frequently and is irrevocable (Solbrig 1991; NRC 1995). Reductions in population size, fragmentation of populations, and alterations in the relative abundance of species are increasingly common phenomena with profound ecological implications (5.2.3). Human introduction of new species into natural communities is also common, and often has profound ecological effects (Drake *et al.* 1989; Vitousek 1990; Carpenter *et al.* 1992; D'Antonio and Vitousek 1992; Carleton and Geller 1993; Huston 1994). How do these changes in diversity affect ecological communities and ecosystems? Can the consequences of deletions or additions be predicted? What patterns are emerging from the plethora of investigations into these complex phenomena?

During recent decades, several hypotheses have arisen to describe the observed or expected consequences of the addition or removal of species. These hypotheses are based in part on observations following species reductions, deletions or additions and in part on predictions from ecological modelling and theory. These hypotheses are often cast as alternatives, but often focus on different aspects of the topic. Some hypotheses emphasize the number of species in the community (Vitousek and Hooper 1993), others the degree of similarity among species in traits that affect community or ecosystem functioning (Menge *et al.* 1986; Walker 1992; Lawton and Brown 1993; Frost *et al.* 1995; Sala *et al.* 1996). Here, we briefly review some of these hypotheses, then present an emerging conceptual framework that integrates and synthesizes the disparate approaches. In reviewing the key ideas, we delineate the hypotheses that centre on the notion of functional similarity among species, suggest how these hypotheses relate to one another, and point out how a number of them have evolved as additional information and understanding have emerged.

5.2.2.2 Relationship between species and the functioning of ecological communities and ecosystems: hypotheses concerning similarity among species

Several hypotheses about changes in species diversity and community or ecosystem responses consider the functional similarity among species, in other words, how similar different species are to one another with respect to their roles in community or ecosystem processes. The different approaches may be viewed as lying along a continuum. At one extreme is the idea that each species is unique and important, such that its removal or loss will have demonstrable consequences to the functioning of the community or ecosystem. At the other end of the spectrum is the notion that species overlap in function to a sufficient degree that removal or loss of a species will be compensated by others, with negligible overall consequences to the community or ecosystem. In the middle of this continuum lies a mixed community, with some unique species and others with substantial overlap in functional properties.

One of the first attempts to address this similarity among species was the notion of 'keystone species' codified by Paine (1969). The central core of the keystone concept is that only one or a few species have uniquely important effects on the community or ecosystem by virtue of unique traits or attributes. Analogous to the removal of a keystone from an arch, removal of a keystone species results in dramatic changes in the functional properties of the ecological system (e.g. changes in diversity, abundance, habitat structure). Paine initially restricted the concept of keystone species to predators of competitive dominants in a community. Building on a series of investigations in a wide range of ecosystems, a recent review (Power and Mills 1995) expands the keystone concept to include any species with an impact on its community or ecosystem that is disproportionately large relative to the abundance of the species (Box 5.2-1). Their review concludes that (a) keystone species have been demonstrated in a wide variety of ecosystems, (b) based on indirect evidence, keystones may be more prevalent than has been demonstrated, and (c) the concept can apply to individual species or groups of species, but that (d) *a priori* prediction of a keystone species remains elusive.

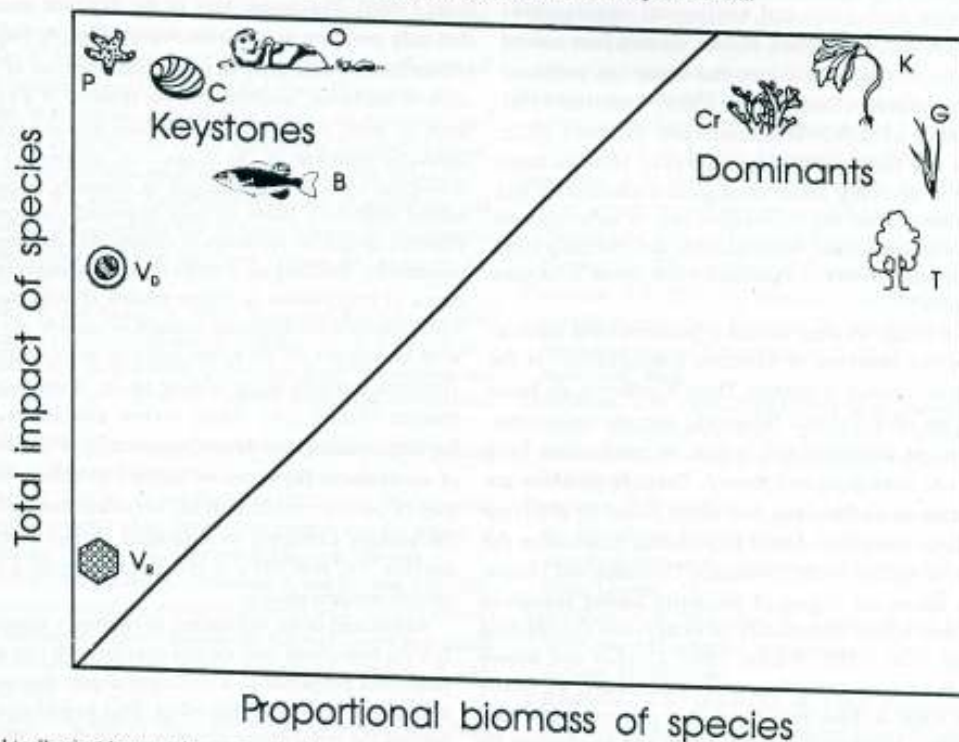
At one end of the continuum of similarity among species lies the hypothesis that species overlap with one another in functional properties to a sufficient degree that loss of any one species has negligible effect. This hypothesis has been termed the redundancy hypothesis (Walker 1992; Lawton and Brown 1993) but others suggest that the term 'functional compensation' hypothesis is preferable (Menge *et al.* 1994; Frost *et al.* 1995). The far opposite end of the hypothetical continuum in similarity is suggested primarily for heuristic purposes. There is no evidence that each and every species plays a unique role such that its absence

Box 5.2-1: Keystone species – what are they and why do they matter?

A keystone species is a species whose impacts on its community or ecosystem are large and greater than would be expected from its relative abundance. This definition is unconstrained by a species' trophic status, mode of impact, or nature of community or ecosystem response. For any species, a relationship exists between the proportional abundance of that species and its total impact on the community or ecosystem. Proportional abundance is normally measured in units of biomass (see graph below). Species whose total impact scales exactly to their proportional abundance fall on the diagonal line ($X = Y$). keystones, in contrast, have total effects that greatly exceed this line of proportional equality. Very rare species with total impacts that exceed the diagonal, but are nonetheless relatively small, are not considered keystones, since their overall effect is minimal. For instance, a very rare rhinovirus that makes a wildebeest sneeze (V_R) might have a total effect far exceeding that expected from its biomass. However, the rhinovirus would not qualify as a keystone species because of its low absolute total effect.

By contrast, an equally rare distemper virus (V_D) that kills lions or wild dogs might have a total impact of sufficient magnitude for keystone designation. The keystone species illustrated in the figure include the sea star *Pisaster* (P), the predatory whelk *Concholepas* (C), sea otters (O), and freshwater bass (B). All are species whose total impact is large and large relative to their abundance. By contrast trees (T), giant kelp (K), prairie grass (G) and reef-building corals (Cr) which dominate community biomass also have total impacts that are large, but not disproportionate to their biomass. These non-keystone dominants are to the right of the line.

Keystone species are usually detected when they are removed or disappear from a system. In the cases illustrated, the absence of the keystone species resulted in dramatic changes to the rest of the community (Box 6.1-1 provides details on the otter example). Keystone species have been reported from a wide variety of ecosystems, all trophic levels and many taxa. Their pivotal impact is often not appreciated until they are absent.



Total (collective) impact of a species (absolute value of community impact \times proportional abundance) of species versus their proportional abundance. Points representing a species whose total impact is proportional to its abundance would fall along the diagonal line ($X = Y$). Keystones are species whose effects exceed their proportional abundances by some large factor and whose total effect exceeds some threshold. Dominants are species which dominate community biomass and whose ecosystem impacts are large, but not disproportionate to their biomass. Letters represent examples of particular species described in the text (Power and Mills 1995).

would immediately result in a dramatic change in the functioning of the ecological system.

Another hypothesis concerning functional consequences of loss of species is the 'rivet hypothesis'. As originally formulated (Ehrlich and Ehrlich 1981), this hypothesis suggested that each species is like a rivet in an aircraft such that each species loss contributes equally to the probability of large changes in community and ecosystem processes. This hypothesis, too, has evolved and now (Chapter 5.1) suggests that, like rivets in critical places in an aircraft, certain species may play more critical roles than others. A number of features are essential to this hypothesis: the number of rivets (= species), their placement, and their immediate neighbours.

5.2.2.3 Key concepts and terms

Consideration of the relationship between species diversity and the functioning of communities and ecosystems requires a clear description of the important terms, e.g. **functional group**, **community patterns**, **community processes**, **ecosystem patterns** and **ecosystem processes**, as given below.

There is no intrinsically unique level at which biotic diversity affects ecosystem processes. The current level of conceptual understanding of the effects of biodiversity on ecosystem processes is so primitive that it is easiest to recognize these linkages at the level of **functional groups**, i.e. groups of species that have ecologically similar effects on ecosystem processes (Woodward 1987; Chapin 1993; Huston 1994). However, no two species or individuals are ecologically identical, so as our understanding improves we expect to recognize situations where species diversity within functional groups (Huston 1994; Cushman 1995) or genetic diversity within species (5.2.1) has important ecosystem consequences. Moreover, because most species belong to more than one functional group and affect species belonging to other functional groups, prediction of the overall consequences of a deletion or addition is complex. For example, large kelps provide the physical structure of a kelp forest in addition to providing a substantial portion of the primary production. Other macrophytes such as algal crusts or turfs and phytoplankton could compensate in part for the loss of production by kelps if kelps were deleted from the system, but would not provide the three-dimensional habitat for a diverse assemblage of invertebrates, juvenile and adult fishes, and marine mammals. Thus compensation by other members in one functional group is not automatically linked to compensation in other functions.

The **community processes** we consider here are species interactions (e.g. competition, predation, mutualism), which we distinguish from **ecosystem processes** — the flows of water, energy, and materials within and among ecosystems (e.g. primary production, microbial

immobilization, nutrient leaching). **Community patterns** are described in terms of the abundance and spatial distribution of species in an ecosystem, whereas **ecosystem patterns** are the quantities and configuration of water, energy and materials in biotic and abiotic components of the system. The same organisms carry out both community and ecosystem processes, so these and other levels of organization are closely linked. For example, introduction of a disease that alters the abundance of a flammable grass (a community change) may depend on genetic variability in disease resistance (genetic diversity) and may alter fire frequency and stand biomass (an ecosystem trait) and the propagation of fire among ecosystems in a watershed (a landscape process).

5.2.2.4 Integrated framework

Here we present a general framework, based on the hypotheses described above, for the information needed to predict the functional consequences of changes in diversity. To understand the community and ecosystem consequences of a species invasion or extinction, we must know at least (1) the approximate number of species in the community, (2) the relative abundance of these species, (3) how strongly a given species differs from other species in the community, (4) the impact of particular species traits on community and ecosystem processes and (5) the indirect effects that a species has on other species in the community. We refer to these as 'critical components of diversity'.

1. The number of species in an ecosystem (species richness) undoubtedly influences some community and ecosystem processes, but we do not know (a) the shape of the relationship between species number and the rate of an ecosystem process or (b) where this relationship saturates (Vitousek and Hooper 1993) (Figure 5.2-1a). If the relationship saturates, and we consider only species richness, we expect species additions or deletions to have their greatest effect when there are relatively few species in the community, as on islands (Cushman 1995).
2. The most abundant species of a community in terms of biomass typically accounts for the greatest proportion of productivity and nutrient cycling (Bormann and Likens 1979; Valiela 1984). Thus, we expect deletion of community dominants to have greater impact on some ecosystem processes than will deletion of species that are small and/or rare (Cushman 1995; Sala *et al.* 1996) (Figure 5.2-1b).
3. The impact of the addition or deletion of a particular species depends on its degree of functional similarity to other species in the community. If a species is

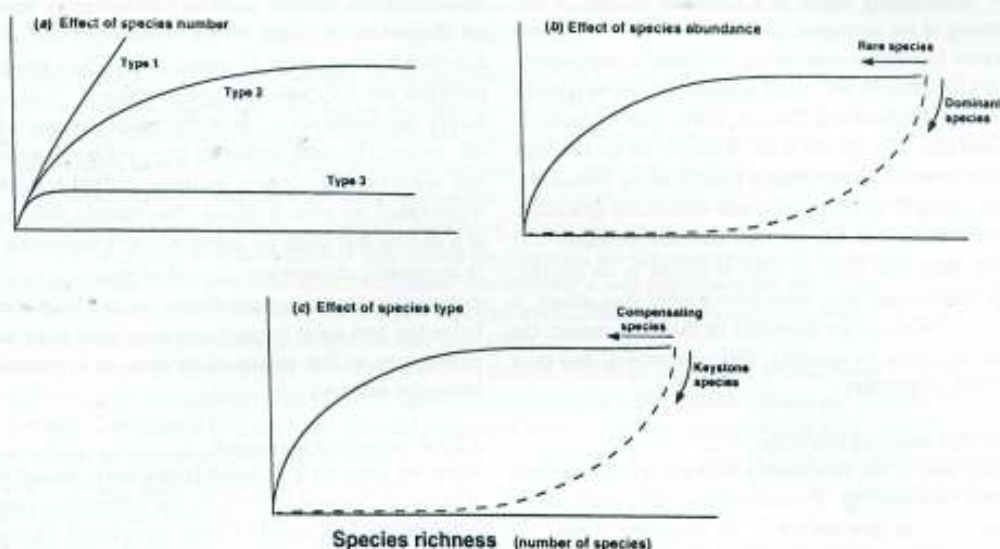


Figure 5.2-1: Some possible effects on ecosystem processes of (a) altering the number of species (ignoring relative abundance and traits of species; Vitousek and Hooper 1993); (b) deleting rare vs dominant species (Sala *et al.* 1996); (c) deleting keystone vs compensating species. The effect of number of species (a) depends on whether changes in ecosystem processes are equally affected by each species addition (Type 1), saturate with addition of new species (Type 2), or have an abrupt threshold with species diversity having no effect on ecosystem processes (Type 3). In (b) and (c), we assume a saturating relationship between ecosystem processes and species number. Arrows indicate the direction of change in ecosystem processes with deletion of species.

functionally similar to other species in the community (i.e. belongs to the same functional group) (Menge *et al.* 1986; Frost *et al.* 1995; Smith *et al.* 1995), its addition or deletion may have less effect than if the species has traits that uniquely affect community or ecosystem processes.

4. Certain traits of organisms have greater ecosystem impacts than other traits. Vitousek (1990) and Chapin *et al.* (1996) suggest that species modify ecosystem processes primarily through their effects on (1) availability of resources in the environment, (2) rates of consumption of resources or prey, and (3) the disturbance regime. In this section we summarize the general reasons for ecosystem sensitivity to changes in these categories of species effects. If a species is unique in the species or resources it consumes or controls (as often occurs at high trophic levels: top-down controls) or affects soil resource pools and supply rates (bottom-up controls, e.g. nitrogen fixation, hydraulic lift, litter quality) or disturbance frequency and intensity (the relative importance of equilibrium and non-equilibrium processes, e.g. digging and burrowing by animals, flammability in plants), gain or loss of such species is likely to have large *amplifying* effects on both community and ecosystem processes. These are the traits most likely to characterize keystone species. By contrast, if species are near the base of the food chain and are similar to other species in their resource (food) requirements, the addition or deletion of a

species generally has a small effect on ecosystem processes because of competitive interactions and *compensatory* responses by the existing or remaining species (Frost *et al.* 1995; Chapin *et al.* 1996). These compensatory changes alter community composition and diversity, but have minor effects on the quantity of resources consumed by the trophic level as a whole (Figure 5.2-1c).

5. Species which themselves have small effects on ecosystem processes can have large indirect effects if they influence the abundance of other species with large direct ecosystem effects. For example, a seed disperser or pollinator that has little direct effect on ecosystem processes may be essential for the persistence of a canopy species with greater direct ecosystem impact (Gilbert 1980; Paine 1980; Cushman 1995).

None of these criteria, taken singly, allow us to predict the community or ecosystem consequences of changes in diversity. However, taken together, these critical components of diversity determine the ecosystem consequences of addition or deletion of species from a community.

5.2.2.5 Effects of diversity per se on ecosystem processes

Species number (the first critical component of diversity) is functionally important because it (1) increases the rate or

efficiency of resource capture under steady-state conditions and (2) provides insurance against large changes in ecosystem processes in response to disturbance or environmental change. When species diversity is extremely low (e.g. a crop monoculture), total nutrient uptake and productivity of a crop, and its consumption by higher trophic levels, is often less than in more complex ecosystems (Swift and Anderson 1993; Vitousek and Hooper 1993; Naeem *et al.* 1994), although forests dominated by a single tree species are not notably less productive than highly diverse forests (Rodin and Bazilevich 1967). In artificial tropical communities, a variety of biogeochemical processes differed strikingly between plots with 0, 1, and 100 species but not among highly diverse plots of differing species composition (Ewel *et al.* 1991; Vitousek and Hooper 1993). Thus, we know that species diversity affects ecosystem processes somewhere between 1 and 100 species, but we do not know where this relationship saturates (Figure 5.2-1a). Artificial communities with differing numbers (1–4) of species per trophic level also differed in productivity (Naeem *et al.* 1994). The challenge in experimental studies is to separate the effects of species number from the effects of the traits of the component species. This is an important area for future research.

Species number is also important because it provides insurance against change in function in the event that a species is lost from an ecosystem. Because each species shows a unique response to climate and resources (Whittaker 1975; McNaughton 1977; Chapin and Shaver 1985), any change in climate or climatic extremes that is severe enough to cause extinction of one species is less likely to eliminate all members from a functional group. For example, Tilman and Downing (1994) showed that, due to the presence of drought-tolerant species, diverse grasslands maintain higher productivity in response to drought than do grasslands whose diversity has been reduced by experimental nutrient addition (see Section 6.1.7.3 and Figure 6.1-3). Conversely, the fewer species there are in a functional group or group of interacting species (e.g. pollinators), the more likely it is that any extinction event or series of such events will alter the ecosystem processes associated with that functional group (Holling 1986; Chapin *et al.* 1996). Thus, genetic and species diversity *per se* is important to the long-term maintenance of community and ecosystem structure and processes. This argues that no two species are ecologically redundant, even if they are similar in their ecosystem effects under a particular set of environmental circumstances.

It is intriguing to ask whether the hierarchical level at which diversity is expressed contributes significantly to the stability of ecosystem processes. Marine ecosystems may have a particularly broad range of physiological and genetic diversity because their diversity occurs at a higher

taxonomic level than in terrestrial systems. For example, 32 of the 33 extant animal phyla occur in the sea (Margulis and Schwartz 1988, Norse 1993) and exhibit a wide array of body plans, compared to the 17 phyla on land. We do not know whether this hierarchical level at which diversity is expressed contributes significantly to the environmental tolerance of ecosystem processes.

Species diversity is important to the maintenance of ecosystem processes over a complete cycle of common disturbance events. Following disturbance, initial colonization by early successional species often stabilizes the substrate, retains nutrients which are later used by other species, or retains moisture which facilitates colonization by less tolerant species. For example, riparian shrubs can stabilize stream banks sufficiently to allow colonization by forest trees (van Cleve *et al.* 1991). Rapid colonization by early successional species following fire or forest cutting retains nutrients which, in the long term, support the growth of late-successional forests (Stark and Steele 1977; Bormann and Likens 1979). The long-term stability and resilience of communities and ecosystems, therefore, probably requires a diversity of species whose ecosystem impact is minimal at most times but critical at certain phases of succession.

5.2.2.6 Mechanisms of community and ecosystem change due to species traits

Species often differ strikingly within and between communities in properties that affect community and ecosystem patterns and processes (Hobbie 1992, Wilson and Agnew 1992, Chapin 1993; van Breemen 1993; Paine 1994). Here we summarize the general reasons for ecosystem sensitivity to the fourth critical component of diversity, i.e. species traits that influence resource availability, resource consumption or disturbance.

(1) Ecosystem processes are highly sensitive to changes in species that influence the *supply or turnover rates* of water, nutrients or space. The supply of soil resources is an important 'bottom-up' control of terrestrial ecosystem processes (Jenny 1980). Similarly, nutrients are critical ecosystem controls in fresh water (Schindler 1978; Carpenter and Kitchell 1993) and in open and coastal marine ecosystems (Lobban and Harrison 1994, Menge *et al.* 1995). Space is a limiting resource in rocky intertidal communities (Dayton 1971; Connell 1978; Paine 1994). Many of the traits that influence resource supply tend to have highly skewed or discontinuous distributions among species in the community, so that a few species tend to have values for the trait that are quite different from those of other species in the community (Figure 5.2-1b,c). Introduction of exotic species with symbiotic nitrogen fixation in Hawaii greatly increased productivity and nitrogen cycling and altered the structure and species

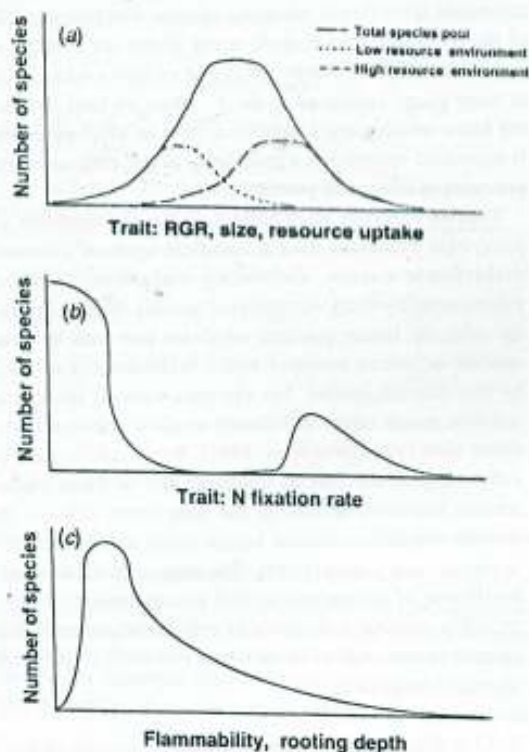


Figure 5.2-2: Typical frequency of occurrence of (a) continuously varying traits, (b) discrete traits, and (c) traits with skewed distribution among species in a community (Chapin *et al.* 1996).

composition of forests (Vitousek *et al.* 1987). Nepalese alder (*Alnus*) increases nitrogen inputs, and bamboo retains newly weathered potassium in Asian slash-and-burn agriculture (Ramakrishnan 1992). Each of the species in these examples differs strongly from other species in the community in its effects on nutrient supply. Similarly, introduction of deep-rooted species, such as *Eucalyptus* or *Tamarix*, can increase access to water and nutrients (van Hylckama 1974), thereby increasing the pool of resources available to support ecosystem productivity (Robles and Chapin 1996). These differences in rooting depth can be important at the regional scale. 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 reduced evapotranspiration and greater dissipation of energy as sensible heat (Shukla *et al.* 1990).

Animals can influence the resource base of the ecosystem by transporting nutrients among microsites within an ecosystem (e.g. concentration of nutrients in polygon troughs by lemmings (Batzli *et al.* 1980), on hilltops by sheep, or beneath desert shrubs by rodents) or by importing nutrients to oligotrophic ecosystems (e.g. nutrient movement from oceans to streams by migratory

salmon or transport of copepod fecal pellets to the deep sea). Species differences in soil microbial communities determine rates of nitrification, denitrification and methanogenesis and, consequently, the loss of trace gases to the atmosphere. Rates of nitrification also influence the susceptibility of N to loss by leaching or denitrification on land. Because these processes are controlled by relatively few species of microorganisms, i.e. the traits are uncommon and discontinuous, changes in their abundance could have large effects on N loss from ecosystems (Frost *et al.* 1995; Schimel 1995).

In terrestrial ecosystems, species also affect the resource supply rate through their influence on the turnover of nutrients in soils. Differences in tissue quality are critical controls over litter decomposition (Melillo *et al.* 1982; Flanagan and van Cleve 1983; Berg and McClaugherty 1989). Litter from low-resource plants decomposes slowly because of the negative effect on soil microbes of lignin, tannins, waxes and other recalcitrant or toxic compounds, reinforcing the low nutrient availability of these sites (Chapin 1991; Hobbie 1992). By contrast, species from high-resource sites produce rapidly decomposing litter with more N and P (Vitousek 1982) and less recalcitrant compounds. Thus, invasion or extinction of a species that differs substantially in litter quality from other species in the community could profoundly alter ecosystem processes. Long-term field experiments suggest that the nutrient content of litter is more important than carbon quality in exerting these ecosystem effects (Berendse *et al.* 1994). Because of the continuous variation in litter nutrient concentration among species (Chapin and Kedrowski 1983), litter-quality effects on ecosystem processes are probably a continuous function of plant traits. Plants can also alter nutrient supply rates through their effects on soil acidity, which is largely a function of the carbon quality of the litter and of the preferred form in which nitrogen is absorbed from the soil (Bormann and Likens 1979). Plants indirectly influence rates of nutrient supply through modification of the micro-environment (Wilson and Agnew 1992; Hobbie 1995). For example, arctic mosses, with their low rates of evapotranspiration (leading to water-logging) and effective insulation (preventing soil warming) indirectly inhibit decomposition (Gorham 1991). These species-specific effects could be important in determining both the pools of resources available to plants and higher trophic levels, and the rate at which these pools turn over.

Species traits that alter the resource supply have just as strong an effect on community processes as on ecosystem processes because resource supply and the balance of available resources determine the competitive balance among species in the community (Berendse *et al.* 1987; Tilman 1988; Aerts and van der Peijl 1993). In rocky intertidal communities, predation and herbivory on species that monopolize space play key roles in determining

community patterns and processes. By preventing mussels from dominating mid and lower shore levels, seastars on the northeastern Pacific and eastern Tasman shores, and snails on southeastern Pacific shores, make space available to a wide variety of invertebrates and seaweeds that would otherwise be outcompeted by mussels (Paine 1966, 1971; Duran and Castilla 1989). Likewise, herbivorous sea urchins and snails control the availability of critical resources (space and access to light) in tide pools by preferentially feeding on competitively dominant seaweeds (Dayton 1975; Lubchenco 1978). In terrestrial ecosystems, an increase in soil resources makes light relatively more limiting, shifting the competitive balance in favour of taller plants (Tilman 1985) and may increase the number of trophic levels that can be supported (Oksanen 1990; Power 1992). Thus, the impacts of resource supply on community structure extend well beyond the primary producers.

(2) The addition or loss of species that differ in their rates of resource consumption or the level to which resources are depleted can have either large or small effects on ecosystem processes, depending on their degree of overlap in resource use with other species in the community. Most plant species are similar to one another in the types of resources used (light, water and nutrients), although there can be specialization by rooting depth (see above), form of nitrogen utilized (Read 1991; Schulze *et al.* 1995), or the level to which soil resources are depleted (Tilman 1988). By contrast, animal and microbial disease organisms commonly vary in their degree of resource specialization and, therefore, in their degree of overlap with other species in a community. In many cases, specific traits of both the consumer and of the plant or prey, as well as characteristics of the environment in which the interaction occurs, determine the specific impact on rate of consumption of the resources or prey (Lubchenco and Gaines 1981).

Traits of plant species that best predict resource consumption are height (or biomass per individual) and relative growth rate (RGR) – traits that vary continuously among organisms (Grime and Hunt 1975) and that are unlikely to be strikingly distinct in any particular species (Figure 5.2-2a). Height (size) enhances resource capture in plants that are rooted to their substrates (e.g. terrestrial plants, aquatic macrophytes and sessile algae) by allowing the plant to reach the top of the canopy where most light is available and to exploit a large soil volume, whereas RGR is correlated with potential for carbon and nutrient acquisition (Olson and Lubchenco 1990; Lambers and Poorter 1992; Chapin 1993). In closed communities, any reduction in the abundance of one species should cause a compensatory increase in the abundance of other species due to release from competition, with little change in the total quantity of resources accumulated by vegetation at the ecosystem level (McNaughton 1977; Chapin and

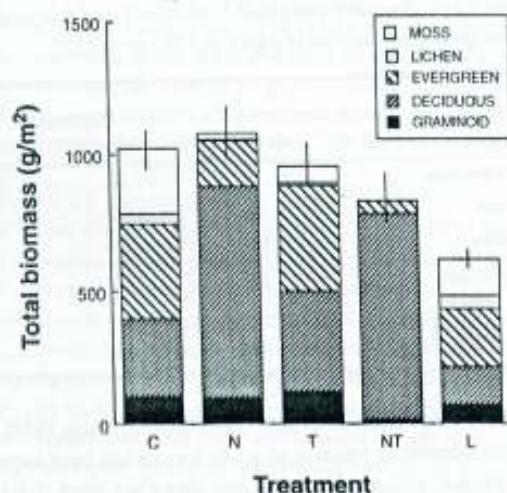


Figure 5.2-3: Total biomass (excluding roots) of plant functional groups in arctic tussock tundra after 9 years of different environmental manipulations: control (C), nutrient addition (N), greenhouse which raised summer air temperature by 3°C (T), fertilized greenhouse (NT), and shading to reduce light by 50% (L) (Chapin *et al.* 1996).

Shaver 1985). Consequently, we expect that the gain or loss of a species will have little effect on biogeochemical cycles within the ecosystem under 'steady-state' conditions (Shaver *et al.* 1995), if these species differ only in resource consumption. This hypothesis is supported by ecological responses to experimental and natural variation in resource supply, both of which show much larger changes in the abundance of individual species than in biogeochemical pools or fluxes measured at the ecosystem level (Figure 5.2-3, Table 5.2-1; McNaughton 1977; Chapin and Shaver 1985; Aerts and Berendse 1988; Chapin *et al.* 1995). In summary, even large changes in species diversity and abundance may have only modest *direct, short-term* effects on pools and fluxes of carbon and nutrients, when species differ only in rates of resource consumption. Similarly, many animal species, particularly grazers, have a broad overlap in diet, such that a change in abundance of one species is compensated by changes in abundance of competing species with minimal effect on the rate of consumption of their common prey species (Frost *et al.* 1995).

Many animal species (and some plant species) differ strikingly from all other species in the community in the resources they consume and, therefore, their effects on community structure. Addition or deletion of these species strongly influences the abundance of the limiting resources or prey that they consume, because they use discretely different resources from other species in the community. These top-down controls are particularly well developed in aquatic systems, where removal of sea otters releases sea

Table 5.2-1: Annual variation in production (% of five-year mean) of major tussock-tundra species and total community above-ground production (Chapin and Shaver 1985).

Species	Production (% of average)					Coefficient of variation (%)
	1968	1969	1970	1978	1981	
<i>Eriophorum</i>	77	58	148	101	116	35
<i>Betula</i>	30	52	55	248	121	88
<i>Ledum</i>	106	138	62	103	91	27
<i>Vaccinium</i>	135	172	96	28	71	56
Total production	93	110	106	84	107	11

urchins which graze down kelp (Estes and Palmisano 1974), or the addition or removal of a fish species can have large 'keystone' effects that propagate 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 wolves can release deer populations which graze down vegetation (Rasmussen 1941), while the removal of elephants or other keystone mammalian herbivores leads to encroachment of woody plants into savannas (Owen-Smith 1988; Wilson and Agnew 1992). Similarly, epidemic diseases, such as rinderpest in Africa, can act as keystone species by greatly modifying competitive interactions and community structure (Bond 1993).

The strong effects of grazers and predators on community structure automatically translate into effects on ecosystem structure, for example by greatly altering the biomass of primary producers (Power 1992), perhaps even on a biogeographic scale (Gaines and Lubchenco 1982; Zimov *et al.* in press). However, we have only fragmentary information on the ways in which this altered ecosystem structure modifies ecosystem processes. Often these top-down controls by herbivores and predators have a much greater effect on the 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, intensively grazed grassland systems such as the southern and southeastern 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 the accumulation of standing dead litter and return nutrients to the soil in plant-available forms (McNaughton 1988). Keystone predators or grazers can thus alter the pathway of energy and nutrient flow and modify the balance between herbivore-based and detritus-based food chains.

We expect these generalizations about the importance of traits determining resource consumption to apply to closed

communities where resource supply rather than colonization determines productivity and nutrient cycling and where multiple species use the same limiting resources. However, disturbance regime strongly influences the expression of these ecosystem effects (Menge *et al.* 1994; see also 5.3.1). As disturbance rate and intensity increase, patterns of resource supply and consumption become less important determinants of ecosystem processes, and the impact of strong biotic interactions and keystone predators is diminished (Menge *et al.* 1994).

(3) Animals or plants that greatly alter disturbance regime can have large effects on ecosystems by decreasing the relative importance of equilibrium processes relative to non-equilibrium processes. This is one of the most important ways in which animals affect ecosystem processes (Lawton and Jones 1995). For example, gophers and pigs create large areas of soil disturbance, creating sites for seedling establishment and favouring early-successional species (Hobbs and Mooney 1991; Kotanen in press), generally leading to a lower biomass and a higher ratio of production to biomass (Shaver 1995). Bivalves that bore into coral reefs increase the rate of bioerosion of coral heads and thus their susceptibility to dislodgment during storms (Highsmith 1980). At the regional scale, disturbances created by overgrazing can alter the albedo of the land surface and change patterns of regional temperature and precipitation (Charney *et al.* 1977; Schlesinger *et al.* 1990).

Plants can also alter disturbance regime through their effects on soil stability and their flammability. For example, introduction of grasses into forest or shrubland ecosystems can increase fire frequency and cause a replacement of forest by savannah (D'Antonio and 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). Plants and animals can also act to decrease disturbance. In early succession, plants are often critical in 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. Similarly, variation in size and shape of seaweeds has a substantial impact on their susceptibility to disturbance from wave forces (Gaylord *et al.* 1994) and, therefore, on community patterns of disturbance and succession (Dayton 1975). Both plant and animal traits that alter disturbance regime tend to be discontinuous, which increases their probability of having a large ecological impact on any given ecosystem. The ecological impact of adding or deleting species which influence disturbance regime depends on whether there are other species in the ecosystem sharing these traits.

Disturbance regime has just as large an impact on structure and processes at the community as at the ecosystem level through its effects on competitive interactions among species with different life-history traits. Disturbance regime determines the competitive balance between early and late-successional species (Olff *et al.* 1993), often resulting in the greatest species diversity at intermediate levels of disturbance (Connell 1978; Sousa 1979; Paine and Levin 1981; see 5.3.1).

5.2.2.7 Ecosystem-level feedbacks to biodiversity of invasions and extinctions

In natural ecosystems, biodiversity may be of greater inherent interest to society than ecosystem processes, because many of the goods and services (direct benefits of species; Ehrlich and Ehrlich 1981) that people derive from ecosystems relate to properties of species rather than to biogeochemical processes. However, the existence and quality of the Earth's atmosphere, climate, water and soil ('indirect benefits' of species; Ehrlich and Ehrlich 1981; Chapter 5.1) depend on biogeochemical processes. We have established that species traits and biodiversity do have implications for ecosystem processes. We also know that species are quite sensitive to their environment and that subtle changes in environment can alter competitive balances or rates of predation or herbivory, leading to changes in species composition and biodiversity (Lubchenco 1978). Perhaps the most important consequences of changes in species traits and biodiversity in natural ecosystems have to do with the largely unknown feedbacks of the altered environment to further changes in biodiversity. For example, invasion by alien grasses in Hawaiian forests resulted in increased fire frequency and a decline in the diversity of fire-sensitive woody species (D'Antonio and Vitousek 1992).

A second, largely unexplored consequence of changing biodiversity involves species-specific interactions with other species that have large ecosystem effects (the fifth critical component of diversity). For example, a seed disperser or pollinator that has little direct effect on ecosystem processes may be essential for the persistence of

a canopy species with greater direct ecosystem impact (Gilbert 1980; Paine 1980). At our present level of ignorance, these indirect effects of species on ecosystem processes are difficult to predict, suggesting that we should be conservative in drawing conclusions about the ecosystem impacts of loss of a given species or level of diversity.

5.2.2.8 Conclusions

Five critical components of diversity required to predict the functional consequences of species additions or losses are (1) the number of species in a community, (2) the relative abundance of these species, (3) how strongly an invading or deleted species differs from other species in the community, (4) the traits of the species and (5) the indirect effects that a species has on other species in the community. The major mechanisms by which species alter ecosystem processes are through changes in soil resource supply, the consumption of resources or food, and disturbance regime.

The gain or loss of a species will have its greatest impact on ecosystem processes when there are few species in the community, when the species gained or lost is a dominant species, and/or when the species differs strongly from other species in the community. When species are similar to one another in their resource requirements, as often occurs with plants and generalist herbivores, the gain or loss of a species has a large effect on community composition but less effect on ecosystem processes because of the compensatory responses of other species to the altered competitive environment. Compensatory responses are most likely to occur where there are many species per functional group. The traits that govern resource acquisition in these species are often continuously distributed among species, so that species differ quantitatively rather than qualitatively in their effects on ecosystem processes.

By contrast, the gain or loss of species that consume unique food or soil resources or that alter resource supply or disturbance regime can have large effects on ecosystem processes, which propagate through the ecosystem through a chain of indirect effects. Traits governing these processes often differ qualitatively among species, so that changes in the abundance of these species have widespread community and ecosystem impacts. Species effects on ecosystem processes are often as large as direct climatic effects and must be included in predictive models of the role of terrestrial ecosystems in global processes.

Species diversity (independent of species traits) is functionally important because it provides insurance against large changes in ecosystem processes and may enhance the efficiency with which resources are captured from the environment and transferred among species. Because each species shows a unique response to climate and resources, any change in climate or climatic extremes

that is severe enough to cause extinction is less likely to eliminate all members of a functional group. The fewer species there are in a functional group or group of interacting species (e.g. pollinators), the more likely it is that any extinction event or series of such events will seriously affect the function associated with that functional group. Although species clearly differ in the magnitude of their impact on community and ecosystem processes, the differences among species in their responses to disturbances and environmental extremes and their indirect ecosystem effects, mediated by species interactions, make it unlikely that there is much, if any, ecological redundancy in communities over time scales of decades to centuries, the time period over which environmental policy should operate.

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5.2.3 Effects of spatial structure on ecosystem functioning

5.2.3.1 Introduction

Species are the building blocks of ecosystems, and as described in Section 5.2.2, the loss of species can lead to changes in ecosystem attributes beyond the species level, e.g. biomass, productivity, disturbance frequency, and the rates of biogeochemical flows. Not all species are equal in terms of their influence on their ecosystem, but Section 5.2.2 indicated some types of species likely to have large impacts: animal species high in the food chain; plant species with a dominant influence on the resource supply, or on the composition of the soil or litter; and species with unique attributes, such as nitrogen-fixing plants in N-poor environments. In Section 5.2.2 it is also suggested that ecosystem attributes depend on the total diversity of the biota, above and beyond the contributions of particular species.

Here the effects of spatial structure on ecosystem functioning are addressed. By spatial structure we mean the sizes and shapes of patches of different types of habitat (here used synonymously with ecosystem), and the distances of these patches from one another. A solid base of theory and empirical evidence shows that spatial structure can profoundly influence the diversity, abundance and interactions of species in ecosystems. In other words, two otherwise similar natural areas, differing only in their spatial configuration, will differ in their species composition and thus in other ecosystem attributes. This is of key importance, since one of humans' most ubiquitous effects on ecosystems is to fragment them. Virtually all natural areas today are not only smaller in total extent, but also considerably patchier than they once were (Groom and Schumaker 1993). Here we explain why patchiness matters, and why spatial structure must be a central consideration in conservation plans.

At the present state of ecological knowledge there is little evidence linking spatial structure directly to flows of

matter and energy, or to other attributes of ecosystems beyond the level of species. This remains an extremely important area for research. However, all ecosystem properties depend ultimately on the biota. Therefore, we review the considerable evidence on the effect of spatial structure on species and their interactions, returning at the end to the possible consequences at other levels of ecosystem organization. (Also see Saunders *et al.* 1991 and Fahrig and Merriam 1994 for excellent reviews of the consequences of fragmentation.)

5.2.3.2 Effects of spatial structure on species diversity and abundance

Local extinction and metapopulations. Ecologists increasingly view most species as consisting of so-called 'metapopulations', i.e. networks of local populations occupying discontinuous habitats, but partly connected to one another by occasional dispersal (see also Section 4.4). Extinctions of these local populations ('local' as opposed to regional or global extinction) may occur frequently in some species, owing to disturbances, changes in the habitat, or natural catastrophes. This implies that the survival of some species may be dependent on the ongoing founding of new local populations. Theory suggests that the chances of persistence for a metapopulation depend on how many local populations and suitable habitat patches there are, the length of time each local population persists before becoming extinct, and the propensity of the species to disperse between habitat patches and found new populations on empty patches (Hanski 1989, 1991; Hanski and Gilpin 1991; Fahrig and Merriam 1994; Hastings and Harrison 1994).

The majority of empirical studies of metapopulations have been on insects and other small and short-lived animals. Similar patterns are likely to be found in other species, but at larger scales of space and time. One common pattern is a 'mainland-island' spatial structure, in which the metapopulation contains one or more local populations large enough to be in no immediate danger of extinction, as well as many smaller populations. The small populations blink in and out of existence, going extinct during droughts, floods, harsh winters or other adverse circumstances, and being recolonized by immigrants from the mainland. If dispersal is blocked, the small populations will cease to exist: if the mainland population is lost, the species will become regionally extinct. Well-documented examples include several species of spiders on small islands (Schoener and Spiller 1987; Schoener 1991), and butterflies on patches of habitat supporting the plants on which their caterpillars feed (Harrison *et al.* 1988; Thomas and Harrison 1992).

In an alternative pattern there is no mainland and all local populations are fairly susceptible to local extinction. In this case the regional survival of the species is much

more precarious: there must be enough populations and available habitat patches within the region, and rates of dispersal among them must be high enough, to allow the founding of local populations can keep pace with their extinction. An excellent example is provided by the pool frog *Rana lessonae* in Sweden, on the northern edge of its distribution. Frog populations in individual ponds naturally become extinct during severe winters, or when succession obliterates the ponds. However, because modern forestry practices are both reducing the number of ponds and obstructing the dispersal of frogs among ponds, the frog may be on its way to regional extinction (Sjögren 1991, 1994). Similar patterns have been observed in other amphibians in temporary ponds (Gill 1978; Sinsch 1992).

Consequences for diversity and abundance. When the metapopulation processes of local extinction and recolonization are important, they lead to an obvious pattern in a species' spatial distribution. Habitat patches that are large and/or close to other patches will support populations of the species most of the time, while small or isolated patches will more often be unoccupied. This pattern is seen in amphibians (Laan and Verboom 1990), birds (Opdam 1990; Verboom *et al.* 1991), mammals (Lawton and Woodroffe 1991; Peltonen and Hanski 1991), and butterflies (Thomas *et al.* 1992) in fragmented European landscapes. Most importantly, when this is the case the regional survival of the species may be highly sensitive to any further changes in the spatial structure of its habitat. It may quickly collapse to regional extinction if the size or number of habitat patches is reduced, the average distances among patches increases, or changes in the habitat between patches make dispersal more difficult.

Based on this evidence, we may expect human-induced fragmentation to reduce the diversity of native species in natural habitats. The types of species most likely to be lost are those with the highest rates of local extinction on small habitat patches, such as the top predators and other species with large body sizes and large area requirements. Also likeliest to be lost are those species with the lowest abilities to disperse among and colonize habitat patches, which include typical late-successional ('climax') species. Conversely, the species likeliest to survive fragmentation will be those best adapted to patchy and frequently disturbed environments, meaning the well-dispersing, early-successional ('weedy') species (Tilman *et al.* 1994). Moreover, even if outright extinctions do not happen immediately, fragmentation will tend to shift species' relative abundances within ecosystems, such that the population densities of weedy species will increase and those of climax species decrease.

We also know that the genetic diversity within species is profoundly affected, and usually reduced, by the

fragmentation, extinction and recolonization of populations (McCauley 1991). What we do not know, as yet, is how much the loss of genetic variation affects the prospects for species' survival (see also 4.2).

5.2.3.3 Effects of spatial structure on species interactions

Pollination. If spatial structure can affect the distributions and abundances of species, it follows that its consequences can cascade through communities of interacting species. Some of the best examples concern the coevolved relationships between plants and the animals that pollinate them, or disperse their seeds (Bawa 1990). In Sweden, the herb *Dianthus deltoides* receives fewer visits by pollinating butterflies, and therefore suffers lower seed set, because of population fragmentation (Jennersten 1988). In small remnant patches of *chaco* (dry forest) in Argentina, numerous plant species experience fewer visits by specialized native pollinators and more visits by generalist introduced honeybees (*Apis mellifera*), leading to reduced seed output (Aizen and Feinsinger 1994a, b). Many similar examples are reviewed by Saunders *et al.* (1991) and Rathcke and Jules (1993). Possible consequences for plant populations include declining abundance, loss of genetic diversity and eventual extinction.

Herbivory. Because of their large area requirements, large mammals are usually among the first animal species to disappear from fragmented forests. Their loss may affect the structure of the entire forest because of the role they play as seed predators and herbivores. Leigh *et al.* (1993) examined small islands of tropical forest formed by the construction of a dam in Panama, and found they had fewer tree species than the forests on the nearby mainland. The islands were dominated by a few tree species whose seeds, on the mainland, were favoured foods of mammals such as agoutis. The absence of agoutis on the islands allowed these trees to become the dominant competitors, reducing overall diversity. Similarly, Dirzo and Miranda (1991) found that the absence of mammalian herbivores from small forest fragments in Mexico led to higher competition among tree seedlings, which led to forests dominated by a few competitively superior tree species.

Predation. Very important ecosystem services are provided by predators that control populations of herbivores, especially herbivores with potentially large effects on biomass and nutrient cycling. Large predators are especially likely to become scarce or disappear from fragmented ecosystems, for the reasons discussed above. Losing lions or cheetahs from fragmented African savannas may have enormous impacts on the vegetation and fire regimes, for example – effects that will be played out over the next several decades or centuries.

This point is best illustrated by predatory insects that can also have large ecosystem effects, but on faster time scales. Many herbivorous insects can undergo outbreaks that

devastate forests or other natural habitats. Ecologists believe that a major natural role in suppressing outbreaks is played by so-called parasitoids, which are insects (usually wasps or flies) that lay their eggs on the bodies of living host insects (which may be herbivorous 'pest' species). The developing larva of the parasitoid subsequently kills the host insect. Roland (1993) found that outbreaks of tent caterpillars lasted longer in heavily fragmented Canadian forests than in less fragmented ones, possibly because parasitoids were less efficient at finding their hosts (caterpillars) in patchy forests. Kruess and Tschamntke (1994) found that in agro-ecosystems as well, fragmentation can lead to fewer parasitoids and more herbivorous insects on plants.

Conversely, fragmentation can also allow natural habitats to be invaded by predators that are scarce in less disturbed situations. Many studies have reported that birds breeding in remnant patches of forest suffer elevated losses of eggs and nestlings to domestic cats, avian brood parasites (e.g. cuckoos), and other predators that thrive in the surrounding human-dominated landscape (Wilcove 1985; Andren and Angelstam 1988; Small and Hunter 1988; Paton 1994). Fragmentation may also influence the prevalence and spread of pathogens (Jarosz and Burdon 1991; Grosholz 1993).

Decomposition. One of the most direct links between fragmentation and ecosystem processes was found by Klein (1989), who examined communities of dung beetles in remnant patches of Amazon Basin forest. Dung beetles are extremely important recyclers of organic matter in nutrient-poor tropical forests. Klein found that forest fragmentation not only altered species composition, with fewer species of dung beetles (and sparser populations) in small patches than in larger tracts of forest, but also led to lower rates of dung decomposition, indicating a significant change in nutrient processing. Although this is an isolated example, it may not be at all unusual. We simply do not know how many changes of ecosystem significance are happening in tropical forests, which are extraordinarily rich in species and specialized interactions, very poorly understood by biologists, and currently threatened by rapid and severe fragmentation.

5.2.3.4 Spatial structure and ecosystems

We have seen that spatial structure has major effects on species composition, abundance, and interactions between species in ecosystems. At present we cannot make definite statements about the consequences of spatial structure at other levels of ecosystem organization, such as disturbance rates or biogeochemical flows. However, we have seen that the kinds of species most sensitive to spatial structure include top predators and other large, area-sensitive species; late-successional ('climax') species, which tend to be poorer dispersers than early-successional ('weedy')

species; and species involved in obligate pollination or seed dispersal mutualisms, which disproportionately tend to be tropical and late-successional. Comparing this with the list of species most likely to have large influences on their ecosystems (5.2.2), we see considerable overlap, suggesting the scope for far-reaching consequences of altering the spatial structure of ecosystems.

The growing recognition by ecologists of the importance of spatial structure is being put into practice in attempts to conserve individual species. As conservationists attempt to design plans for large-bodied, fragmentation-sensitive species such as the northern spotted owl, the core principles are to make individual patches large enough for the rate of local extinction not to be too high, as well as close enough together (or connected by 'corridors' of habitat) for rates of dispersal and recolonization to be adequate (Doak 1989; Lamberson *et al.* 1992; but see Harrison *et al.* 1993).

However, one general problem with these strategies is that the responses of individual species to fragmentation are highly dependent on details of the species' demography and dispersal behaviour (Fahrig and Merriam 1994; Harrison 1994). We know too few of these idiosyncratic details, for any species, to predict with any confidence whether it can survive in a given fragmented landscape. Worse yet, a landscape that supports a viable metapopulation of one species may easily fail to do so for many others. Few principles exist yet to guide us in the conservation of entire fragmented ecosystems, except that, almost certainly, the less additional fragmentation we impose on them the better they will function at all levels of organization.

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5.2.4 Biodiversity at landscape to regional scales

5.2.4.1 Introduction

Most of the current emphasis on biodiversity has been focused on taxonomic or functional diversity. Even at the scale of ecosystems, the largest proportion of effort has

been focused on the relationship between species diversity and ecosystem functioning. While such work is of critical importance, it does not capture larger-scale patterns and processes, specifically those at the landscape to regional scale. At these large spatial scales, the appropriate biological unit that confers diversity is the ecosystem. Landscapes are composed of an assemblage of interacting ecosystems. A diverse landscape or region is one with many different ecosystems (richness component), or one in which the area occupied is similar for all ecosystems (evenness component). The key characteristic of a diverse landscape or region is that its constituent ecosystems perform different functions – physical, biological or human-related. Here, we do not address species or population diversity that occurs at large scales, nor heterogeneity induced at the scale of individuals (i.e. 'gap dynamics'), nor patchiness within an ecosystem. Rather, we focus our discussion at scales that are relevant to processes that occur at the landscape to regional scale: watershed dynamics, gaseous and energy exchange with the atmosphere, and socioeconomic and political dynamics.

These processes are responsible for the interactions between ecological units and global change, and we will refer to them as 'landscape or regional functions'.

Humans have demonstrated world-wide that alteration of the constituent ecosystems within landscapes and regions through land-use management can fundamentally alter local and global-scale hydrological cycles, atmospheric chemistry, terrestrial carbon storage, soil erosion rates, water quality and human welfare. A careful analysis of the role of biodiversity at large scales is therefore important for understanding and managing long-term global sustainability.

Our objective here is to explore the conditions under which biodiversity at landscape to regional scales is important for the large-scale system functions identified above. We will first set forth some ideas about a general relationship between biodiversity and landscape to regional function, providing examples from a diverse literature. Second, we will assess the types of landscapes or regions in which rare ecosystem types contribute largely to ecosystem functioning. Finally, we will assess the relationship of human land-use diversity to the functioning of both ecological and human systems.

5.2.4.2 Diversity and ecosystem functioning at landscape to regional scales

Conceptual framework: The extent to which biodiversity matters in a landscape or region is at least partly dependent upon the linkages among ecosystems. The currency of these linkages includes wind, water, trace gas exchange, plant and animal movements and human products and revenues. Certain ecosystems within a landscape or region may serve as sources of materials, energy or biota (Pulliam 1988), while others may serve as sinks, Risser (1987) and

Forman and Godron (1986) suggested that disturbances increase the rate of material flow among landscape units, but that fragmentation may also reduce flows and linkages.

The relationship between diversity and system functioning at large scales has strong analogies to generalizations made for the scale of species and functional-type diversity and ecosystem functioning by Sala *et al.* (1996). First, to understand the relationship between ecosystem diversity and landscape or regional function, one must understand the contribution of the various ecosystems to the specific function of interest, i.e. element export, gaseous flux, revenue, etc. Once this is understood, the relationship between diversity and function becomes clearer: deletion, disturbance or increases in the abundance of the ecosystem that contributes the most to the specific function will have the largest effect. In many cases the most abundant ecosystem will be the one that contributes the largest proportion to landscape or regional function. In some specific cases, there may be 'keystone' ecosystem types that are relatively rare within the landscape or region, but that provide a disproportionate contribution to function at that scale.

In many landscapes or regions, the presence of several ecosystem types that have high proportional land cover is most important in determining large-scale system functioning, for instance in susceptibility to disturbance. Human activity in such landscapes often preferentially reduces the abundance of one or more of these dominant ecosystem types, and thus may impact system functioning significantly. High-productivity ecosystems, such as the fertile tropical rain forests of the Amazon and the tallgrass prairie of North America are among the most likely to be cultivated or harvested. The impacts of reducing such dominant ecosystem types may be highly significant for landscape and regional function, resulting in large-scale habitat changes, alteration of storage or runoff of water, and associated consequences for sediment production, or altered carbon and nitrogen balance. In addition, in landscapes or regions that contain 'keystone' ecosystems, human interference with ecosystem functioning may have very dramatic influences, such as complete elimination of a crucial ecosystem function such as water storage.

Examples: Ecosystem diversity at landscape and regional scales is controlled by the interactions among large-scale patterns in climate and large and small scale heterogeneity in the physical environment. A diverse array of ecosystems within landscapes or regions may be important for providing both sources and sinks of propagules, fauna, sediments, water or nutrients. If the array contains an adequate balance of ecosystems that serve each of these functions, the function at the landscape or regional scale is likely to be able to persist in the face of disturbances. We will provide four examples, with particular attention to the

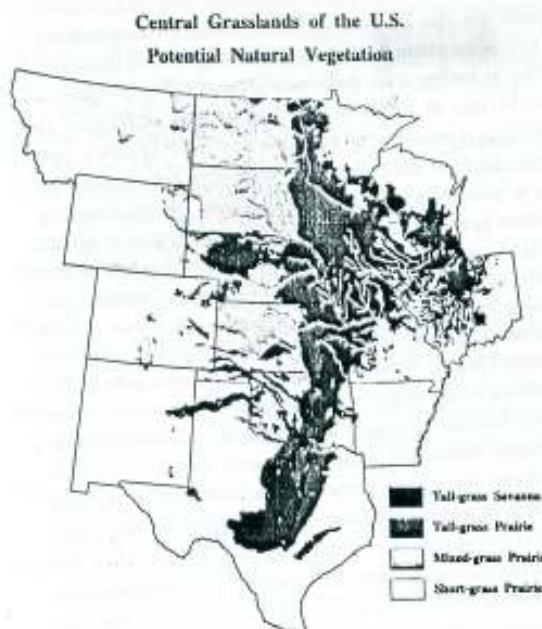


Figure 5.2-4: Potential natural vegetation of the central grasslands of the USA. Revised from Küchler 1964.

central grassland region of the USA, the system for which we have the most information and experience.

In central North America there is a strong west-east gradient in mean annual precipitation from the eastern foothills of the Rocky Mountains to the Mississippi River. Additionally, there is a nearly orthogonal north-south gradient in mean annual temperature. These gradients interact to provide regional-scale patterns in ecosystem types (Figure 5.2-4). These regional-scale patterns interact with small-scale patterns of topography and parent materials to produce an increasingly complex pattern of ecosystems as one scales down from the region to individual landscapes. At a mesoscale level (hundreds of km²), the Sand Hills of Nebraska provide a classic example of the effect of parent material on ecosystem development. Because of their effect of reducing evaporative losses and therefore increasing the effectiveness of precipitation (Noy-Meir 1973), these deep sandy soils (Figure 5.2-5) result in a westward extension of the tallgrass prairie into an area in which the typical vegetation is classified as northern mixed prairie (see Figure 5.2-4). Here, landscape-scale topographic gradients can result in gradients in ecosystem types over tens of metres.

This complex of scales of heterogeneity in both environments and ecosystems provides the grassland region with enormous response potential to certain large-scale disturbances such as climate change. This complex geographic mixing of ecosystem types changes the nature of the responses that will be necessary for the region to

adapt to new climatic changes. Instead of requiring regional-scale migration of species adapted to the new climate, response to climate change will in many cases only require local-scale dispersal. In addition, it is important to note that this regional distribution of soils and of ecosystem types has developed over many thousands of years: consideration of long time scales may be important for any assessment of the origin and maintenance of large-scale diversity.

A second example of the importance of landscape-scale heterogeneity occurs in systems that are subjected to large-scale fires. In coniferous subalpine forests, topographic variability results in a complex of ecosystem types, including forest successional stages, meadows and xeric vegetation (Romme and Knight 1981). This landscape-scale heterogeneity in ecosystem types, caused by physical patterns in drainage and nutrient availability, as well as by successional dynamics, results in natural fire-breaks which may reduce the likelihood of very large fires (Romme and Knight 1981; Romme 1982). Recent work in Yellowstone National Park in the USA has suggested that heterogeneous landscapes are more resistant to large fires than homogeneous landscapes, and that once burned, they have a greater ability to maintain water quality (Knight and Wallace 1989).

A third example is found in the interaction of migratory and other large fauna and the structure and function of landscapes and regions. A very large proportion of the world's fauna in subtropical to arctic regions depends upon multiple habitats which are used seasonally. Wild ungulate movements have been shown to influence significantly the patterns of net primary production, forage utilization and nutrient cycling (Ruess and Seagle 1994) at both landscape and regional scales. Coughenour (1991) suggested that for antelope (*Saiga tatarica*) in southern Asia, wildebeest in the Serengeti, and bison in North America, migration helps to conserve forage and protect landscapes from overgrazing. Interference in the ability of these ungulates to utilize a diversity of habitats through spatial constraints or habitat elimination has had very large impacts on ecosystem functioning, through local overabundance of herbivores or by removal of natural grazing (reviewed by Coughenour 1991). Maintenance of corridors for faunal migration may significantly enhance the ability of organisms to distribute their habitat use across broad regions (Forman 1987).

Landscape diversity and function may rely upon population dynamics of a single species. For example, beaver (*Castor canadensis*) in the boreal forest of North America have been shown to alter the distribution of hydrologic zones (forest, wet and dry meadows and ponds) (Naiman *et al.* 1994). The net effect of increasing beaver populations has been to convert forests into meadows and ponds, increasing the abundance and cover

of these ecosystems from minor constituents to the majority of land cover (Bridgham *et al.* 1995). The anaerobic conditions created by these ecosystems have altered regional biogeochemical processes, potentially doubling or tripling methane flux from the boreal forest (Bridgham *et al.* 1995), a significant constituent of the global flux. In addition, beaver activity influences the movement and accumulation of nutrients and water through alteration of drainage networks, an effect that may last for decades or even centuries (Naiman *et al.* 1994). In this example, a previously minor ecosystem type has increased in abundance and brought about change in a large-scale function.

Finally, landscapes in many areas of the world are subjected to anthropogenic inputs of sulphate and nitrate, causing net acidification. Within such landscapes, some of the ecosystems, such as coniferous forests, streams and oligotrophic lakes, have a very high sensitivity to such inputs. The presence of other ecosystems within these watersheds, capable of providing a sink for acidity or of providing a source of basic cations, has been demonstrated to be crucial for the continued functioning of these systems. This has been shown to be true particularly for streams and lakes in mountainous regions (Johnson *et al.* 1981; Charles 1991). Acidity that falls in mountainous regions is often not sufficiently filtered until it has passed through the soils of deciduous forests or subalpine bogs. Streams and lakes are dependent upon a relatively large areal extent of 'sink' systems in order to resist large-scale biological impacts resulting from net acidification.

5.2.4.3 Keystone ecosystems

There are several examples of ecosystems that contribute specialized functions to landscapes or regions despite being very small. The presence of such an ecosystem may add only a small increment to an index of 'diversity' based upon richness or evenness of ecosystem types, but may have a very significant influence on large-scale system functioning. Human interference with such 'keystone' ecosystems may occur at very small spatial scales, but may have dramatic effects at landscape to regional scale.

Riparian ecosystems, because of their physical and biological components, have a specialized function in landscapes and regions. They are well recognized for their abilities to filter sediments in overland flow, and to retain nutrients in overland flow and subsurface water movement (Gregory *et al.* 1991). For example, in an experimental watershed in Maryland, USA, croplands released considerable proportions of nitrogen and phosphorus received in a given year (92% and 59% of inputs, respectively), while riparian forests maintained most nutrient inputs (releasing 11% of nitrogen and 20% of phosphorus inputs) (Peterjohn and Correll 1984), including

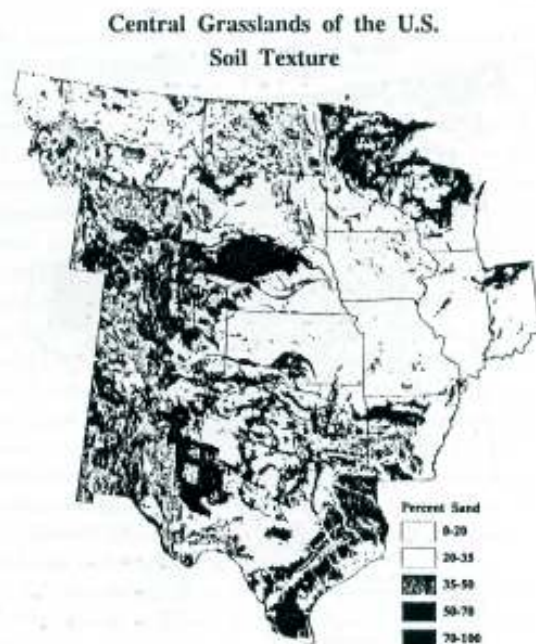


Figure 5.2-5: Sand content in the central grasslands of the USA. Data from USDA Soil Conservation Service 1989.

those received from adjacent croplands. When riparian biota are disturbed or destroyed, severe sedimentation and nutrient loading may occur. Riparian systems may be one of the best examples of 'keystone' elements in landscape diversity, because their influence is out of all proportion to their size.

Wetlands have long been recognized as providing a key role in absorption of phosphate and other materials that are harmful to aquatic systems (Verry and Timmons 1982; Urban *et al.* 1989). Anthropogenic sources of phosphate have major implications for the functioning of natural aquatic systems (e.g. Schindler 1974, and many others), causing algal blooms, increased consumer activities, oxygen deficits and large-scale fish kills. Although wetlands may provide a critical function in phosphate absorption, Richardson (1985) demonstrated that wetlands may saturate with phosphate under very high input more rapidly than ecosystems that have high levels of amorphous iron oxides in soils. These results suggest that a diverse array of surrounding terrestrial ecosystems may make critical contributions to the functioning of landscapes undergoing extreme stress.

Many other keystone ecosystems have been documented in the literature, for instance prairie potholes (Poiani and Johnson 1993) and tropical lagoons or mangroves (Morell and Corredor 1993). Clearly, identification of keystone ecosystems and their relationship to landscape or regional functioning should be a high priority.

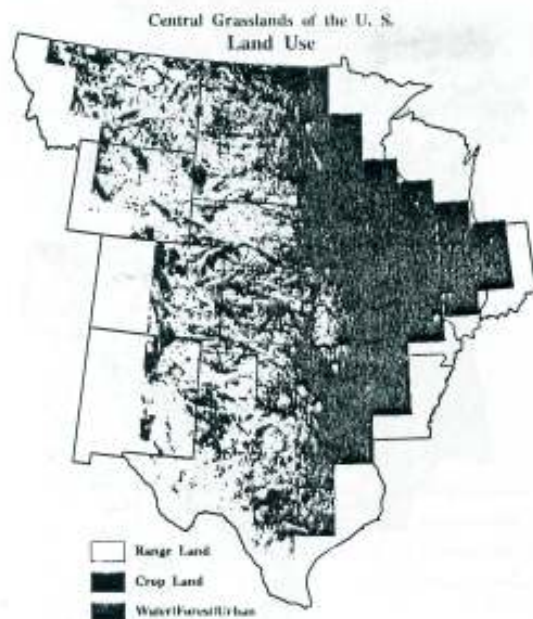


Figure 5.2-6: Land use in the central grasslands of the USA. Data from USDI US Geological Survey 1986.

5.2.4.4 Land-use diversity

One of the distinctive properties of landscapes or regions, as opposed to smaller units, is the extent to which humans must be considered a part of the system. Ecosystems are managed at spatial scales from landscapes to regions. Humans change the character of the ecosystems they manage by altering their properties with respect to exchange of nutrients, energy and sediments, and with respect to additional substances such as toxins or fertilizers. Inclusion of human processes as part of landscape and regional functioning is therefore necessary for any understanding of causes and effects at these scales (Naveh 1971). Furthermore, the structure of landscapes and regions has a large impact on patterns of human occupation, on land-use decisions, and on cultural and economic conditions. An integrated approach to human and ecological systems is the most appropriate approach to understanding landscape and regional functioning.

Probably the clearest examples of landscapes and regions that include a large diversity of ecosystem types are found in areas in which some of the natural ecosystems have been replaced with intensively managed ecosystems producing commodities such as timber or grain. This heterogeneity has tremendous consequences for landscape or regional-scale processes, including nutrient and sediment redistribution, and gaseous exchange with the atmosphere. Here, we will identify the causes of large-scale heterogeneity in land-use management practices, and discuss the significance of the

resulting heterogeneity for the functioning of landscapes and regions.

Heterogeneity in land-use is the result of interactions between climatic and edaphic constraints and human socioeconomic forces. Macroclimatic zones generally determine the range of land use management practices that are biologically and economically feasible in a region and therefore have a large influence on ecosystem diversity. For example, in the central grasslands of the USA (Figure 5.2-6), the distribution of cropland versus rangeland is generally controlled by precipitation, but patterns are modified locally by soil texture and depth, and by the availability of surface or ground water for use in irrigation. Qualitative evaluation of Figure 5.2-6 suggests an ecosystem analogue to the relationship that Whittaker and Niering (1975) reported for species diversity along a moisture gradient.

It appears that land-use diversity is low in the driest and wettest parts of the central grassland region. In the driest areas, along the eastern margin of the Rocky Mountains, landscapes are dominated by native grasslands because water availability limits crop production. In the wettest parts of the region, landscapes are dominated by cropland ecosystems because water availability is so favourable for crop production. The intermediate areas are mixtures of grassland and cropland ecosystems and have the highest landscape diversity. Social, cultural and economic conditions interact with environmental constraints to produce these observed patterns of land use (Riebsame *et al.* 1994).

In highly managed regions, human systems may be best maintained where land-use management practices have resulted in a pattern of ecosystem types that confers functional diversity for both ecological and economic systems. Cultivated ecosystems generally function as sources of sediments, as sources of trace gases such as ammonia, as areas that have net reductions in carbon storage, and as sources of cash revenue. To maintain regional functioning, we suggest that these systems must be balanced by ecosystems that can capture sediments, produce less (or even consume) trace gases, and serve as net carbon sinks. Naveh (1971) argued that human activity in Mediterranean ecosystems may be directed to the maintenance of a sufficient level of ecological diversity. We provide below two examples of systems that may be considered sufficiently diverse for ecosystem and human system functioning, and an example of one that may not.

The central grasslands of North America comprise a mosaic of land use, ranging from intensively cropped dryland systems to irrigated cropland and native grassland used for beef production. An index of land-use diversity for the region would probably be high, given the spatial complexity and the number of crop types distributed throughout the region. In terms of ecosystem functioning, the presence of native grasslands in this matrix, rather than

the diversity *per se*, may be extremely important. Cultivation results in significant regional losses of carbon through increasing decomposition and erosion which reduce the amount of organic matter in the soil (Burke *et al.* 1991). The presence of native grasslands is important for minimizing those carbon losses at a regional scale. The grasslands evolved in the presence of large generalist herbivores and appear to be well adapted to withstand domestic livestock grazing (Milchunas *et al.* 1988). In addition, cattle feedlot operations in the region produce large amounts of methane. While all soils in the region have net methane consumption, the grassland systems have significantly higher methane consumption than cultivated areas, and the presence of such sinks reduces the net regional methane contribution to the atmosphere (Mosier *et al.* 1991). In this case, diversity of land uses does not produce a 'better' balance of trace gas emissions (i.e. the lowest possible level of emissions), but, given that humans must use the area for grain production, the presence and distribution of the native grasslands is crucial for minimizing regional human impacts.

If we consider the dynamics of human populations, the presence and distribution of both grassland and cropland ecosystems may also be important for social and economic stability. Climatic variability in the region has produced large fluctuations in ecosystem production, economic welfare and land-use management (Albertson and Weaver 1944). For example, during the 1930s, a prolonged period of low precipitation resulted in failures of the winter wheat crop in the southwestern part of the region. Winter wheat requires sufficient soil water in the autumn to germinate and establish and enough water during the winter to promote tiller survival. Spring moisture is required for plant growth, flowering and grain production. By contrast, early and mid-summer soil water is necessary to promote forage production by the native grasslands. The probability of failures of both the winter wheat and forage crops in any given year is relatively low. Hence, the stability of human socioeconomic systems in the region is greater in the presence of both ranching and farming operations than it would be if only one land-use type were available.

Tropical deforestation in the Brazilian Amazon provides an example of the genesis of spatial patterns of ecosystems as a result of human use. In this case, a region dominated by a single ecosystem type (forest) is being made more diverse by adding a variety of crop and pasture ecosystem types. Skole and Tucker (1993) used satellite data to estimate that the area of the Amazon affected by deforestation increased from 78 000 km² in 1978 to 230 000 km² in 1988. This was accompanied by an increase in the total area of forest fragments (<100 km²) from 5115 km² to 16 228 km², suggesting that large blocks of forest are increasingly being broken up into smaller blocks. The 1990 IPCC estimate of net release of carbon to

the atmosphere as a result of tropical deforestation is 1.6 ± 1.0 Pg (Houghton *et al.* 1990). Initial studies of the effects of deforestation on other trace gases suggested that conversion to pasture was resulting in increases in N₂O-N of up to 1 Tg per year (Luizao *et al.* 1990). However, recent work has significantly altered our understanding by assessing the interactions of successional dynamics with trace gas fluxes. Keller *et al.* (1993) demonstrated that nitrogen oxide fluxes increase following conversion to pasture, but that these fluxes decrease to levels below those in forests after ten years. Similarly, they found that forest soils consume methane, and that recent, moist pastures are net producers of methane; however, these fluxes are reduced to predisturbance levels during secondary succession (Keller and Reiners 1994). Clearly, deforestation is altering regional and continental-scale processes; however, it is very important to note that the relationship of successional dynamics to these processes is complex and deserving of further study.

A final example of an intensively managed region is the Loess Plateau of China. Here, the spatial pattern of land-use management is apparently very diverse. There are large numbers of cultivated patches on valley bottoms, slopes (terraced or unterraced) and some remnant uplands, and grazing lands are located on the very steep dissected slopes. However, the ecological stability of the region is extremely low, due to the intensity with which each hectare of land is used. Many of the slopes are cultivated without building terraced fields, and the natural grasslands and shrublands on slopes have been so severely grazed that the vegetation is sparse and in many places the soils are bare. These land-use patterns combine with unfavourable natural conditions – namely loess consisting mainly of silt with porous structure and well-developed cleavages, and precipitation that is concentrated in the summer usually falling as high-intensity storms. Thus, the region is subjected to very high rates of erosion, and high rates of sediment loss. As a result, the Yellow River leaving the Loess Plateau carries an enormous sediment load (approximately 1.6×10^9 tonnes per year) (Integrated Scientific Research Team of the Loess Plateau of CAS, 1990), which makes it unsuitable for most natural biological activity and causes enormous deposition problems downstream. Human populations in the region are large, and expanding rapidly, which is placing increasingly heavy demands upon an already intensively utilized landscape. Inhabitants continue to cultivate more hillslopes and to graze the degraded grassland and shrubland ecosystems more intensively. Many of the flocks of sheep and goats are kept for personal status, not for food production, so over many areas the intensive grazing that is degrading the ecosystems adds relatively few commodities to the market-based economy of the region. In the Loess Plateau region, the fact that the landscape is diverse does

not alter the fact that almost the entire region serves as a net source of sediment.

5.2.4.5 Summary

Human use of ecosystems has sparked a world-wide concern for its effects on biodiversity. To a large extent the focus of concern has been on losses of species from ecosystems, and this in turn has raised the issue of the relationship between species diversity and ecosystem functioning. While this concern and effort is warranted and important, it does not deal fully with the issue of biodiversity. What is missing in this approach is the investigation of the diversity of ecosystems in landscapes and regions.

Diversity at the scale of landscapes and regions is related to hydrological balance, biotic interactions, trace gas fluxes and other large-scale processes, but the nature of the relationship appears to be landscape- or region-specific. Human activities have greatly altered broad-scale patterns of diversity, and a significant challenge remains regarding how to balance ecological functioning with human needs. Which ecosystems within landscapes play keystone roles? And how do we maintain natural processes, and hence diversity, while meeting the human demands of landscapes and regions?

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5.3 Drivers and dynamics of changes in biodiversity

5.3.1 Overview of disturbance

The relationship between biodiversity and disturbance has several important aspects. First, there can be both direct and indirect relationships between the two phenomena, although the indirect relationships are not yet well understood. Secondly, both biodiversity and disturbance are hierarchical concepts (Table 5.3-1), with different expressions at different levels of organization, such as organisms, populations, communities and ecosystems (Pickett et al. 1989). This indicates that the relationship between them may change as one focuses on different

levels of organization. Thus, events that disturb a community may not disturb a landscape. Thirdly, in order to understand the relationship between biodiversity and disturbance, several important clarifications about disturbance must be borne in mind. (1) Discussion of disturbance cannot be productive without an explicit, if perhaps tentative, model of the components, interactions and scale of the system of interest (Kolasa and Pickett 1989). Otherwise it will be impossible even to say what is or is not a disturbance or to disentangle the effects of disturbance and stress. (2) Assessment of disturbance requires a reference state (Rykiel 1985). Such reference states can be arbitrarily set, culturally determined, or derived from historical or palaeo-ecological records as long as the important past or external determinants of the system are known (Pickett et al. 1992) (3) Non-arbitrary reference states can be supplied by models of the system that specify the components and interactions of the system that are needed for that system to persist. Even in transient systems that are accidents of a certain time and place, such a model can be valuable in discerning disturbance and stress. Without substantial progress toward the rigour outlined above, the relationships between biodiversity and disturbance may be difficult to discover, let alone generalize or apply to management. Generalization must not, for example, mix different hierarchical levels of organization at which the expressions and mechanisms of interaction between biodiversity and disturbance are necessarily different.

Given the caveats above, disturbance is most generally defined as a physical disruption of the structure of a system. The system must be represented by an explicit model that specifies the components and the interactions within it. Placing the model in a hierarchical context indicates how particular disturbance events may or may not spread or affect other levels of organization or scale. The discussion that follows focuses on the ecological rather than the evolutionary impact of disturbance.

5.3.1.1 Characteristics of disturbance

It is important to specify the several dimensions characterizing disturbance (White 1979). The first characteristic is the identity of the event(s). What are the types of disturbance that act in a system? A caution to be applied here is that labelling events simply as fire or flood, for example, may not be adequate. Certain kinds of fire, or certain kinds of flood, may have both qualitatively and quantitatively different impacts on ecological systems at different levels of organization. The need for a model of the system must be re-emphasized here. It is simply impossible to say what is a disturbance without an explicit model of the system that specifies scale and organizational level.

Disturbance has intensity or severity (White and Pickett 1985). Although some might wish to characterize intensity

Table 5.3-1: Disturbance and biodiversity as expressed at different ecological levels of organization. Note that the scale at which an agent of disturbance acts may change the level of organization it impacts. Therefore the same agent may or may not act as a disturbance on different levels of organization.

Level	Illustrative element of biodiversity	Example of disturbance agent
Individual	Genotype	Predation
Population	Age structure	Disease
Community	Successional status	Lightning strike
Landscape	Patch type	Grazing exclusion
Biome	Ecoregion	Climate shift

by the amount of energy expended by the disturbance event, such a strategy will leave much of what is ecologically important about the disturbance hidden. It is not simply the force expended in blowing down a forest, for example, that is important in determining the response to that disturbance. It is also the nature of the substrate that results (White and Pickett 1985). How much of the soil is exhumed with the upturned roots of trees as opposed to merely being covered with debris resulting from the snapping of trees? In the case of fire, how patchy is the surface that is burned, and how much legacy remains from before the fire? And in another scenario, how many trees are defoliated by a herbivore at outbreak densities? Certainly, comparing vastly different intensities of disturbances as measured by energy expended by the event may lead to important generalizations about the nature of the template the disturbance leaves and the subsequent reorganization of the system, but at this stage in the development of disturbance theory, measuring intensity as energy expenditure alone seems inadequate. Joint characterization of disturbance events by energy expenditure and the nature of the habitat template they produce may be more promising (Barry and Dayton 1991).

Disturbances return to sites with some characteristic frequency (White and Pickett 1985). To speak figuratively, lightning does strike repeatedly at a site, and the ecological question is – how often? Stratifying the frequency by intensity is valuable additional information. Frequency can be specified in absolute terms or in terms relative to the temporal extent of the process or longevity of the system of interest. Typically, old-growth mesic, broad-leaved forests in many parts of the world experience treefalls at a given point once in 100 to 120 years (Hartshorn 1978; Reiners 1983). Boreal forests, having fire as the dominant disturbance, experience shorter return times (e.g. Heinzelman 1973). Montane coniferous forests in wet environments generally turn over more slowly (Dale *et al.* 1986), although there is considerable variation based on site and community characteristics (Zackrisson 1977). Insect populations reach outbreak levels and disturb forest

canopies at intervals dependent on landscape and climate (Nothnagle and Schultz 1987).

The spatial scale and distribution of the disturbance is important as well (White and Pickett 1985). How large are the individual events relative to the size of the system? How are the events distributed in space? Are they near one another, or isolated? Answers to these questions about scale will help explain and predict the impact of disturbances on systems. For example, a checkerboard pattern of clearcuts intended to retain intact forest patches in a landscape is actually less likely to maintain old growth forest interiors in the Pacific Northwest than is contiguous cutting of an equivalent area (Franklin and Forman 1989).

Combining type, frequency and scale characterizes a disturbance regime (White and Pickett 1985). The term 'regime' could be replaced by pattern, as there is no necessity for constancy of pattern. Yet, different environments, landforms, human and natural landscapes, and regions can be characterized by the kind, recurrence and spatial pattern of disturbances within them. The term alerts ecologists to be prepared for regularities in patterns of disturbance that can evolutionarily select (Huston *et al.* 1988) or ecologically assort species (Noble and Slatyer 1980), in the same way that general patterns in climate may do. Indeed, natural disturbance regimes owe much of their regularity or repeatability to climatic patterns. Such a link points out the potential sensitivity of disturbance regimes to global climate change. Models that rely on the relative repeatability of disturbance regimes can successfully account for species distributions and behaviours (Waring and Schlesinger 1985; Horn *et al.* 1989). This is an important intersection between biodiversity and disturbance.

5.3.1.2 Relationship of disturbance to other ecological processes

In one system of characterizing disturbance, two additional factors are considered. Given the conceptual refinements above, these factors are more appropriately applied to stress, or to the inclusive concept of perturbation which includes both disturbance and stress.

One feature – the point of impact or point of pressure on a system – is a partial substitute for not having a specific model of the system, as discussed above. In both approaches, the idea is that different aspects of the natural world will be differentially sensitive to disturbance. Indeed, some will be immune to certain common events. This differential sensitivity must be known to study the relationship between biodiversity and disturbance.

The second feature that is more appropriate to the concept of stress or the inclusive concept of perturbation is duration. Disturbances are by definition discrete events (White and Pickett 1985). They may of course emerge from cumulative effects of stress, as when a grassland community is opened catastrophically by the aggregate effects of drought stress (e.g. Weaver and Albertson 1943). But the event of opening the canopy and root mat of the grassland community is discrete relative to the long persistence of such communities. It is important to recognize that the temporal patterns of disturbance as indicated by frequency, and the unusual juxtapositions of usual disturbance events in time, may result in ecological effects that are qualitatively or quantitatively different from the customary disturbance regime.

One of the emergent insights about disturbance is that it can operate in a similar way to predation as a disrupter of competitive exclusion and equilibrium species composition that would result from unchecked competition (Denslow 1985). This insight is encapsulated in the term 'non-equilibrium coexistence' (Connell and Keough 1985; Huston 1979) (see Chapter 4.5). Of course, coexistence determined by predation and by disturbance (acting with other factors) can establish an equilibrium composition. The term 'non-equilibrium' emphasizes the need to include other factors that can maintain communities in an equilibrium different from that achieved exclusively as a result of competition (Pickett 1980). The continued study of disturbance has confirmed this early insight (Loucks 1970).

5.3.1.3 Principles of disturbance

Most generalizations about disturbance currently stand as hypotheses, and focus on intermediacy of intensity, but more commonly, of frequency (Connell 1978; Lubchenco and Menge 1978; Huston 1979). The insight that diversity is expected to be maximized at intermediate frequencies or intensities of disturbance is called the 'intermediate disturbance hypothesis'. A majority of species could not survive very intense disturbances. Nor could most species persist in the highly competitive communities that arise when disturbance is infrequent or very mild (Horn 1974). Likewise, productivity can show the same pattern (Reiners 1983). These generalizations must be constrained by underlying fertility gradients (Tilman 1988; Grime and Hodgson 1992; Grace 1993), the life histories of the species

available, and the existence of competitive hierarchies (Connell and Keough 1985). In systems where competitive hierarchies exist, higher fertility is expected to increase the rate of exclusion of poorer competitors, and higher rates of disturbance are thus required to reduce competitive exclusion in such environments. Furthermore, life-history features of the species pool determine the mode and success of reinvasion or persistence in a site after disturbance.

Models of population extinction and recolonization in a patchy environment have shown the importance of effective recolonization rates of poorer competitors, spatial aggregation of superior competitors and alternative local equilibria, among other factors (Hanski 1995). Source-sink relationships in a metapopulation are key causes of species coexistence in patchy landscapes (Pulliam 1988; Opdam 1991).

The temporal and spatial patterns of disturbance, and the responses of communities and ecosystems to them at the landscape scale, can be summarized as patch dynamics. Disturbed patches can be treated as populations, with birth, growth, size and age distributions, and death of patches (Levin and Paine 1974; Whittaker and Levin 1977; Pickett and Thompson 1978; Levin 1986). On the ground, the pattern would appear as a shifting mosaic (Bormann and Likens 1979; Remmert 1991) which may, if the patches are not too large relative to the size of the entire landscape, come to a steady state. Some landscapes may not produce an equilibrium distribution of patches (e.g. Romme 1982). Such patterns of patches and their dynamics can represent important sources of biodiversity in landscapes (Pickett and Thompson 1978; Foster 1980; Gilbert 1980). In many landscapes, successional species (Pickett 1976), certain desirable wild flowers (Little 1977; Menges 1990) and keystone mutualists (Gilbert 1980), among others, may depend to some extent on new or recently disturbed patches. Likewise, some heath communities, or prairies and savannas in moist climates (Jordan 1993) require disturbance among their defining parameters.

The requirement of certain desirable or rare species, or of interesting community types for the existence of disturbance in the landscape, points out an important way in which disturbance is ecologically significant. At the community level, disturbances create opportunities for some species and at the same time can disadvantage other species. Because community disturbance alters resources and environmental signals and regulators, it shifts the community niche space, or environmental determinants, at least temporarily. At the least, disturbance may temporarily disadvantage competitively superior species, giving less competitive species a respite that permits them to persist in the community (Denslow 1980; Pickett 1980). If the occurrence of disturbance is regular enough, it can, as stated above, act as a selection pressure and drive the specialization of species on the conditions it creates. Thus

some degree of fugitivity exists in many plant species that are denizens of even closed communities (Harper 1977).

What creates opportunity for some species almost always creates a limitation for others (e.g. Connell 1978). Only in the most physically extreme environments where a very few species are able to surmount the problems of making a living will this generalization not be expected to hold. Thus limitation and opportunity are opposite sides of the same coin. The principle of allocation (Cody 1966), which states that

organisms must allocate their limited stores of assimilated energy among mutually exclusive structures or functions, explains the generality of this relationship. It is such a powerful principle that it provides the basic foundation of many ecological theories and models that are used to predict species distribution in time and space (e.g. Tilman 1988).

In relating disturbance to biodiversity at the community level, it is important to know what species in a community are favoured, and which ones are disfavoured, by

Box 5.3-1: Thresholds in ecosystems.

In many of the world's biomes, ecosystems can exist in two or more alternative states which may differ with respect to their species composition, ecosystem functioning or ability to provide some ecosystem service. Each state may appear stable because modest perturbations have small or short-lived effects. Large perturbations, however, may shift the ecosystem from one state to another. Such state shifts can have important policy implications if ecosystems are transformed from desirable to undesirable states. (Perceptions of desirability or undesirability are value judgements related to societal goals or expectations, which are also subject to change through time.) If the undesirable state is stable, substantial policy changes or enormous resource commitments may be needed to restore the ecosystem to the desirable state.

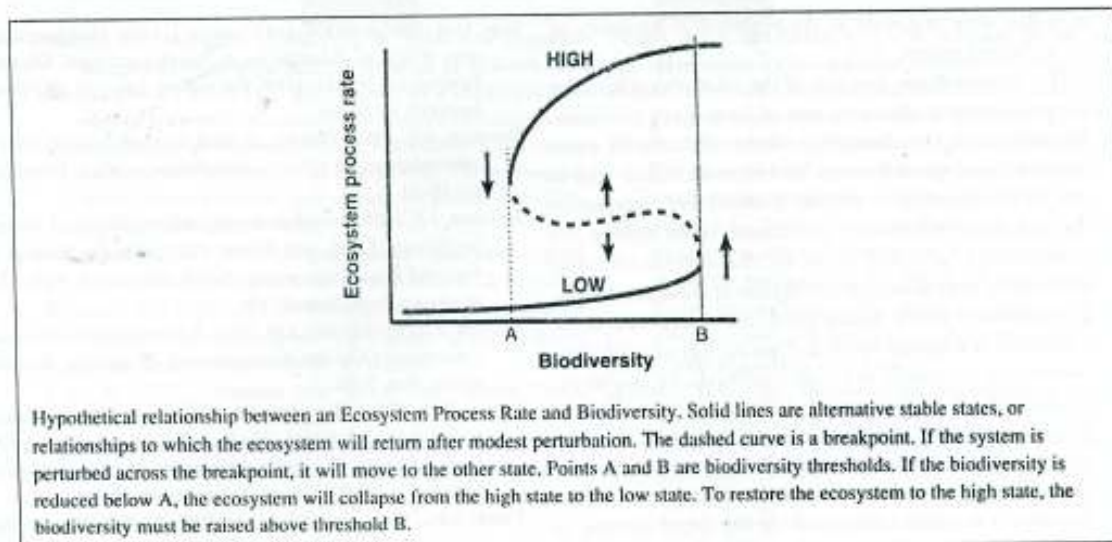
Examples of alternative states are known from both terrestrial and aquatic ecosystems. Semi-arid grassland can remain productive as long as grazer density is modest (Noy-Meir 1975). When grazer density rises above a threshold, community composition changes rapidly and the ecosystem shifts rapidly to a state of degradation and low productivity. Once this occurs, the range will remain unproductive unless managers reduce grazer density substantially while the ecosystem recovers to a productive state. Forests subject to outbreaks of grazing insects also exhibit alternative states, in which outbreaks are either suppressed or spread rapidly (Ludwig *et al.* 1978). In lakes, changes in nutrient inputs and fish stocks can shift the ecosystem between states of good or poor water quality (Scheffer 1991; Carpenter 1992; Scheffer *et al.* 1993). Alternative states that differ in productivity may also exist in marine ecosystems (Steele and Henderson 1984; 1992; Knowlton 1992).

When exploitation of living resources is modest, the resource exists in a high-productivity state and yield is high (Clark 1976; Walters 1986). When exploitation rate rises above a threshold, the ecosystem shifts to a state of low productivity and yield remains low. Large and sustained reductions in exploitation are necessary to return the ecosystem to the high-productivity state, and significant economic losses can occur during the collapse and recovery stages. Adaptive management techniques can be used to detect and avoid thresholds (Walters 1986) when the political and social circumstances are favourable (Lee 1993).

Thresholds in the relationship between biodiversity and ecosystem functioning are hypothetical but plausible (see graph below). When biodiversity is relatively high, the ecosystem follows the limb of the curve labelled 'high'. The ecosystem process rate, which corresponds to production or some other ecosystem service, is relatively high but declines smoothly as biodiversity declines. When biodiversity decreases to level A, the ecosystem process rate falls abruptly to the limb of the curve labeled 'low'. Along this lower limb of the curve, the ecosystem process rate remains relatively low but increases slightly as biodiversity rises. To return the ecosystem to the state with high process rates, it is necessary to increase biodiversity above level B. If species have been lost permanently, restoration may be impossible. Species conservation maintains restoration options.

A threshold hypothesis is consistent with much of the evidence about ecological consequences of species' extinction (Ehrlich and Ehrlich 1981). However, there is considerable scientific disagreement about the particular shapes of the curves and the locations of the thresholds (Schulze and Mooney 1993). There is also uncertainty about whether particular species are crucial in determining the location of thresholds (Schindler 1990; Frost *et al.* 1994). At present, scientific capacities to predict thresholds in ecosystem behaviour are poorly developed.

Thresholds have significant implications for resource economics, ecosystem restoration and sustainability of ecosystem services. When ecosystems are driven across thresholds to undesirable states, losses can be long-lasting or even permanent. Costs of ecological restoration in economic, energy or material terms can rise steeply if ecosystems must be forced across a threshold to restore them. In some cases, restoration may simply be impractical. Where biodiversity is reduced by global extinctions, opportunities for restoration may be permanently lost.



disturbance (Bazzaz 1983). Managers have long recognized contrasting categories of plant species, such as increasers and decreaseers relative to grazing, and fire sensitive versus fire dependent species in certain forests, shrublands and grasslands. It would be inappropriate to argue that disturbance is good for all species in an assemblage. The insight that emerges from the last twenty years of new study, and synthesis of the insights of previous generations of ecologists, is that disturbance is 'good' for some species and ecological processes, not that it stimulates all natural or socially desirable species, ecological phenomena and systems. In other words, the role of disturbance is large in many systems, and biodiversity at various levels bears the stamp of disturbance. Successful management, restoration, conservation and sustainable development require that the role of disturbance in the target system and for critical processes, or for threatened and endangered species, be evaluated (Pickett *et al.* 1992). As a further elaboration of the analysis of the nature of disturbance, Carpenter (Box 5.3-1) discusses the importance of thresholds in perturbations to biodiversity as related to ecosystem processes.

5.3.1.4 Disturbance and management

Disturbance of ecosystems has implications for the maintenance and restoration of biodiversity at all hierarchical levels (McNaughton 1989; Walker 1989; Pickett and Parker 1994). The important role of both human agents (Mooney and Godron 1983; Naveh and Lieberman 1984) and natural agents of disturbance in a landscape is recognized here. Management involves the manipulation of existing systems, the restoration of a lost state (Hughes 1994), or the amelioration of an existing state of a system, while development, in the most positive sense, is the interpolation of anthropogenic and natural

systems. Every decision a manager makes (or neglects!) favours some species or ecological phenomena and disfavors others. This is the inexorable operation of the principle of allocation, and its resultant contrasts in the genetically determined strategies of organisms in the world as people now interact with it. No management (to use that word now to represent also restoration and sustainable development) can favour all species or states simultaneously. It is critical that management avoid damage to native and specialist species and their evolutionary potential. Management likewise must not neglect important processes and phenomena in landscapes, which is the *de facto* scale at which humans manage. In addition to understanding the biogeographic and evolutionary characteristics of the biota, successful management requires an understanding of the role of the disturbance regime in assembling the communities and ecosystems, and in driving ecosystem processes on which biodiversity depends. Management may sometimes have to maintain existing natural disturbance types, compensate for unavoidable natural disturbances, replace missing natural or pre-industrial human disturbances, or compensate for novel human stresses or reduced spatial extent of the system (Botkin 1991; Pickett *et al.* 1992). This list suggests that attention to the different kinds of disturbances, and the interactions among different anthropogenic and natural disturbances and stresses, is fundamental to successful and sustainable management, which must seek to maintain or recreate the multiplicity of opportunity that exists in the 'patch dynamic' natural world. The maintenance and importance of biodiversity are intertwined with these processes, and in order to use disturbance effectively, managers must know whether anthropogenic disturbances or stresses mimic the natural

ones that were important in the evolution or assembly of an ecological system.

Our understanding and use of the relationship between disturbance and biodiversity, rest on several key principles. Disturbance is the disruption of the structure of some specified ecological system. The most desirable way to specify the system is to provide a model that incorporates the system components, the connections among the components, and the scale of the system. Natural disturbance is an important and persistent component of the environments under which biodiversity evolved at the population and species levels and has been assembled at the community, ecosystem and landscape levels. Of course, the events that act as disturbance at each of these levels of organization differ in kind, frequency and scale. At some scales, apparently disruptive events become incorporated into the systems of interest, and the disturbance regime becomes a defining component of the larger system. In such situations disturbance must be maintained. Alternatively, if human management has prevented natural disturbance events, those events must be restored or substituted to permit the system to continue to exist. Thus, disturbance is a component of sustainability in some ecological systems and landscapes, but the type, intensity, frequency and scale must be properly applied if it is to remain a positive force in sustaining biodiversity.

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5.3.2 Human-induced perturbations biodiversity

5.3.2.1 Introduction

Human perturbations affect biodiversity both directly and indirectly through changes in land and water use (Figure 5.3-1). Such changes have a direct impact through habitat destruction and over exploitation of resources such as occurs in overfishing and overgrazing, and an indirect impact through their effects on the composition of the atmosphere and the climate, both of which directly affect biodiversity. Changes in biodiversity in turn modify the functioning of populations, ecosystems and landscapes. Finally, these changes feed back into land-use patterns, atmospheric composition and climate, accelerating or decelerating the rate of global change and the impacts of human activities. Here we focus on the effects of land use, atmospheric composition, and climate on the different components of biodiversity whereas most of Sections 5 and 6 of the GBA analyse the effects of changes in biodiversity on ecosystem functioning.

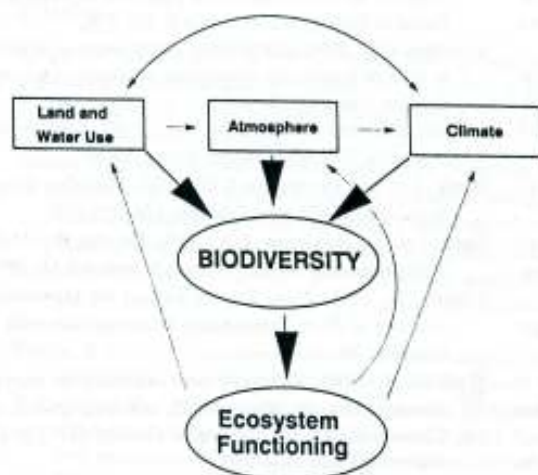


Figure 5.3-1: Conceptual model of the effects of human-induced perturbations on biodiversity and ecosystem functioning. Changes in land and water use directly affect biodiversity and simultaneously modify the composition of the atmosphere and the climate. The alterations of land and water use include the overexploitation of resources such as in overfishing or overgrazing as well as drastic transformations such as the conversion of forests into croplands. Changes in climate and in the composition of the atmosphere also directly alter biodiversity.

5.3.2.2 Changes in land and water use

Forests, grasslands, savannahs, and deserts have been altered drastically by human activity. Over the last three centuries, forests have decreased by 1.2 billion ha or 19%, and grasslands by 560 million ha or 8% (Richards 1993). This is mainly the result of increase in croplands of 1.2 billion hectares and the growth of urban areas. The rate of land-use change is accelerating very rapidly, as is demonstrated by agricultural expansion which was greater during the period 1950–80 than during the entire 150-year period between 1700 and 1850 (Richards 1993). Land-use change also includes changes associated with the over exploitation of resources which are ubiquitous and more difficult to quantify. For example, livestock overstocking has resulted in severe degradation of rangelands (referred to as desertification), bush encroachment or brush invasion altering large areas of North America, Africa and Australia (Buffington and Herbel 1965; Walker *et al.* 1981; van Vegten 1983; Archer 1989).

Marine environments have been and still are being drastically modified by human action. Changes in water use are usually not reflected in qualitative shifts like those we observe in terrestrial environments but in steady and quantitative changes of their chemical, physical and biological properties. Anthropogenic additions of nutrients are most obvious in relatively shallow coastal seas such as the Baltic or the North Sea in Europe, or Puget Sound along the open coast of the state of Washington in North America (Jickells *et al.* 1993). As a result of the discharge of wastes from heavily populated and industrialized areas, the nutrient content of the oceans has increased significantly. For example, phosphate concentration in the Baltic increased by a factor of 3 in the period 1958–80 (Jickells *et al.* 1993). Increases in nutrient availability stimulate the growth of plankton which in turn consumes dissolved oxygen as it decomposes (Lancelot *et al.* 1987). Simultaneously with the increase in nutrient availability, dissolved oxygen in the deep waters of some parts of the Baltic Sea decreased from 3 ml/l at the beginning of the century to almost zero at present (Jickells *et al.* 1993). Besides pollution, humans also drastically alter marine environments by over-exploiting resources. Overfishing has resulted in the elimination of substocks of herring, cod, ocean perch and salmon in several regions of the world (Ludwig *et al.* 1993).

Changes in land use are the major causes of habitat destruction and fragmentation, and these in turn are the major causes of recent extinctions, and constitute a major threat to biological diversity (WCMC 1992; Skole and Tucker 1993). A clear indication of the importance of habitat destruction in accounting for changes in biological diversity is that one way of estimating current and predicted losses of species diversity is based solely on combining information on current and projected

deforestation rates with information on species richness per unit area in tropical forests (Ehrlich and Wilson 1991; see also Section 4.4). The assumption that global terrestrial species extinction rates can be assessed from tropical forest extinction rates is justified on the assumption that most terrestrial species occur in tropical moist forests. Independent exercises using different approaches have estimated extinction rates to be of the same order of magnitude as those estimates based on species-area relations and the rate of habitat loss (Smith *et al.* 1993; Heywood *et al.* 1994).

Although drastic changes in land use such as large-scale transformations of forests into grasslands or grasslands into croplands usually result in reductions in global species diversity, more subtle human-induced changes sometimes increase local species diversity. For example, some grasslands that evolved under low grazing pressure have shown increases in species diversity as a result of the introduction of livestock and the consequent increase in grazing intensity (Sala *et al.* 1986; Milchunas *et al.* 1988). This pattern is accounted for mainly by the introduction of alien species better adapted to grazing conditions, without the disappearance of native grasses. Further increases in grazing intensity have reduced diversity as introduced grazing-tolerant species have become dominant. Human activity is mostly neutral or negative with respect to genetic or species diversity. Only recently – by means of biotechnology – have humans increased diversity. However, at the community and landscape levels human activity may either increase or decrease diversity. Naveh (1971) suggested that human-induced livestock grazing has increased plant, community and landscape level diversity in the Mediterranean Basin.

5.3.2.3 Changes in atmospheric composition

Recent changes in the composition of the atmosphere are a clear indication of the major disruption of biogeochemical cycles that have occurred as a result of human activities (Schlesinger 1991). First, scientists pointed out the perturbations of the carbon cycle and the resulting sharp increase in the concentration of carbon dioxide in the atmosphere (Keeling 1986). Next in importance is the disruption of the nitrogen cycle as evidenced by the magnitude of human-induced nitrogen fixation, the increase in nitrous oxide emissions, and the high values of nitrogen deposition over most of the developed world (Matson and Vitousek 1990; Vitousek 1994). These alterations of biogeochemical cycles have always resulted in ecosystem enrichment and, in most ecosystems, nutrient enrichment results in a sharp reduction in species diversity. Experimental fertilization of shortgrass steppe, tallgrass prairie, tundra and deciduous forest has always resulted in decreases in plant species richness (Lauenroth *et al.* 1978; Schulze 1989; Tilman 1993).

The increase in atmospheric CO₂, and the corresponding CO₂ fertilization effect, results in an ecosystem carbon enrichment which is modulated by nutrient and water availability (Mooney *et al.* 1991). Carbon enrichment can be expected to have effects on biodiversity similar to those that have been demonstrated for the enrichment of ecosystems with nutrients. Because our ability to perform CO₂ enhancement experiments in whole ecosystems is relatively recent, there is no experimental evidence to assess the effect of CO₂ fertilization on biodiversity. Experiments under controlled environmental conditions support the hypothesis that CO₂ enhancement changes plant-plant interactions, and alters the competitive balance among species, which might lead to a decrease in plant species diversity. Elevated CO₂ field experiments based on open-topped chambers showed a distinction between the response of C3 and C4 species in a salt-marsh (Curtis *et al.* 1989). Morse and Bazzaz (1994) also exposed two species with different photosynthetic pathways to elevated CO₂ concentrations and found that the C3 species (*Abutilon theophrasti*) showed a larger response than the C4 species (*Amaranthus retroflexus*). Based upon experiments under controlled environmental conditions, Polley *et al.* (1994) suggested that the invasion of the C4 grasslands in the southwestern United States by woody C3 mesquite (*Prosopis glandulosa*) during the past 150 years can be related to the observed 27% rise in atmospheric CO₂. Species-specific differences among CO₂ responses of forest trees have been reported for temperate zones (Williams *et al.* 1986; Norby *et al.* 1992) although not for tropical ecosystems (Körner and Arnone 1992). Phillips and Gentry (1994) speculated that increased CO₂ may favour vine growth in tropical forests, which may explain the observed increase in tree mortality.

5.3.2.4 Climate change

The indirect effects of changes in the composition of the atmosphere and changes in land-use patterns occur via changes in climate. Changes in land-use and atmospheric composition have already been detected and will affect ecosystems and humans sooner than changes in climate. However, climate change has been the first global change phenomenon to attract the attention of scientists and policy-makers. Scientists agree that an increase in the atmospheric concentration of greenhouse gases such as CO₂ and methane will result in an increase in global temperature and a change in the global distribution of precipitation. Current uncertainties are related to the geographical patterns of those changes and the speed with which they will occur (Mitchell *et al.* 1990). Predicted changes in climate for a doubling of atmospheric CO₂ are quite significant for most regions in the world. Models that relate average climatic variables to the distribution of vegetation types are ideal tools for assessing the potential effect of climate change

Box 5.3-2: Management for sustainable biodiversity.

To manage and exploit the environment effectively, and sustainably, scientific information must be translated into management plans and actions. However, promoting the wise use of ecological concepts in managing the Earth's biodiversity is neither simple nor straightforward. It requires not only specific scientific skills, but also considerable leadership qualities in co-ordination, integration and advocacy. On the other hand, the challenges and opportunities for a decisive involvement of the ecological sciences in environmental management are greater than ever, given that the Convention on Biological Diversity and the *Agenda 21* document signed at the UNCED Rio summit in 1992 provide ample political support at the highest level. How do we translate ecological research into management? Here, some key aspects of the research/management interface are discussed.

1. *The available options are limited.* The options available to managers are restricted by practical feasibility, environmental acceptability, economic desirability, and in many cases political advantage (Saunders and Burbidge 1988). Time is a key constraint. Decisions need to be made within a given (and usually short) time horizon, and typically with only incomplete information available. In the case of biodiversity, for example, the rate of loss of both species and habitats is growing exponentially, leaving less and less time for detailed, long-term studies (Meadows *et al.* 1992).

2. *Management for sustainable biodiversity must be based on the precautionary principle.* The precautionary principle, and the associated notion of reserved rationality (Perrings 1991; see Section 12), apply to those decision-making problems in which both the level of fundamental uncertainty and the potential costs are high. Examples include the use of environmental resources in novel ways and at high levels of magnitude. Both principles imply the need to proceed cautiously to safeguard against the possibility of unexpectedly severe future costs when there is ignorance as to the probability distribution of the magnitude of the negative impacts. In other words, when dealing with decisions that have the potential to destroy crucial life-supporting systems, it is prudent to have some margin for error (on the conservative side) as one learns the outcomes of a given management policy. It is also prudent to make allowances for the potential, although uncertain, future losses associated with the resulting use of environmental resources and services. By necessity, the precautionary principle implies a high value-driven judgment about the responsibility borne by present generations toward future generations (Perrings 1991). Therefore, and acknowledging that at present we do not have all the answers we need, the only prudent policy to assume today is that while there is clearly redundancy in the role of species in delivering some services, there may also be an extinction threshold which, if crossed, will result in unacceptable deterioration of ecosystems services (see 5.1). Accordingly, the precautionary principle indicates that extreme care should be taken before labelling any species as 'redundant'. Since the precautionary principle entails a cost for human societies, decisions need to be made about how much the precautionary principle would have to be stretched or how much insurance different societies can afford to buy. These kinds of decisions will be greatly aided by a better understanding of the relationship between biodiversity and ecosystem functioning.

3. *The relationship between science and management is a two-way process.* There is no such a thing as a definite, prescription regarding environmental management. Management is a continuous, dynamic and interactive process involving research, implementation and monitoring. Therefore, a continuous feedback between researchers, managers and users is clearly necessary. Accordingly, the following basic steps are required in a well planned project: (a) planning and developing goal-orientated research, (b) dissemination of results, (c) implementation of management practices and policies, and (d) monitoring and feedback.

An important component of this two-way process is the adaptive management approach, i.e. using management practices as a research tool to obtain information and insight to fine-tune management practices. Use of management as a research tool has considerable potential, providing access to semi-experimental situations at a scale and degree of realism well beyond the possibilities of 'traditional' experiments (Holling 1978). Furthermore, the management project itself can be used as an experimental probe as, for example, when manipulating grazing pressure as a way of understanding vegetation dynamics in savannas or grasslands. The adaptive management approach is particularly useful when decisions need to be made in situations where data are incomplete and uncertainty is great, requiring an ongoing, flexible, and sometimes opportunistic process. A particularly important challenge for researchers on the functional role of biodiversity is the need to develop sustainable management models for each of the Earth's biomes, in which both ecological services and human use are made compatible (see for example Milton *et al.* 1994 for a discussion on savannas). Furthermore, involvement in real-world situations favours interdisciplinary work, while providing a better insight into the constellation of factors (biological, economic and social) affecting the system under management.

under equilibrium conditions. One of the earliest models of this kind is the one developed by Holdridge (1947) (see Section 2.3). Analysis of the distribution of vegetation in equilibrium with the new climatic conditions showed big shifts of vegetation types under a double CO_2 climate (Emanuel *et al.* 1985; Kramer and Leemans 1993). The main result is a poleward shift of vegetation patterns. Approximately 30% of the vegetation of the Earth will experience a shift as a result of the predicted climate change. Although the climate change is expected to be significant, the major threat for biodiversity is the speed with which this change will occur. Changes of the magnitude predicted for a doubling of CO_2 have occurred during the Earth's climate shift from glacial to interglacial periods. However, while these changes occurred over millennia, the expected human-induced changes will occur in less than a century (Watson *et al.* 1990). The rapid change in climatic conditions will hamper the ability of individual species to migrate to regions with climatic conditions similar to those of the present. Moreover, in some cases such as the Arctic, the area favourable for the survival of an individual species will be largely reduced. The reductions of suitable areas for a large number of species, and a change in climate faster than the migration rate of most species, is certain to result in a drastic reduction of global species diversity.

5.3.2.5 Conclusions

Human-induced perturbations differ quantitatively and qualitatively from natural perturbations. Humans have increased the frequency and severity of natural disturbances to the extent that their impact is now greater than that of most natural ones (Likens 1991). The duration of human disturbances is also usually much longer, and the frequencies are much higher, than natural ones (Reiners 1983; Woodwell 1983). Among the major threats to species diversity are the qualitatively new kind of disturbances for which no specific adaptations have yet evolved. Humans have synthesized new chemical substances which have reduced the stratospheric ozone layer at higher latitudes in the Southern Hemisphere as well as at mid-latitudes (Farman *et al.* 1985; Stolarski *et al.* 1991). A reduction in the ozone layer allows increased quantities of short wave radiation (UV) to penetrate through the atmosphere. There is evidence that increased UV results in major negative effects on primary producers as well as on the next trophic level (Caldwell *et al.* 1989; Smith *et al.* 1992; Bothwell *et al.* 1994). Equally new is the ability of humans to exchange floras and faunas which has resulted in rapid and major invasions of exotic plant and animal species (Drake *et al.* 1989). Increases of some insect, plant pathogen and weed pests may be associated with the increase in CO_2 and temperature (Pimentel *et al.* 1992).

All the human-induced perturbations described here result in reductions of global species and genetic diversity, although some human manipulations may result in local increases in genetic, species, community, ecosystem and landscape diversity. Human-induced perturbations under the term 'global change' directly affect ecosystems, and humans who depend on ecosystem services (Ehrlich and Mooney 1983). Global change reduces species diversity which in turn (as described in Sections 5 and 6) may affect ecosystem functioning. The truly irreversible nature of the loss of genetic and species diversity is what it makes it so important for humans (Vitousek 1994). In contrast, the changes in atmospheric composition and climate and to a large extent land use are reversible. Reducing of 'human forcing' will result in a slow return of the atmosphere and the climate to approximately original conditions. In contrast, the loss of population and species diversity is permanent. The combination of genes that results in a variety of morphologies and behaviours will be lost for millions of years or even forever. The issue of how to satisfy the increasing demands of human societies for goods and services and simultaneously to ameliorate the rate of species and populations loss, is discussed in Box 5.3-2.

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5.4 Conclusions

5.4.1 Background

Fundamentally, we wish to answer the simple question: Does biodiversity matter in the functioning of ecological systems? This question should be addressed with respect to the four major principles introduced in Section 5.0: (1) the levels of biological and ecological organization and their interactions, (2) the numbers of different biological units within each level, (3) the influence and degree of similarity in the traits or roles that biological and ecological units within each level play, and (4) the spatial configuration of the units within any level. We have thus summarized the conclusions of the chapters in Section 5 with respect to these four principles. We then proceed with a synthesis of these conclusions with respect to the influence of human actions and implications for management. The summary and synthesis take the form of several simple questions.

5.4.2 What are the influences of genetic diversity on ecosystem functioning?

Ehrlich (5.1) and Templeton (5.2.1) both point out that intraspecific genetic variation can be, and has been, exploited to change quantitative aspects of ecosystem functioning, e.g. by increasing crop yields. In addition, intraspecific genetic variability confers some adaptive capability to those species, and thus increases the possibility that their functional roles can continue to be expressed in ecosystems that are undergoing environmental variability or stress. There is very little information on whether the genetic similarity of populations influences ecosystem functioning. Templeton (5.2.1) points out that

the phenomenon of local adaptation of populations to their environment is well known, and thus the spatial configuration of genetic variability might be important. Reintroduction of species to areas from which they have been lost is generally most successful if the reintroduced individuals are from populations that originated close to the original area. It is not unreasonable to suppose that there are ramifications of these observations for ecosystem functioning, but direct experimental evidence or observations are lacking.

5.4.3 What are the influences of species diversity in ecosystem functioning?

In many cases, species clearly matter. This is primarily because the species plays an important and unique role in its ecosystem. Removal or addition of the species results in a dramatic and obvious change in the other species in the ecosystem or in a key ecosystem process. The evidence for this conclusion is compelling; the number of examples is increasing as more systems are examined; and these keystone species (Chapin *et al.*, 5.2.2) have been reported from a wide range of ecosystem types. However, in spite of the widespread existence of the phenomenon, no species characteristics have emerged that allow prediction of which species will play keystone roles. In fact, some small or cryptic species have been found to play a keystone role.

In many other cases, however, there appears to be substantial overlap among species with respect to their functional roles. Their removal or addition appears to have little demonstrable effect either on other species or on an ecosystem process. Other species compensate for the absence of the target species, at least in the short term. However, it is not known with certainty if all functions of the species in question are compensated for (in fact, it is rarely understood what the full range of functions is for each species). For this reason, it is probably inappropriate to say that species are 'redundant'.

Ecosystems with greater overlap among species with respect to any particular process will be more resistant to change than otherwise comparable systems characterized by little compensatory potential. This stability is predicted to be a direct result of the fact that species that overlap with respect to a particular function probably differ with respect to their responses to environmental changes such as temperature, salinity, ultraviolet radiation (UV-B), or exposure to toxic compounds. Compensatory overlap is thus suggested to provide 'insurance' in the sense that key functions are more likely to continue despite changes that result in the loss of some species. There is some evidence for this prediction, but it is a very difficult phenomenon to demonstrate. There is no evidence that contradicts the predictions. This is an area where further research is needed.

The above conclusions focus on particular traits of species and the extent to which the traits are unique to a

species or not. A separate question of importance is whether the number of species *per se*, apart from their specific traits, has a strong influence on ecosystem properties. The number of species in an ecosystem is functionally important, independent of the traits of the species, for two reasons: (1) more species generally increase the rate or efficiency of resource capture under steady-state conditions, and (2) more species provide insurance against large changes in ecosystem processes in response to disturbance or environmental change (Chapin *et al.*, 5.2.2).

The spatial structure of species populations within ecosystems has influences on their interactions, their diversity and abundance, and therefore on ecosystem-level processes (Harrison, 5.2.3). Changes in spatial structure, especially fragmentation of habitats, act differentially on different kinds of organisms, depending in part on body size, trophic level, life-history characteristics and successional stage. Fragmentation reduces the diversity of native species in their natural habitats and the types of species most likely to be lost are those with the highest rates of local extinction on small habitat patches (e.g. top predators and other species with large body sizes and large area requirements). Also likely to be lost are species with lower abilities to disperse 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 'weedy' species characterized by short life-span, rapid growth rate, and high reproductive and dispersal capacity. This, in turn, is expected to result in numerous ecosystem-level consequences: faster turnover and leakier systems with respect to nutrients, nitrogen, and carbon; higher litter quality and therefore faster decomposition rates; simpler spatial structure; less overall protection from herbivory; and different kinds of chemical defences against herbivory, tending to low molecular weight compounds.

Thus, the assessment is revealing that in many cases 'species matter' in a fashion that can be demonstrated; in others, species appear to be sufficiently similar to other species with respect to their functional roles that their loss should have no immediate consequences, but unequivocal demonstration that they will or will not 'matter' over a longer period of time is difficult and unlikely to occur. This does not mean that every single species matters in every single situation. There are certainly examples where species have been lost and there has been no demonstrable change to the ecosystem's functioning. It is difficult to say, however, that no change occurred; the evidence available does suggest that there was no catastrophic change.

5.4.4 What are the influences of landscape diversity on ecosystem functioning?

At a landscape or regional scale, the key processes to understand are those that regulate the movement of materials (e.g. nutrients, water, trace gases, etc.), energy fluxes, and dispersal of organisms among the constituent ecosystems, and between the ecosystems and the atmosphere and hydrosphere (Burke and Lauenroth, 5.2.4). The number of different types of ecosystems on a landscape has obvious effects on the total functioning of the landscape. Those ecosystems that cover large areas obviously have important roles; however, some ecosystems on a landscape have functional importance out of proportion to their abundance (Burke and Lauenroth, 5.2.4). This is true of riparian areas and wetlands, particularly in respect of their capabilities to purify water before it reaches streams and rivers, and also for marine systems such as coral reefs, mangroves and kelp forests.

Because of climatic, topographic and geological variation; historical differences; and disturbance frequency, severity and extent (Pickett, 5.3.1; Burke and Lauenroth, 5.2.4), the arrangement of ecosystems on the landscape can be extremely complex, and this complexity affects the total functioning of the landscape. Many of the transfers across landscapes are the result of directional processes, such as wind and water flow, and therefore the total effect of the processes in a region may depend critically on the actual spatial arrangement of the ecosystems, and how that array is orientated with respect to these abiotic factors. The fragmentation of habitat associated with human activities can alter landscape/regional diversity by affecting the spatial patterns of ecosystems on the landscape, by fragmenting the landscape, in effect creating new, disturbed areas, and/or by decreasing the total area of different ecosystems on the landscape. Each of these effects may have characteristic results for different types of species, and thus for ecosystem processes. For example, the spatial pattern of the fragmentation results in the provision of dispersal corridors for some organisms, but reductions in available habitat and opportunities for dispersal and migration for others, and can have a great effect both on overall levels of biodiversity and on ecosystem functioning across the landscape.

5.4.5 What are the human influences on ecosystem functioning?

Human-induced changes in biodiversity are characterized by their increased frequency (rate of change), severity (magnitude of change), and increased spatial extent (Sala, 5.3.2). At a local scale, human activities can have negative (local population eradication), neutral (sustainable harvesting), or even positive (e.g. increase in the number of landscape units) effects on biodiversity. When viewed at a global scale, though, human activities reduce biodiversity

at genetic and species levels, and species' extinctions are completely irreversible. In addition, human activities can create environmental changes for which biota are not at all adapted, for example increased surface UV-B flux due to reduction in stratospheric ozone, or the proliferation of novel, but extremely toxic compounds in the environment.

Extractive activities, such as agriculture and forestry, tend to increase the fluxes of materials in ecosystems across a landscape, often leading to increased losses of nutrients, increased surface water flow, increased sedimentation in streams and rivers, and long-term reductions in soil carbon and soil fertility. These activities clearly affect landscape functioning through their effect on the diversity of ecosystems within a landscape. Other human activities, such as the construction of dams for water control, have very different effects at landscape scale, often resulting in the concentration and immobilization of nutrients and sediment in particular parts of the landscape. Still others, such as fire control in forests, have the effect of dramatically changing the disturbance regime, resulting in widespread changes in landscape functioning.

5.4.6 What are the management implications for goods and services?

To manage and exploit the environment effectively and sustainably, scientific information needs to be translated into management plans and actions. However, there is great difficulty in managing to provide goods and services simultaneously while maintaining diversity at prudent, sustainable levels. Several important principles can be used to guide the implications for management: (1) practical constraints on feasibility, environmental acceptability and economic desirability must be clearly understood; (2) a goal-orientated approach must be applied that recognizes that there are always multiple objectives in any management scenario; (3) an iterative process, analogous to that of adaptive management in forestry, should be employed in order to integrate the knowledge

gained from earlier management decisions into a continually improving management scheme; and (4) when uncertainty about the resource base or the knowledge base is predominant, the precautionary principle should be employed, thus avoiding whenever possible decisions that close off future options.

5.4.7 Summary

Section 5 has laid out in broad detail the important concepts governing the study of the relationships between biodiversity and ecosystem functioning. The importance of considering biodiversity at multiple levels of organization is emphasized, as is the degree of influence and similarity in traits, and the spatial arrangement of biological units within any level of organization. Redundancy of function of species within ecosystems and ecosystems within landscapes cannot be assumed; indeed, some species and ecosystems have unique functional roles that are significant out of all proportion to their abundance. The main consequence of diversity at all levels seems to lie in the degree of adaptive insurance it provides for the maintenance of ecosystem processes against environmental variation and/or stress.

The human influences on biodiversity and ecosystem functioning have largely taken the form of rapid, large, and frequent changes in land and resource use, increased frequency of biotic invasions, reductions in species numbers, creation of novel stresses, and the potential for change in the climate system. Although disturbance is a critical element controlling the composition and functioning of ecosystems, human influences have increased its pace and extent well beyond previously known levels. The major implications for the continued provision of ecological goods and services are to create and use management strategies in an adaptive fashion, to ensure that sufficient resources are maintained in the system to provide resilience, and to be cautious about making potentially irreversible decisions.