6 Biodiversity and Ecosystem Functioning in Grasslands

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6.1 INTRODUCTION

Grasslands are the potential natural ecosystem type on approximately 25% $(33 \times 10^6 \, km^2)$ of the land surface of the earth (Shantz 1954). Current estimates of the global extent of grasslands range from 16% (Whittaker and Likens 1973, 1975) to 30% (Ajtay *et al.* 1979). The difference between the estimates of the potential extent of grasslands and the current extent provides an indication of the degree to which humans have, and are, modifying this ecosystem type. In the temperate regions much of the area of natural grasslands has been converted to cropland. In the subtropical and tropical regions the area occupied by savannas is increasing as a result of conversion of forest to pasture for domestic livestock. Humans have had an enormous influence on the structure and function of grasslands worldwide.

The scope of this chapter employs a broad definition of grasslands encompassing those regions covered by natural or seminatural herbaceous vegetation, predominantly grasses, with or without woody plants (Singh *et al.* 1983). The largest areas of grasslands are found in central and southern Asia (Lavrenko and Karamysheva 1993; Singh and Gupta 1993; Ting-Cheng 1993), southern South America (Soriano 1992), Africa (Herlocker *et al.* 1993; Le Houkrou 1993a; Tainton and Walker 1993) and central North America (Coupland 1992) (Figure 6.1). Smaller areas occur in Europe (Lavrenko and Karamysheva 1993; Le Houkrou 1993a) and Oceania (Gillison 1993; Mark 1993; Moore 1993).

To a large extent the potential distribution of grassland ecosystems is determined by climatic variables, principally temperature and precipitation (Whittaker 1975). In general, grasslands occur between forests and deserts. They are located in areas in which water availability falls below the requirement for forest at some time during the year but is sufficient to support grasses as the dominant plant type. Many grasslands have an important
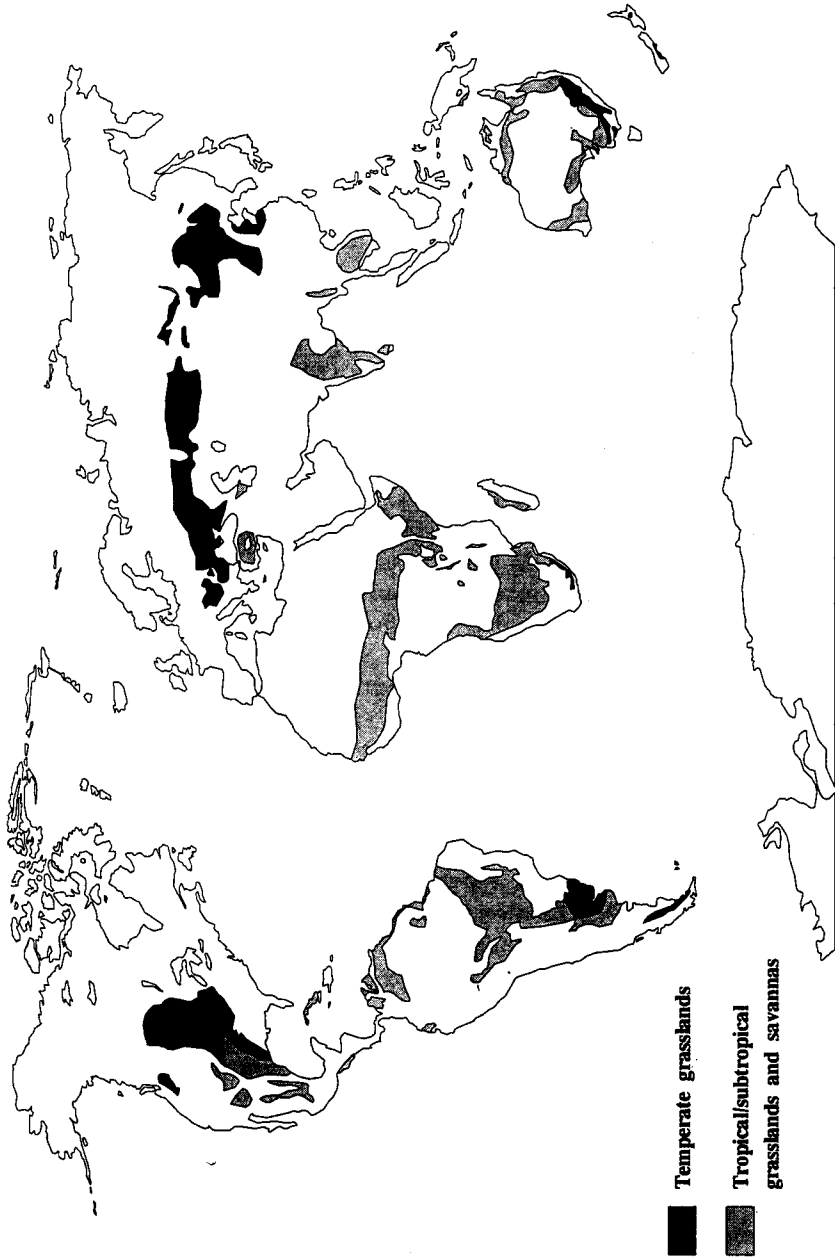
Figure 6.1 Map of the global distribution of temperate grasslands (adapted from Bailey 1989)

Temperate grasslands

Tropical/subtropical grasslands and savannas

woody plant component. In temperate and subtropical regions, shrubs often provide the woody component of grasslands.

Three factors of grassland environments distinguish them from other ecosystem types (Anderson 1982; Milchunas *et al.* 1988), these are drought, fire, and grazing by large ungulate herbivores. The influence of these three factors on grasses and grasslands has resulted in some of the most characteristic features of grasslands. All three factors provide selection pressures for high turnover of above-ground plant organs, location of perennating organs near the soil surface, and a large fraction of biomass and activity belowground. The influence of any one of these factors on the structure and function of grasslands depends upon the details of the particular environment. Drought is a more frequent influence on dry grasslands than it is on those in humid regions. Conversely, fire is a much more frequent force in shaping grasslands in humid regions than it is in dry regions. Grasslands in humid regions have higher fire frequency because they have higher production and accumulate more fuel than those in dry regions. The effect of grazing is also related to the dry-to-humid gradient but in a different way from fire. Grazing can be an important evolutionary force across the moisture gradient, but its specific influence depends upon the moisture status of the site (Milchunas *et al.* 1988). In dry areas, the effects of drought provide a selection pressure that is complementary to that of grazing – that is they select for a similar set of characteristics. If fire was an important force in dry areas, it effects would also be complementary. In humid regions, drought is a less frequent control on ecosystem structure and function than in dry areas. One result of this is that the structure of plant communities in humid regions depends as much, or perhaps more, on a species ability to compete for above-ground resources (light) than its ability to compete for below-ground resources (water and nitrogen). Therefore, selection pressures exerted by the need to compete for canopy resources and those of grazing by large herbivores are antagonistic. For example, competition for light selects for tall plant types and grazing selects for short ones. Fire is an antagonistic selection pressure to competition but at a different temporal scale than grazing.

6.2 THE GLOBAL DISTRIBUTION OF GRASSLAND BIODIVERSITY

The most thorough compendium of comparative data on grassland biodiversity comes from the World Conservation Monitoring Centre (WCMC) (1992), which assembled data from a wide variety of sources to achieve preliminary, working comparisons both of grasslands on different continents and grasslands with other types of ecosystems. WCMC (1992) estimated that

only 5% of the world's bird species and 6% of the mammal species were primarily grassland-adapted, since many of the species with abundance centers in grasslands also range over broad geographic areas and utilize a variety of different ecosystem types. Still, the grasslands of Africa are major biodiversity locations for large grazing, browsing and predatory mammals, and many birds that breed in Eurasia winter in African grasslands (Williams 1963). Mares (1992), in a provocative paper entitled "Neotropical mammals and the myth of Amazonian diversity" documented that the drylands of South America have a more diverse mammalian fauna than any of the other major South American ecosystem-types, including tropical rainforest, particularly when considering endemic mammal species. As Redford *et al.* (1990) observed in relation to threats to the South American Chaco, "The concentration on rainforests. . . has led to the neglect of other severely threatened ecosystems." Chief among those regions are grasslands.

The WCMC (1992) ranked the Earth's natural grasslands in the following order of decreasing importance as repositories of biodiversity of indigenous plants and animals: African savanna; Eurasian steppe; South American savanna; North American prairie; Indian savanna; Australian grassland. Surprisingly, the plant species density of African savanna grasslands in regional geographic blocks is not far below that of African rainforest (Menaut 1983). At present, of course, there are very few, if any, surviving primary grasslands in India, and much of those elsewhere have been converted to other land-uses.

6.3 DISTURBANCE AND GRASSLAND BIODIVERSITY

Disturbance is such an intrinsic property of grassland ecosystems that it could be argued that the true disturbance is a lack of disturbance. It has been suggested that degradation of Australian grasslands may be as much a consequence of improper fire regimes as of overstocking (WCMC 1992), and the treelessness of North American prairies was due in significant part of both lightening-caused and Amerindian-set fires (Sauer 1952). Perhaps rather than characterizing environmental fluctuations in grasslands as disturbance, we should recognize them as integral stochastic factors. Chief among these in pre-Colonial grasslands were grazing and browsing by both large and small mammals, abundant seed-eating and insectivorous birds, stochastic precipitation on seasonal, interannual and decadal times, fire, trampling, and nutrient harvest over large areas accompanied by deposition in small areas due to foraging, defecation and urination by grassland animals. In a thorough examination of the literature on the effects of grazing on species composition changes in the Earth's grasslands, Milchunas and Lauenroth (1993) concluded that those changes were associated with, in order of

decreasing importance, the intrinsic above-ground productivity of a grassland, the evolutionary history of grazing at each location, and the level of consumption. Thus, high primary productivity, generally associated with grasses of greater stature, was associated with greater changes in species composition when grazed as the tall species were replaced by shorter, more grazing-tolerant, grasses. There can be little doubt that stochastic environmental fluctuation has been a fundamental feature contributing to grassland biodiversity (McNaughton 1983).

Large-scale environmental modification of habitats by humans, particularly in Europe and North America, has been instrumental in range expansion of grassland species in historical times. Once reduced to small pockets of distribution in the Eurasian steppe, the steppe marmot *(Marmota bobac)* has expanded throughout farmlands since the 1940s, and many steppe animals expanded into Europe as it was deforested and portions were converted into pasture (WCMC 1992). Similarly, tremendous range expansions by the brown-headed cowbird *(Molothrus ater)* and coyote *(Canis latrans)* have carried them far beyond their native Great Plains in North America, and brood parasitism by the cowbird is believed to be a significant contributor to songbird declines in the cowbird's newly exploited habitats (Trail and Baptista 1993).

Thus, disturbance has disparate effects on grassland biodiversity. Environmental fluctuations intrinsic to the grassland climate and the co-existing biota are fundamental to grassland biodiversity. Conversely, the transformation of grasslands to cultivated croplands has obliterated such once-extensive grasslands as North America's tall-grass prairies and parts of the Eurasian steppe. Overstocking and other improper management policies have degraded grasslands on all continents. Exotic diseases have also had drastic effects upon the biodiversity and function of grassland ecosystems, modifying their organization substantially far beyond the susceptible organism as the consequences are transmitted through food weds (McNaughton 1992). Finally, expansion of cultural pastures into previously forested regions had led to major range expansion of some grassland organisms, sometimes contributing to detrimental changes in the biodiversities of invaded communities.

6.4 CONCEPTUAL MODEL

The relationship between biodiversity and ecosystem function in grasslands can be described by two general hypotheses (Lawton and Brown 1993); the "redundant species hypothesis" which states that species richness is irrelevant for ecosystem function (under existing conditions), and the alternative hypothesis that each and every species plays a unique role in the functioning

of the ecosystem. Experimental evidence does not support either of these extreme hypotheses. Most ecologists prefer a model with a threshold in species richness, below which ecosystem function declines steadily, and above which changes in species richness are not reflected in changes in ecosystem function (Figure 6.2) (Vitousek and Hooper 1993).

A fundamental problem with this model is that it suggests that all species are equally important, and that what matters is the number of species, and not the characteristics of the species that are added or deleted. Evidence suggests that there is a large asymmetry in the contribution of individual species to ecosystem processes (Lauenroth *et al.* 1978; Sala *et al* 1981; Franklin 1988; Komarkóvá and McKendrick 1988; MacMahon 1988). For processes such as primary production, decomposition, nutrient cycling or transpiration, there is a good relationship between the abundance of a species and its contribution to ecosystem function. Rank−abundance diagrams demonstrate how asymmetry in the abundance of species is a common feature across many ecosystems (Figure 6.3) (Whittaker 1965). While these diagrams were originally constructed using primary production as the response variable, the same relationship probably holds for nitrogen uptake, decomposition and other components of ecosystem function. A small number of abundant species account for a large fraction of ecosystem function, whereas a large number of rare species account for a large fraction of species richness but only a small fraction of ecosystem function (Golluscio and Sala 1993).

We suggest that the relationship between biodiversity and ecosystem function and the rank−abundance models are intimately related. The model depicted in Figure 6.2 holds only under the assumption that species are deleted in rank order, from the least abundant to the most abundant. The
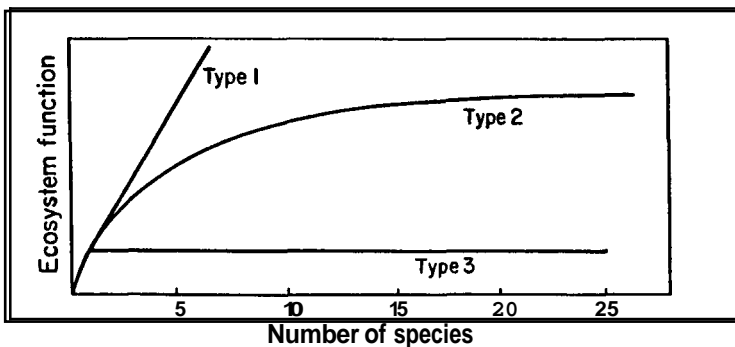

Figure 6.2 A model relating species richness to ecosystem process (after Vitousek and Hooper 1993). Ecosystem process is a generic term which represents processes such as primary production, decomposition, mineralization, evapotranspiration, etc.
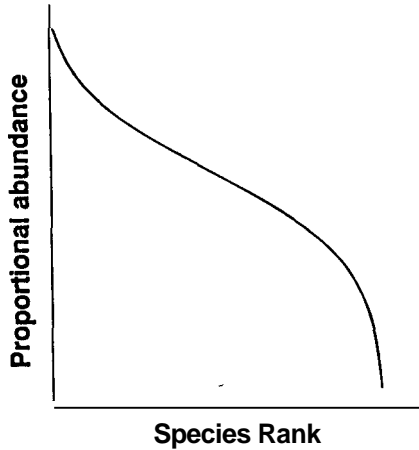
Figure 6.3 Log of the abundance of individual species ordered along the *x*-axis from the most abundant to the least abundant

rarest species is deleted first from the system, followed by the next species in the rank, in what we call an ascending fashion (ascending along a rank-abundance curve) (Figure 6.3). Our contention is that the biodiversity-ecosystem function model has a different shape if species are deleted in a descending fashion along rank–abundance diagrams (Figure 6.4A). Deleting the most abundant species first, i.e. the one that channels the largest fraction of primary production, could result in an abrupt change in ecosystem function (Figure 6.4B). The biodiversity-ecosystem function model has the opposite pattern when species are deleted in a descending fashion, with large changes in ecosystem function as a result of few changes in species richness, followed by a plateau at lower richness levels where further deletions do not result in further alteration of ecosystem processes.

The large impact on ecosystem function of deleting the dominant species is the result of deleting the species which is best adapted to modal environ-mental conditions, and is not the result of deleting a large fraction of biomass. A prediction of the model is that deleting the amount of biomass of the dominant species but from all species in proportion to their abundance will have a small ecosystem effect in comparison with removing the same amount of biomass but from only one species, the dominant one. For example, the model predicts that the removal of the dominant species in a hypothetical ecosystem which accounts for 40% of the biomass will have a larger effect on ecosystem function than removing 40% of the biomass from each individual species. In both cases the amount of biomass removed is the same, but in one case the removal is spread over all the community and in
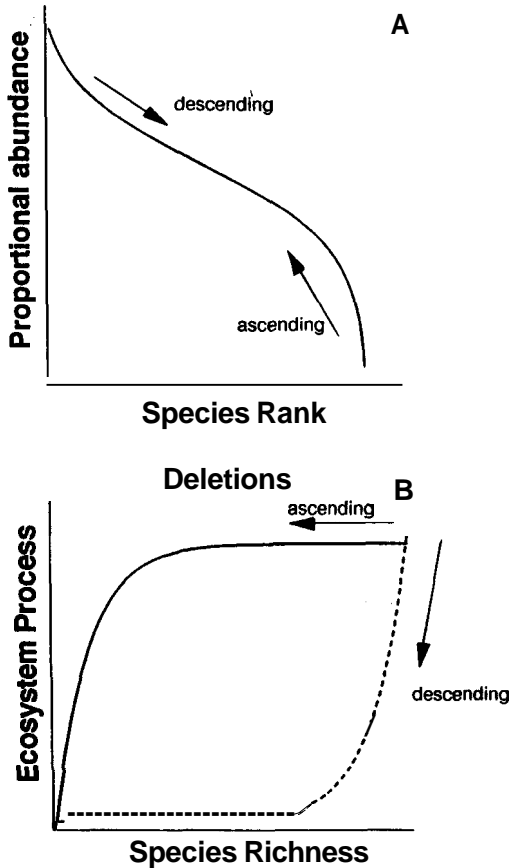
Figure 6.4 (A) Rank–abundance diagram showing two alternative patterns for species deletions: an ascending pattern where the rarest species is deleted first followed by the next species in the rank, and a descending pattern where the most abundant species is deleted first followed by the next species in the rank. (B) The effect on ecosystem processes of deleting species in an ascending or descending fashion

the other it is concentrated on the dominant species. We suggest that the latter has a larger ecosystem effect than the former.

There is an infinite number of models of biodiversity-ecosystem function, defined by the order in which species are deleted. The ascending and descending cases are the boundary cases. From this information the relationship between biodiversity and ecosystem function can be specified for any particular case simply by knowing the rank order of the species to be deleted.

Time is an important consideration in our conceptual model. The size of the response of ecosystem function to the deletion of one or more species will depend upon the time at which the response is measured. As the time between the deletion and the measurement increases, the size of the response should decrease. The explanation for this decrease lies in the compensatory response of the remaining species. The rapidity and magnitude of the compensatory response will be process- and ecosystem-specific. For example, deletion of the dominant plant species in the short-grass steppe of North America will have a large effect on net primary production during the year of the deletion and perhaps for several subsequent years. In less than 10 years the remaining plant species will probably completely compensate, and net primary production will be back to pre-disturbance levels. In this case compensation is complete. Other processes or ecosystems may respond differently to the deletion of the dominant species. We can speculate that deletion of the dominant microbial species that accounts for nitrogen mineralization may produce a very different response depending upon the presence of other species that can perform the same function. If alternative species are not present, nitrogen mineralization will be decreased and over time the compensatory response will be small or absent.

Time is also related to environmental variability: the longer the time-scale of observation the greater the range of environmental conditions experienced by an ecosystem. The effect of removing species on ecosystem function depends on the prevailing environmental conditions. For example, removing drought-resistant species during a wet year will have small effects on ecosystem processes. However, removing them in a dry year may have major ecosystem effects. Therefore, the greater the time-period over which ecosystem responses are observed, the higher the probability of observing an effect of changes in biodiversity. This greater probability will be attenuated by the compensatory potential, which will also increase with time.

So far, our discussion has assumed that all species have similar roles and their impact on ecosystem function is solely related to their abundance. However, ecologists have long recognized the existence of similarities among species and the convenience of defining functional groups (Humboldt, von 1806). Species within functional groups share morphological, physiological and/or phenological characteristics which result in a common ecological role (Sala *et al.* 1989). Therefore, the deletion of an entire functional group could have a larger impact on ecosystem function than deleting the same number of species but drawing from a variety of functional groups. A species may belong to more than one functional group, and consequently the impact of deleting one species may be related to the number of species already existing in the functional group(s) and on the number of functional groups to which the species belongs. Again, the effect on ecosystem function is not simply related to the number of species, but to which species are added or deleted.

Functional groups within a community account for different fractions of total ecosystem processes. For example, perennial shrubs account for a large percentage of total above-ground net primary production in the Chihuahuan desert of North America (MacMahon 1988). We could rank functional groups according to their abundance and their contribution to individual ecosystem processes and construct a rank−abundance diagram for each. Functional groups can be deleted from the least to the most important in an ascending fashion along the rank−abundance curve, or alternatively from the most important to the rarest. Deleting entire functional groups should result in abrupt changes in ecosystem function (Figure 6.5). The decrease in ecosystem function should be largest when deleting first the most abundant functional group.

So far we have considered the effects of changes in species richness which occur as a result of deleting species. This exercise assumed an initial condition of a system in the richest stage, and evaluated the effect of deleting species in different fashions. This follows the most common experimental approach to this question (Ewel *et al.* 1991; Tilman and Downing 1994). Equally important is the effect of species additions on ecosystem function. In most cases, the models developed for the species deletion case should be applicable for the species addition problem. There are three possible outcomes of species additions: increase, decrease, or no change in ecosystem processes. Increases in ecosystem processes should occur in those systems which have previously lost some species. The effect on eccosystem functioning of species additions
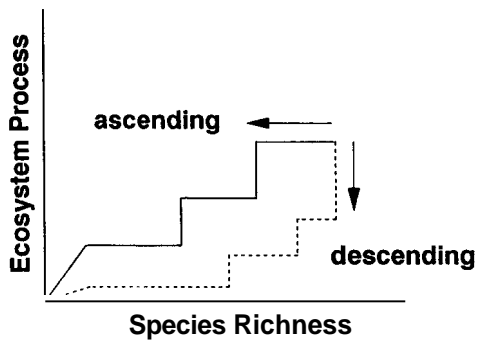

Figure 6.5   The effect on ecosystem processes of deleting entire functional groups in an ascending or descending fashion. Deletions in an ascending fashion means that the first to be deleted are all species from the rarest functional group, followed by all the species in the next functional group. In this case, species within functional groups are also deleted in an ascending fashion. Deletions in a descending fashion represent the opposite pattern, where functional groups and species within functional groups are deleted from the most abundant toward the least abundant
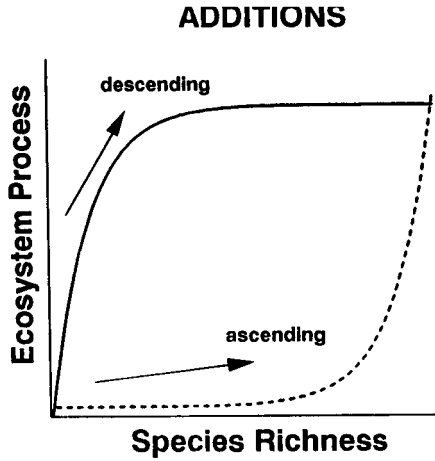
ADDITIONS

Figure 6.6   The effect on ecosystem processes of adding species in an ascending or descending fashion. Additions in an ascending fashion indicates that the rarest species in the intact system is added first, followed by the next in the rank. Additions in a descending fashion indicates that the most abundant species is added first

will depend upon the order in which different species are added (Figure 6.6). Beyond the species richness threshold, further increases result in the partial or total replacement of one species by a new one, but processes remain at a constant level. Finally, we can envision cases in which introduction of a new species will decrease ecosystem processes.

The model developed here describes the relationship between ecosystem function and diversity within a trophic level. The same model is appropriate to describe the diversity-ecosystem function relationship within any trophic level, but different trophic levels cannot be combined. The model assists us in predicting the differential ecosystem effects of removing one plant species versus another plants species, or removing one herbivore species versus another herbivore species, but does not allow us to compare the effects of removing one plant species against removing one herbivore species.

This analysis of the effects of biodiversity on ecosystem function has focused on the species level and has only evaluated the effects of changes in species richness. We suggest that the framework developed at the species level is equally applicable at lower and higher levels of organization, and that the changes in the diversity of populations, functional groups, communities and landscapes affect functioning in the same manner that species richness affect ecosystem functioning.

The definition of the relevant ecosystem processes changes across scales as the definition of biodiversity changes across scales. Some processes are

meaningful only at one scale, while others retain importance at broader levels of organization. For example, we can analyze transpiration at the population, functional group and community levels, but we can only study evapotranspiration at the community level or at larger scales. This is because bare soil evaporation is largely dependent on cover, an attribute which emerges only at the community or larger scales. As rank–dominance curves describe the distribution of species within communities, we can construct rank–dominance curves in a similar way for individuals within populations, and communities within landscapes.

Our contention is that the model described in Figures 6.4 and 6.6 depict the overall relationship between biodiversity and function across a broad spectrum of scales. The effects of adding or deleting individuals, species, communities or landscape units upon processes such as transpiration, evapotranspiration, watershed dynamics, production, nutrient mineralization, airshed dynamics, etc. follow the general model (Figure 6.4) and depend on the sequence in which species, communities or landscapes are deleted or added. If we start by deleting the landscape units which account for the smallest fraction of the relevant processes, no changes will be observed at the landscape level until several of these units are deleted. From that point forward, deletions will result in a steady decrease in function. Conversely, if the deletion starts with the most important units, the landscape will show rapid functional changes followed by a plateau where further changes in landscape diversity are not reflected in functional changes.

Up to this point we analyzed the effects of reducing or increasing species richness upon ecosystem function. We will now consider the opposite relationship: that is the effect of ecosystem function on species richness. The relationship between productivity and diversity has been explored in a number of studies. At the scale of regions, a pattern is emerging: as productivity rises, diversity first increases and then declines (Currie 1991; Rosenzweig and Abramsky 1993; Wright *et al.* 1993). In striving to increase productivity, human beings have manipulated resource availability through means such as fertilization and irrigation. Hence, human intervention has inadvertently led to less diverse and functionally simpler systems (Mellinger and McNaughton 1975; Berendse 1993).

6.5   IMPACTS OF CHANGES IN BIODIVERSITY UPON ECOSYSTEM FUNCTION

The previous section presented a conceptual model of the effects of changes in biodiversity on ecosystem function. This sections summarizes experimental evidence for this relationship. We organized this section according to different ecosystem processes, such as primary production, decomposition,

water distribution, atmospheric properties, landscape structure and biotic linkages. Our use of the term ecosystem processes includes not only water, energy and nutrient cycling, but also atmospheric properties, landscape structure and biotic linkages which overlap with the major biogeochemical cycles. This partitioning allows us to deal explicitly with large-scale processes which show a large impact from human activity.

6.5.1   Productive capacity

Our model suggests that a decrease in species richness, with initial deletion of the rarest species, results in no change in primary production until a threshold is reached, beyond which there is a steady and substantial decrease in production. Removal of rare species in the Serengeti grasslands resulted in full compensation of production by the remaining species (McNaughton 1983). Deletion of species of intermediate abundance resulted in only partial compensation in production. Finally, removal of dominant species which accounted for 70% of the initial biomass resulted in a significant decrease in production.

Grasslands provide several examples in which the relationship between diversity and primary production has been assessed experimentally. The sites studied are geographically diverse, and include California annual grasslands, old fields in New York and grasslands in the Serengeti (McNaughton 1993). Results are contradictory: a negative relationships was observed between productivity and diversity in the annual grasslands of California and the old fields of New York, whereas no relationship between productivity and diversity was found in the Serengeti. The effects of species diversity on production should be assessed with reference to which species have been deleted, and with respect to the driving forces behind the observed changes in diversity, rather than the diversity itself. In the case of the Serengeti, differences in diversity resulted from differences in grazing regime, while in the old fields in New York the diversity differences were a consequence of a successional process.

The diversity–stability hypothesis (McNaughton 1977) suggests that perturbations will result in a larger change in ecosystem function in simple systems than in diverse systems. There is experimental evidence to test this hypothesis in grasslands. McNaughton (1993) analyzed the response to a perturbation caused by fertilization along a diversity gradient which emerged as a result of a successional process. The experiment consisted of fertilizing with N, P and K old fields that were in different successional stages and therefore had different diversity. Similarly, Tilman and Downing (1994) analyzed the response to a perturbation caused by a severe drought along a diversity gradient. They created the diversity gradient by fertilizing the native prairie. Diversity was maximum in the native system and decreased as

fertility increased. In both cases, the effect of perturbation on production was maximum in simple systems and minimum in the most diverse systems.

6.5.2   Decomposition and soil structure

The effects of biodiversity on decomposition in grasslands can be viewed from the plant perspective or the microbial perspective. Microbial diversity is not well documented in grasslands, and its effect on decomposition is even less clearly understood. The effects of plant species diversity on decomposition result mainly from differences in litter quality among species. Several experiments have demonstrated the importance of species characteristics on total soil nutrients, nutrient availability and the rate of decomposition (e.g. Matson 1990; Wedin and Tilman 1990; Hobbie 1992). For example, abandonment from grazing or mowing usually result in losses of forbs and in the dominance of grasses which have different litter quality (Heal *et al.* 1978). Ter Heerdt *et al.* (1991) found that C/N ratios of fresh dead material increased significantly in sites with decreasing grazing intensities.

6.5.3   Water distribution and balance

Important input and output flows which determine water balance and distribution of water change with the scale under consideration. At the ecosystem level, the major flows are transpiration, bare soil evaporation, deep percolation, run-on, run-off and precipitation. At the plant level transpiration is the only relevant flow, but at higher levels of organization watershed variables become dominant. All the output flows of water at one scale are intimately related, and although the biotic components directly affect mainly absorption and transpiration, they indirectly affect all other components of the water balance.

Reduction of transpiration as a result of species deletions is related to species-specific characteristics that affect water dynamics. Rooting depth, phenology, maximum transpiration rate, drought resistance or avoidance are all species characteristics that affect water balance. Species with deep roots are able to absorb water located in a different portion of the soil profile than species with shallow roots. Species with different phenological patterns (early vs. late season) are able to use water available during different portions of the year. In addition, many of these characteristics are self-associated. For example, late-season phenology is associated in several systems with xerophytism or deep-root systems (Gulmon *et al* 1983; Golluscio and Sala 1993).

Experiments and associated models of grassland water dynamics have shown how removal of functional groups such as perennial grasses or shrubs can result in alterations of ecosystem water balance (Knoop and Walker

1985; Paruelo and Sala 1995). Deep percolation losses can increase as a result of a decrease in the abundance of one of the functional groups, and the distribution of water in the soil profile can change as a result of deleting deep- or shallow-root functional groups. In the Patagonian steppe, only a fraction of the water freed by the removal of a functional group was used by the remaining functional group (Sala *et al.* 1989). Most experiments have focussed on the deletions of entire functional groups, providing no experimental evidence for the effects of deleting individual species.

6.5.4   Atmospheric properties

Atmospheric CO_2 is an importance trace gas and a major component of the carbon cycle. We have described how biological diversity from species to landscapes affect production and decomposition, which are the major processes driving the carbon cycle. We are not aware of studies relating species diversity to atmospheric properties. However, Burke *et al.* (1991) calculated the effects on the carbon balance of converting a large fraction of the North America Central Grassland Region into cropland. They also estimated, by means of a simulation model, the effects of changes in climate as predicted by global circulation models upon the carbon balance of grassland ecosystems. They compared the observed losses in carbon as a result of cultivation against those which may result from climate change. Cultivation resulted in a net release of carbon from soil organic matter which was larger than the expected loss as a result of climate change.

6.5.5   Landscape structure

Croplands have expanded dramatically during this century from 9.1×10^6 to $15 \times 10^6 \, km^2$ (Richards 1990). This expansion altered landscape heterogeneity in grasslands. Habitat selectivity by domestic livestock has differentially influenced riparian ecosystems and therefore altered landscape diversity. Domestic livestock, and especially cattle, tend to congregate in the topographically lowest portions of the landscape (Senft *et al.* 1985; Pinchak *et al.* 1991). Such habitat selectivity has negative effects on the plant and animal diversity of riparian ecosystems (Kauffman and Krueger 1984; Smith *et al.* 1992). The reduction in diversity of the stream-side vegetation and its productivity have negative effects on both physical and chemical indicators of water quality (Kauffman and Krueger 1984). Reduction in the diversity and productivity of the herbaceous vegetation layer can change the velocity and erosive energy of the stream flow. Losses of the woody overstory has large effects on water temperature. Both the overstory and understory vegetation layers have important effects on the rates and kinds of aquatic processes that occur in a stream (Kauffman and Krueger 1984). Diversity

and productivity of invertebrates and fishes are profoundly influenced by the diversity of the stream-side vegetation.

6.5.6 Biotic linkages/species interactions

Invasions in grasslands are common and in some cases have been associated with changes in grazing regime. Examples of grasslands which have been invaded by exotic species are the California grasslands and the intermountain west of North America, the Pampas in South America, and the savannas in tropic South America (Sala *et al.* 1986; D'Antonio and Vitousek 1992). Invasions in grasslands usually occurred in association with the increase in grazing intensity and/or a change in dominant grazer. Vulnerability to invasions associated with grazing appears to be related to moisture availability and the grazing history in evolutionary time (Milchunas *et al.* 1988). Grasslands which evolved under light grazing conditions and under mesic conditions are more vulnerable to invasions than those which evolved under heavy grazing in xeric environments. Semi-arid grasslands of northwest US and southwest Canada have a short evolutionary grazing history, and before the introduction of cattle they were dominated by perennial tussock grasses (Tisdale 1947; Daubenmire 1970). The inability of these grasses to cope with heavy grazing resulted in the invasion and dominance of many areas by Eurasian weeds (Daubenmire 1940, 1970; Ellison 1960; Mack 1981; Mack and Thompson 1982). Invasions often disrupt competitive interactions (D'Antonio and Vitousek 1992), which results in changes in species composition with the ecosystem effects described above.

6.6 CONCLUSIONS

On a world-wide basis the response of grasslands to the major human use, domestic livestock grazing, has been variable (Milchunas and Lauenroth 1993). In some areas where the native vegetation is well adapted as a result of evolution, changes in biodiversity have been very small (Milchunas *et al.* 1988). In other areas changes have been very large. In some cases, and especially in tropical and subtropical grasslands, the large changes have involved a shift from a grass-dominated vegetation to one dominated by woody plants (Walker *et al.* 1981; Van Vegten 1983; Archer 1989). In other cases the large changes have involved invasions of exotic plants that have profoundly altered the ecosystems. Conversion of grasslands to croplands or seeded pastures has also had a major influence on biodiversity and ecosystem function. In many cases these converted grasslands have become net sources of carbon and nutrients accelerating global change. These major

transformations of grasslands and their effects on biodiversity modify the water, carbon and nutrient cycles to an extent that significantly contributes to jeopardizing the earth's life-support system.

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