

Biodiversity and Ecosystem Functioning: Ecosystem Analyses

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EXECUTIVE SUMMARY

1. Ecosystems provide services to humans that are crucial for their well-being. These services are not widely recognized, nor are they properly valued in economic, or even social terms.
 2. The Earth is covered by a myriad distinctive ecosystems all of which are increasingly impacted by human activity.
 3. Human-driven perturbations to ecosystems are altering their structure, depleting stores of resources that fuel productivity, disconnecting populations and disrupting species interdependencies.
 4. The accidental introduction of species can have major, and often detrimental, impacts on the functioning of ecosystems. Successful establishment of invaders is greatest in those systems that are biotically simple, such as islands, and those that have been disturbed by human activity. The potential success of a particular invading species is difficult to predict but its ecosystem impact depends on whether it utilizes or produces a resource unique to its new habitat.
 5. All ecosystem services are affected to one degree or another by reductions in diversity. This fact follows simply from the greater resource capture, i.e. of energy, water, nutrients, sediments, of diverse systems compared to simple systems. However, depending on the time dimension and functional types present, the exact relationship between diversity and function will vary.
 6. Certain ecosystems, such as arid and arctic ecosystems, and those found on islands, appear particularly vulnerable to human disruptions and hence alteration of their functioning. These sensitive systems all have low representation of key functional types (organisms that share a common role).
 7. The types of connection among ecosystems within a landscape greatly influence the exchange of nutrients, water, sediments and genetic material. Ecosystems, and the services they provide, must be considered in a total landscape context and in some cases even on an intercontinental basis.
 8. As society exerts ever greater control and management of the ecosystems of the world, great care must be taken to ensure their sustainability, which is due in large part to the buffering capacity provided by biotic complexity.
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6.0 Introduction

6.0.1 Background

In this section, the general principles outlined in Section 5 are used to assess our current knowledge of the ecosystem-level consequences of human-induced changes in biodiversity. We provide separate assessments for a selection of the major biomes of the world because the human impacts on biodiversity and the associated ecosystem consequences differ among biomes and because decision-makers will require different information for each. Our sample includes freshwater, marine and terrestrial systems that represent a significant portion of the ecosystems on Earth.

6.0.2 Biome essays and ecosystem processes

For each of the 15 biomes surveyed, the authors provide information on the consequences of human-induced changes in biodiversity for seven ecosystem processes and/or properties:

- Productive capacity and biomass
- Soil structure, nutrients and decomposition
- Water distribution, balance and quality
- Atmospheric properties and feedbacks
- Landscape and waterscape structure
- Biotic linkages/species interactions
- Microbial activity

These topics involve key ecosystem processes, such as carbon, water and nutrient cycling. They also recognize the importance of higher levels of integration in ecological systems; interactions between the Earth's surface and atmospheric properties; biotic linkages, because they result in the provision of many essential ecosystem services; and microbial activity, which fuels many ecosystem-level processes. More extensive discussions of these points with respect to each ecosystem can be found in the forthcoming SCOPE volume (Mooney *et al.* 1996).

The biome essays provide biome-specific information on (a) the drivers of change in biodiversity, (b) the impact of these drivers on biodiversity at multiple levels, and (c) the ecosystem consequences of these changes in biodiversity. For example, as outlined in the coral reef essay (6.1.10), a major driver of change in these systems is overfishing by the growing human populations that inhabit the adjacent coastlines. The impact of this driver on biodiversity is to reduce greatly the abundance and diversity of algae-grazing fishes. A significant ecosystem consequence of this change is the transformation of reefs from coral-dominated to algae-dominated systems. These changes have direct and immediate feedbacks to people who depend on coral reefs: in addition to buffering coastal environments from storms, coral reefs provide an array of highly specific taxa that are important in commercial and subsistence harvesting.

6.0.3 Cross-biome comparisons and syntheses

After considering each of the 15 biomes in our sample, the authors generate cross-biome comparisons of the ecosystem consequences of human-induced impacts on biodiversity. These seven essays provide comparative analyses of the functional consequences of an increasingly modified world. We then synthesize the findings of the individual biome essays and the cross-biome comparisons to derive our final conclusions.

We have attempted throughout to provide a synthesis of our conclusions that is in a form accessible to both policy-making and scientific communities. Inevitably, our current ability to address all the questions for which one would like answers is limited in some cases. However, the hope is that future efforts will benefit from an articulation of these questions and from knowing where the gaps in scientific knowledge exist.

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6.1 Biome essays

6.1.1 Arctic and alpine systems

6.1.1.1 Introduction

Arctic and alpine ecosystems are cold-dominated ecosystems lacking trees. These ecosystems occupy about 8% of the terrestrial surface of the globe (5% Arctic, 3% alpine) but support only about 4% of the global flora (1500 Arctic species, 10 000 alpine species) and fauna. Species diversity of plants and animals in Arctic and alpine regions declines with increasing latitude and altitude, but genetic diversity within species appears unrelated to climatic severity. Within both regions species diversity of plants and animals is concentrated in areas of high vertical relief, lacking a well-developed organic mat. The vast expanses of peat-covered landscape in the Arctic and in level terrain in alpine regions have very few species (generally <10 vascular plant species per m²), and these species have a widespread geographic distribution. Landscape diversity strongly influences terrestrial-aquatic exchanges, particularly in permafrost-dominated Arctic terrain, where water and nutrients flow laterally among ecosystems (Kling 1995).

6.1.1.2 Productive capacity, biomass, decomposition and nutrient cycling

Human impacts on biodiversity. Other than the direct impacts of land use, the most profound human impacts result from activities outside Arctic and alpine ecosystems, such as CO₂-induced climatic change, which may increase

reproductive output and growth in the high Arctic (Wookey *et al.* 1993) and cause major changes in growth-form composition in the low Arctic (Chapin *et al.* in press) and alpine regions. CO₂ has little direct effect on Arctic or alpine plant growth (Tissue and Oechel 1987) or ecosystem CO₂ flux (Oechel *et al.* 1994; Körner *et al.* 1995). Arctic haze derived from pollutants produced at low latitudes could reduce the cover of mosses and lichens (Lechowicz 1987), which provide the major insulating layer protecting permafrost integrity (Tenhunen *et al.* 1992).

Ecosystem consequences of impacts. In the Arctic, changes in the relative abundance of current species generally have little direct effect on productivity and nutrient cycling because reduced abundance of some species is balanced by increased abundance of others (Chapin and Shaver 1985). Overall productivity is strongly constrained by climate and nutrient supply, so that energy and nutrient cycling are relatively insensitive to large changes in relative abundance of species and growth forms. However, these changes in species composition can have long-term effects on nutrient cycling and productivity through changes in litter quality and rates of decomposition (Shaver *et al.* 1995) or nitrogen inputs by lichens and the blue-green algae associated with mosses. Climatic warming increases the abundance of shrubs which have higher litter quality than the mosses they replace (Chapin *et al.*, in press). Similarly, reduction in moss cover resulting from pollutant inputs could increase energy inputs to soil and soil temperature (Tenhunen *et al.* 1992; Zimov *et al.* 1993a). Warmer soils enhance decomposition and the nutrient supply to vascular plants (Nadelhoffer *et al.* 1991). Lichens, which are important both as a source of N fixation and as winter food for caribou, are particularly sensitive to shading by shrubs (Chapin *et al.* in press) and to air pollutants (Lechowicz 1987). Changes in grazing can also modify the diversity of plant functional groups. For example, large mammalian browsers increase in response to increased shrub growth. In the boreal forest, these browsers speed the rate of succession by removing highly palatable species, leaving species with lower litter quality and associated declines in decomposition and nitrogen mineralization (Pastor *et al.* 1993). Thus, the major effects of climatic warming may operate primarily through changes in composition of plant and animal communities and litter-quality feedbacks to nutrient supply rather than directly on the productive capacity of vegetation.

6.1.1.3 Soil structure and nutrient pools

Human impacts on biodiversity. Soil structure and nutrient pools are most strongly dependent on human activities that influence long-term ecosystem persistence. In both the Arctic and the alpine, human disturbance that destabilizes soils (e.g. tourist developments in the alpine and use of tracked vehicles in the arctic) increases the

physical interactions among landscape units. For example, destabilization of slopes in the alpine causes down-slope delivery of avalanche debris. In the Arctic, permafrost degradation associated with mining and oil development expands beyond the initial zone of disturbance due to heating of adjacent soils, melting of ice, impoundment of water, and slumping of soils (Billings 1973; Walker *et al.* 1987).

Ecosystem consequences of impacts. This shift in landscape structure from mesic to wet tundra results in lower productivity, lower decomposition and greater carbon storage than does the original tundra from which it was formed (Chapin *et al.* 1980; Oechel and Billings 1992). Some of the biologically richest ecosystems in the lower alpine zone in Eurasia have developed over millennia of traditional cattle grazing or mowing but are losing species with the current abandonment of lands. This loss of diversity affects slope stability and drainage. In both Arctic and alpine ecosystems, return to the original ecosystem type following soil destabilization can require hundreds to thousands of years.

6.1.1.4 Water distribution, balance and quality

Human impacts on biodiversity. Human impacts on ecosystem integrity and landscape diversity (see above) strongly influence water quality and distribution. Destabilization of alpine slopes reduces plant cover and increases the quantity and seasonal variation in runoff to rivers, presumably affecting aquatic community structure and trophic dynamics. In the Arctic, human-induced melting of permafrost can lead to siltation of rivers and to formation of new ponds (Walker *et al.* 1987).

Ecosystem consequences of impacts. Even small anthropogenic nitrogen or phosphorus additions to Arctic lakes and streams substantially increase algal and fish production, increase production by benthic mosses, and greatly alter the species composition of zooplankton (lakes) and insect grazers (streams), shifting from a detritus-based to an algae-based food web (Peterson *et al.* 1993).

6.1.1.5 Feedbacks to atmospheric properties

Human impacts on biodiversity. Recent climatic warming is already causing upward migration of alpine species (Grabherr *et al.* 1994) and is predicted to cause northward and up-slope movement of treelines (D'Arrigo *et al.* 1987; Briffa *et al.* 1990). This represents a major change in distribution and diversity of species and functional groups in cold-dominated ecosystems. If climatic warming leads to drier soils, this would change landscape diversity, which at present is largely determined by topography and soil water movement.

Ecosystem consequences of impacts. Northward and upward movement of treelines would substantially increase annual energy absorption by northern ecosystems by

masking snow and reducing albedo. This would act as a positive feedback to regional climatic warming, an effect that would be most pronounced at high latitudes, but could extend to the tropics (Bonan *et al.* 1992). The current net CO₂ efflux observed in Arctic ecosystems may depend directly on soil drying (Oechel *et al.* 1993) in the wet Arctic of North America (with diversity playing little role), but the increased CO₂ efflux in the drier Russian Arctic could reflect a reduction in cover of pollutant-sensitive mosses, whose insulative properties govern the soil temperature regime (Zimov *et al.* 1993b). Arctic wetlands and associated loess sediments are large terrestrial sources of methane (Reeburgh and Whalen 1992; Fukuda 1994), and changes in landscape diversity, as a result of soil drying, could reduce methane efflux. Changes in the abundance or species composition of sedges, which transport most methane from Arctic soils to the atmosphere (Torn and Chapin 1993), could alter fluxes of this greenhouse gas and, therefore, the role of methane in atmospheric warming (Whalen and Reeburgh 1992).

6.1.1.6 Landscape and waterscape structure

Human impacts on biodiversity. Human agricultural (alpine) and industrial (arctic) developments have substantially altered landscape structure and diversity. For example, in the Arctic, the building of roads and pipelines has altered patterns of water drainage, and the relative abundance of waterlogged and well-drained soils. In the alpine regions, the construction of ski runs has smoothed the landscape and introduced new plant communities. Such land-use change can alter hydroelectric yield. These indirect impacts of energy development are many times larger than the direct impact of development (Walker *et al.* 1987).

Ecosystem consequences of impacts. For ecosystem consequences, see the above sections on soil structure and water distribution.

6.1.1.7 Biotic linkages and species interactions

Human impacts on biodiversity. Increasing demand by non-Arctic people for Arctic animal products, combined with increasing hunting efficiency, has resulted in a greater human harvest of marine and terrestrial mammals, in many cases causing or contributing to population declines. This is often combined with changes in human social structure which might otherwise have placed limits on the exploitation of these animal resources (Young and Chapin 1995). In addition, human-induced climatic warming is altering the competitive balance and diversity of plant species within the Arctic (see productive capacity) and could decouple the phenology of plants and their pollinators, leading to elimination of plant species that may have important ecosystem effects (Inouye and McGuire 1991).

Ecosystem consequences of impacts. In cases where animals (e.g. sea otters) are keystone predators, over-

hunting produces effects that propagate through the entire ecosystem. Human hunting of the Pleistocene megafauna may have triggered the change from grass-dominated steppe to less productive moss-dominated tundra at the end of the Pleistocene (Zimov *et al.* 1995). Changes in abundance of reindeer or herding practices in Russia and Scandinavia greatly influence lichen cover and, therefore, the vegetation structure and productivity of these landscapes (Andreev 1978). Geese and other waterfowl determine productivity, nitrogen input and cycling rates, and disturbance regimes, in Arctic salt marshes (Jefferies and Bryant 1995), and recent changes in the abundance of geese have totally altered the structure and dynamics of these coastal ecosystems. Little is known about the ecosystem impacts of possible changes in pollinator abundances. Insect-pollinated species are concentrated in areas of vertical relief, which contribute little to carbon storage or methane flux but are important in slope stability.

6.1.1.8 Microbial activities

Human impacts on biodiversity. Human impacts on microbial activity are mediated primarily by changes in species composition and litter quality (see productive capacity) and secondarily by the introduction of contaminants from oil spills and pollution.

Ecosystem consequences of impacts. Most Arctic and alpine ecosystems have a similar spectrum of enzymatic potentials to degrade common substrates such as lignin, cellulose and proteins, despite large differences in litter chemical composition (Schimel 1995). Ecosystems do differ, however, in their capacity to produce or consume methane, petroleum products and many anthropogenic pollutants. Changes in microbial diversity are thus more likely to be important in the production and degradation of unusual substrates than in the normal processing of plant litter and soil organic matter.

6.1.1.9 Summary and relevance to human activities

Arctic and alpine ecosystems are particularly vulnerable to human impacts on species diversity, because there are few species in the most widespread vegetation types, so the loss or gain of even one or two species has a large proportional impact on diversity. Furthermore, landscape diversity is easily altered by human impact, due to the sensitivity to disturbance of steep alpine slopes and the sensitivity of Arctic soils to permafrost degradation. Resulting ecosystem changes affect local inhabitants primarily by reducing the productivity of various animal species (reindeer, marine mammals, fish) on which they depend. In alpine and down-slope ecosystems, these changes influence run-off, landslide danger and the quality of drinking water. Other effects of human-induced changes on Arctic and alpine ecosystems are indirect, resulting from potential positive

feedbacks of CO₂ and CH₄ emissions to climate warming. Because human impacts on the Arctic and alpine regions originate primarily outside these regions, they are generally decoupled from, and unresponsive to, the effects they cause.

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6.1.2 Tropical forests

6.1.2.1 Introduction

Tropical forests grow in frost-free regions between the Tropic of Cancer and the Tropic of Capricorn. In the New World, evergreen forests of the humid tropics extend from the border of the San Luis Potosí-Veracruz States of Mexico (Dirzo and Miranda 1991a), south to the east coast of Brazil. In Africa, these forests are confined to the Guinea coast, the Zaire Basin and the eastern part of Madagascar. In Asia, they are found in the monsoon areas north to the southern slopes of the Himalayas, in southeastern India, and in Malaysia, Indonesia, the Philippines, Thailand, and New Guinea. Evergreen tropical forests extend south in a narrow discontinuous strip on the east coast of Australia.

Most tropical forest regions, even the wettest ones, have dry seasons during which one to several months may receive <100 mm of rain. Only in Malaysia and Indonesia are there large areas that are always wet (i.e. >100 mm of rainfall per month) (Walter 1973). Tropical areas with longer dry seasons are typically found poleward from wet forest regions, but they also exist in regions that are dry for topographic reasons. If these areas have not been heavily disturbed, they support moist and dry deciduous forests. In tropical and subtropical regions with lengthy dry seasons, rainfall reaches its maximum at the time the sun is at its zenith; the winter months, which are only slightly cooler than the summer months, are relatively dry.

Rainfall increases with elevation on the slopes of tropical mountains except in areas that lie in the lee of tall mountains. Clouds form on most days around 1500 metres above sea level, with the result that cloud forests prevail between 1000 and 2500 m on mountain slopes. Precipitation decreases rapidly above the cloud belt. Forests above the cloud zone have short stature and the leaves of trees are smaller and more xeromorphic than those at lower elevations. Above these low-stature forests is a zone dominated by scleromorphic shrubs (Grubb 1977).

One of the most distinctive features of tropical forests is their biological richness, particularly in numbers of species. The world records for species richness are 473 tree species (considering only individuals with a diameter at breast height (dbh) of 10 cm or more) in a 1 hectare plot in Amazonian Ecuador (Valencia *et al.* 1994), which supersedes the previously known and highly publicized record of 300 woody species (trees and lianas dbh >10 cm) in a 1 ha plot in Ecuador (Gentry 1988) (see also Section 3.2 and Latham and Ricklefs (1993) for an analysis of tree species diversity) and 1200 species of beetle collected from a single tree species in Panama (Erwin 1982). Fourteen of the 18 areas on Earth with unusually high degrees of plant endemism lie within the moist tropics. Their collective expanse, which is smaller than California, constitutes less than 5% of the remaining undisturbed forests. These forests contain more than 37 000 endemic plant species, or 15% of all plant species, in less than 311 000 km², or just 0.2% of the Earth's land surface (Myers 1988, 1990). Plant life-forms are also exceedingly diverse in tropical forests and include trees, shrubs, herbs, epiphytes, hemi-epiphytic trees, epiphytic cacti, terrestrial and climbing palms, climbing herbs, bamboos and more (Richards 1952; Whitmore 1975; Gentry 1990). These impressive figures of tropical biodiversity should not conceal the fact that our current knowledge is still very limited. Two splendid accounts of our ignorance on this subject are those of Gentry (1992) for plants and Gaston (1991) for insects. The following statements taken from these two sources provide compelling examples. In the supposedly well-collected region of Iquitos, Peru, nearly 70% of extracted timber comes from a tree first described in 1976, and the most common climbing species in the inundated forests of this area was first discovered in 1976. For insects, estimates of the proportion of tropical species still not described range from a low of perhaps 65%, to a high of 99% (see Section 3.1.2).

For unknown reasons, these forests are relatively resistant to invasions; invaders tend to be restricted to disturbed rather than natural areas (Rejmanek 1989; Whitmore 1991).

6.1.2.2 Human impacts on biodiversity

Considerable attention has been directed towards tropical forests because their rate of loss is currently very high (Myers 1989; Lanly *et al.* 1991; Whitmore and Sayer

1992). According to the last published calculations of FAO (1990), tropical closed forests were being destroyed at a rate of at least 110.5 million ha per year. Rates of loss of forest cover vary greatly by continent and habitat type, and true deforestation rates are difficult to determine because satellite data are incomplete and ground truthing is available for relatively few areas (Myers 1994). In Central America, more than 95% of tropical dry forest has been converted to agriculture, whereas a much higher percentage of evergreen humid forest still remains (Janzen 1988). If recent rates of destruction of tropical forests continue, massive extinctions of populations and species are expected to occur in the coming years and decades (Wilson 1992; Whitmore and Sayer 1992).

The extensive conversion of forests to pastures and agricultural lands as well as shifting cultivation and forestry plantations in Southeast Asia greatly reduce biodiversity at both local and landscape scales. Few of the many species that make tropical forests the richest habitat type on Earth can survive in the croplands, pastures or second-growth forests that replace the forests. However, some of them can be extremely successful in those habitats (e.g. *Cecropia* spp. and *Ochroma pyramidale*, among other plants (Gómez-Pompa and Kaus 1992). In addition, because of their narrow ranges many tropical species are vulnerable to extinction from loss of forests in local areas. For example, many species of cloud forest plants in tropical Latin America are endemic to isolated sites smaller than 10 km² (Gentry 1992) while among the birds of tropical forests in South America, 440 species (25% of the total) have ranges of less than 50 000 km². In contrast, only eight species (2% of the total) of bird species in the United States and Canada have such restricted ranges (Terborgh and Winter 1980).

6.1.2.3 Productive capacity, biomass, decomposition and nutrient cycling

Primary productivity of tropical forests is apparently positively correlated with plant species richness only when the number of species is far below that which characterizes most mainland tropical forests, even those that are fragmented and highly disturbed (Vitousek and Hooper 1993; Wright in press). However, some tropical forests, especially those growing on unusual soils, are dominated by one or a few species of trees (Connell and Lowman 1989; Hart 1990). Examples include *Mora excelsa* stands adjacent to mangrove forests (Richards 1952); *Eperua* forests in South America (Richards 1952; Klinge and Medina 1978; Klinge and Herrera 1983; Herrera *et al.* 1984; Cuevas and Medina 1988), and the *Pterocarpus officinalis* or *Celaenodendron mexicanum* forests of Mexico (Martijena 1993). These forests have not been studied well enough to determine whether their productive capacity is influenced by their low species richness. Recent

studies have failed to detect significant differences in nutrient levels of soils between forests dominated by *Celaenodendron mexicanum* and adjacent mixed (diverse) patches of seasonally dry forests (Martijena 1993) or between evergreen forests dominated by single species and mixed forests in India (Kadambi 1942), Zaire (Hart *et al.* 1989; Hart 1990) and Malaysia (Whitmore 1975).

None the less, biodiversity may influence tropical forest productivity if there is much variation in weather and if disturbances are relatively frequent or severe. Annual productivity is higher and less variable in species-rich than in species-poor temperate grasslands because some species perform better during wet years, while others do better during dry years (Tilman and Downing 1994). It is possible that a similar variation in performance occurs among tropical trees, but we are unaware of any relevant data. Gathering such data may be difficult because little variation is expected in the number of leaves produced per unit area. The rate of biomass accumulation depends strongly on the nature and intensity of disturbance, and species differ in the speed with which they respond to disturbances. Therefore, although there are no data available to test the hypothesis, species richness may influence the rate at which biomass accumulates after disturbance (Denslow 1995).

The consequences of forest disturbance for ecosystem productivity and nutrient cycling depend on the scale and frequency of the disturbance. In the Atlantic lowlands of Costa Rica, intermediate-scale experimental clear-cutting of forests on residual soils resulted in rapid, short-term increases in nutrient concentrations in soil solutions, increased percolation of water through the soil, and increased losses of soil nutrients (Parker 1994). With no additional disturbance, the large pulse of nutrients lost below the rooting zone in percolating water was transient: concentrations returned to pre-disturbance levels in less than two years. Small-scale disturbances, such as in natural or artificial treefall gaps, do not result in increased soil nutrient availability (Vitousek and Denslow 1986) or solution losses (Parker 1994) compared to the intact forest. On the other hand, large-scale, long-term conversion of forests to grasslands or cropland results in major changes in nutrient pools and the soil biota (Olson 1963; Hamilton and King 1983; Macedo and Anderson 1993; Henrot and Robertson 1994). In combination with extraction of nutrients in harvested biomass, these changes cause the productivity of the transformed tropical agro-ecosystems to decrease rapidly.

Litter decomposes so rapidly on the floor of lowland tropical wet forests that there is no interannual accumulation of decomposing litter (Barrow 1991). Hence, tropical trees may not influence the development of soil profiles in highly species-specific ways as strongly as they do in high-latitude forests. However, tropical trees differ markedly in tissue chemistry (Rodin and Basilevich 1967;

Golley 1983a, b), suggesting that they differ in what they remove from the soil and what they deposit on the soil surface. Soils under the legume *Pentaclethra macroloba* at La Selva, Costa Rica, have lower pH values than soils away from individuals of this species, presumably because the trees fix nitrogen, which is then nitrified (Parker 1994). Soils under female *Trophix involucreta* individuals have higher phosphorus concentrations than soils under males (Cox 1981). The meager evidence so far available suggests that trees of different species may generate significant differences in the soils in the areas affected by their roots and litter fall, but whether these differences are important for regeneration, growth, species richness and productivity of tropical forests remains to be determined (Parker 1994).

6.1.2.4 Water distribution, balance and quality

Deforestation, agricultural practices and soil erosion reduce landscape complexity and diversity and also result in the pollution of many rivers and streams that flow through tropical forests. Pollution can alter species diversity and trophic dynamics considerably, as in the case of lead- and mercury-polluted segments of the Orinoco River caused by gold mining (Pfeiffer and De Lacerda 1988).

Alteration of landscape structure and diversity affect water distribution and balance in terms of the seasonal variation in runoff to rivers and lakes and associated nutrient inputs. Water distribution and quality are also affected by the type of management techniques and the diversity components associated with management practices. For example, in a seasonally dry forest in Mexico, soil erosion within the forest was negligible (< 2 Mg/ha/yr), whereas conversion to maize and grassland increased erosional losses up to 130 Mg/ha/yr (Maass *et al.* 1988). In this study, as much as 185 k/ha of nitrogen, 27 k/ha of phosphorus, and 378 k/ha of calcium were lost via erosion within a year of deforestation, whereas less than 0.1 k/ha of each element was lost from the intact forest. Presumably, the nutrients eroded from deforested soils end up in neighbouring rivers and lakes where they alter water quality. In addition, runoff from cut-over forests leads to erosion along tropical coasts, which may cause death to corals.

6.1.2.5 Atmospheric properties and feedback

Tropical deforestation and subsequent conversion to other simplified systems (largely grasslands) lead to changes in the rates of fixation and storage of carbon in vegetation. Tropical forest destruction and burning is currently a net source of atmospheric CO₂, but this is due to reduction of the total acreage of forests and to extensive burning (Detwiler and Hall 1988; Hall and Uhlig 1991; Houghton 1991) and not to loss of species *per se*. In general, tropical wet forest deforestation contributes more to carbon emissions than does cutting of seasonally dry forests

(Maser *et al.* 1992). Conversion to grassland, the most common type of forest conversion in the tropics, contributes the largest amounts of carbon emissions (Maser *et al.* 1992). Because tropical plantations can and do accumulate carbon at rates similar to those of natural species-rich forests (Cuevas *et al.* 1991; Ewel *et al.* 1991; Lugo 1992), there is no reason to expect that carbon budgets of tropical forests are strongly influenced by species richness.

Tropical wetland areas are a major global source of methane, but upland tropical soils can be significant methane sinks. Conversion of upland tropical forests to agriculture can transform these soils from methane sinks to net methane sources. Agricultural activities and development projects that alter, destroy or create (artificial) tropical wetlands also affect biodiversity components of these systems with potential atmospheric effects. Methanogenic bacteria in tropical wetlands are responsible for 60% of the total global methane emissions from natural sources, but gut symbionts of termites are also a significant source of methane (Wassmann *et al.* 1992; but see Martius *et al.* 1993). How emission rates of methane and other chemicals vary with biodiversity is unknown, though ongoing research indicates that emission rates vary with the species of termite.

6.1.2.6 Landscape and waterscape structure

Deforestation is dramatically altering tropical forest landscapes and waterscapes (Shukla *et al.* 1990). However, although deforestation is causing reductions in species diversity, there is no evidence that species loss is, in turn, influencing the structure of landscapes or waterscapes. It has been established that, in Amazonia, tropical landscape modification in the form of transformation of forest to grassland may alter local climate, particularly through the intensification of rainfall seasonality (Shukla *et al.* 1990).

6.1.2.7 Biotic linkages and species interactions

Deforestation, fragmentation and isolation, edge effects, contemporary defaunation (*sensu* Dirzo and Miranda 1991a), and reduction of forest habitat size (Lovejoy *et al.* 1986) have profound effects on biotic linkages and species interactions. Most tropical plants are animal-pollinated (Bawa 1979; Bawa and Beach 1981; Baker *et al.* 1983; Bawa and Hadley 1990); they are fed upon by a wide variety of generalist and specialist herbivores (Dirzo 1987); and they also depend upon animals for dispersal of their seeds (see Estrada and Fleming 1986). Flowering plant species inhabiting forest fragments can experience severely reduced rates of pollinator visitation which can lead to reduced seed production and/or genetic diversity of progeny (Aizen and Feinsinger 1994a, b). Similar effects may be operating as a consequence of reductions in the abundance of critical pollinators, such as Euglossine bees

in Amazonian forest fragments (Lovejoy *et al.* 1986), or the outright loss of hummingbird species on Panama's Barro Colorado Island (Karr 1982). Reduction or loss of other species or functional guilds as a consequence of forest fragmentation (e.g. seed-dispersing birds and bats) may also affect plant reproductive biology, forest structure and forest dynamics. Fragmentation and isolation also alters the guild of vertebrate seed consumers in fragmented tropical landscapes, thereby affecting floristic composition (Cox *et al.* 1991; Dirzo and Miranda 1991a; Leigh *et al.* 1993). Contemporary defaunation (due to habitat alteration and hunting) of medium- to large-sized understorey vertebrates is correlated with local reductions of floristic diversity and the occurrence of monospecific seedling carpets in tropical forests (Dirzo and Miranda 1991b). Although the long-term ecosystem consequences of such changes have not been studied, biodiversity disruptions such as defaunation and creation of local monocultures probably affect patterns of litterfall deposition and possibly nutrient dynamics. Long-term ecosystem consequences of alterations of biotic diversity in the tropics warrant further study.

Secondary productivity is potentially highly sensitive to species richness because different plants allocate their primary production in highly distinctive ways. Plant species differ strikingly in the proportion of primary production allocated to defences; which defensive compounds are synthesized; the quantities and composition of tissues that function to attract mutualists (Coley *et al.* 1985; Davidson *et al.* 1991) and the chemical composition of their wood. Because tropical climatic conditions allow heavy herbivore pressure throughout the year, tropical woody plants allocate relatively large amounts of energy to the production of chemical defences (Levin 1978; Levin and York 1978; McKey 1979) and to the production of resources that attract predators and parasites of herbivores (Simms 1992). Consumers may increase primary productivity by maintaining individual plants and plant populations in rapid growth phases, by reducing the accumulation of living plant biomass, by reducing respiratory losses, and by recycling nutrients, but the relatively small amount of new primary production typically consumed by herbivores in tropical forests probably has little effect on total net primary production (Huston 1994).

'Mobile link' species (i.e. animals necessary for the persistence of plant species that in turn support otherwise separate food webs – Gilbert 1980, pp. 19–20), such as pollinators, seed dispersal agents and plant defence mutualists, alter fluxes of energy and materials very little in ecological time, but they may be critical to the maintenance of the species richness of tropical forests. Many species in tropical forests depend upon a small suite of frugivores for dispersing their seeds. Loss of these species, many of which disappear when forests are fragmented, may

adversely affect the long-term population viability of many tree species (Howe and Smallwood 1982; Terborgh 1986).

6.1.2.8 Microbial activities

Fungi and bacteria are involved in a wide range of fundamental processes in tropical ecosystems, from global geochemistry to decomposition and nutrient cycling (Hawthornth *et al.* 1996). However, the taxonomy of tropical microbes is so poorly understood that we know very little about the functional roles played by individual taxa and how sensitive ecosystem processes are to human-induced deletions of these species. Although we know very little about the effects of tropical deforestation on microbial biodiversity, it is clear that microbial activity declines considerably in cleared areas. One possible way in which microbial activity may be affected is by differential effects of human activities on plant species that associate with nitrogen-fixing bacteria, but there is no evidence of such effects in tropical forests. However, we speculate that in forests remaining near deforested areas the edge effect, which is known to increase tree falls and forest turnover rates, may indirectly affect microbial diversity through the creation of advancing fronts of secondary plant species, with leaf chemistry and litterfall characteristics different from those of the mature forest. Deforestation and fragmentation which threaten the entire guild of nitrogen-fixing microbes may directly affect productivity and nutrient cycling in tropical forests.

In mature forest patches, in comparison to gaps, plants grow slowly, use nutrients efficiently, and produce relatively low-quality litter that decomposes slowly and may deter litter herbivores. Gap pioneer species, in contrast, grow rapidly, produce comparatively more degradable litter, and are easier to use by litter feeders — thus enhancing rates of nutrient cycling (Hobbie 1992). In addition, positive feedbacks to nutrient cycling may arise due to species differences in carbon deposition and competition with microbes for nutrients in the rhizosphere.

6.1.2.9 Summary and relevance to human activities

Humans are impacting biodiversity in tropical systems primarily through forest destruction, largely for conversion to pastures, cropland and plantations. Current rates of habitat loss and associated species loss are higher in tropical regions than elsewhere in the world (Janzen 1988; Raven 1988; Whitmore and Sayer 1992). Reductions of intraspecific genetic diversity are poorly documented, but they are certainly taking place, perhaps at a very serious level. Other human activities that affect biodiversity and ecosystem functioning include water pollution and development projects such as dams, but the ecosystem consequences of such perturbations are poorly known. It is sometimes assumed that the profusion of species in tropical forests may compensate for the loss of some or many of

them. However, given the paucity of data on many critical aspects of the relationships between biodiversity and ecosystem processes, such an assumption is unwarranted and may be dangerous.

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- North and South America and on the islands of New Zealand and Tasmania. In Western Europe and in the eastern part of the United States and Canada, precipitation is equitably distributed as snow or rain throughout the year. In eastern Asia, under a monsoon climate, most of the precipitation falls in the summer. Along the Pacific coasts of North and South America, where the climate is more Mediterranean, precipitation occurs mainly during the winter months. The forests are dominated by deciduous and, to a lesser extent, evergreen broad-leaf and needle-leaf trees encompassing a potential area of about 18.6×10^6 km² (Melillo *et al.* 1993), more than 50% of which has been converted to cultivation (Matthews 1983). In total, more than 1200 tree species are represented. Differences in history since the Tertiary have caused large variations in tree diversity in the four regions. East Asia, in spite of extensive reduction in forest area, has six times as many species as North America, eight times more than Europe, and eighteen times more than Chile.

6.1.3.2 Productive capacity, biomass, decomposition and nutrient cycling

Human impacts on biodiversity. For centuries the temperate forest regions have experienced intensive human activity. The East Asian forests of China were the first to be largely cleared for agricultural development before 3200 BP (Teng 1927). Clearing followed much later in Europe, North America and much of the Southern Hemisphere (Perlin 1989). In addition, many native forests have been converted to plantations of a few species, largely represented by conifers. Human activities have affected biodiversity in forests to a lesser extent by introducing pests and pathogens, by creating air and water pollution, and by selectively harvesting various products (tree species, game animals, mushrooms and litter). If, through consumption of fossil fuels, humans induce predicted climatic change, the biodiversity of temperate forests as well as other biomes will be substantially altered (Peters and Lovejoy 1992).

Ecosystem consequences of impacts. A major consequence of clearing activities is a reduction in ecosystem carbon stores, in both biomass and soil organic matter. Globally, temperate forests today, although much smaller in extent than originally, are thought to be a net sink for carbon dioxide exchange (Tans *et al.* 1990). If so, this is mainly the result of faster growth rates associated with younger forests (Wofsy *et al.* 1993). The total biomass, both alive and in dead woody material, is much less in young forests than in older ones (Waring and Franklin 1979). Although biodiversity in plantations is usually reduced, growth rates are generally increased due to genetic selection and intensive management. Air and water pollution, pest and pathogens, and most harvesting practices tend to increase the rates at which minerals cycle

6.1.3 Temperate forest systems

6.1.3.1 Introduction

Temperate forest ecosystems of the mid latitudes occupy a climatic zone with pronounced variation in seasonal temperatures. Distribution is mainly in the Northern Hemisphere, in Europe, East Asia and eastern North America. In addition, representatives of this biome exist in a narrow band of rain forest along the Pacific coasts of

and nutrients are lost from the forest ecosystem. Genetic and species diversity is usually sufficient, however, for maintenance of net primary production, given time for re-establishment of a full canopy (Shugart and West 1977). Immediately following forest clearing the microbial system is able to sequester critical nutrients and prevent their loss by leaching (Vitousek and Matson 1985; Griffiths *et al.* 1994).

6.1.3.3 Soil structure and nutrient pools

Human impacts on biodiversity. Frequent disturbances associated with thinning and harvesting activities modify the surface litter and may compact the soil, which causes surface runoff and erosion from steep ground. The increasing use of fertilizers in forestry and agriculture, combined with nitrogen and sulphur in the atmosphere derived from consumption of fossil fuels, add to wet and dry deposition of these elements (Galloway *et al.* 1987). Unpaved roads create dust, and winds distribute calcium, potassium and other elements across wide areas (Hedin *et al.* 1994). Where ozone levels are high, and combine with atmospheric deposition of heavy metals, the recycling of nutrients through decomposition may be slowed, and may eventually limit the production of organic matter (Tyler 1972). Pests and pathogens, on the other hand, have fewer long-term effects and generally increase the rate at which minerals and nutrients cycle through soils (Waring and Schlesinger 1985).

Ecosystem consequences of impacts. The practice of clear-felling all the trees in a watershed temporarily increases the export of nutrients into groundwater, lakes and streams (Likens *et al.* 1978). Unless land is permanently cleared, however, the soil organic matter content is not substantially reduced (Gholz and Fisher 1982). The microbial system associated with shrubs and other vegetation may survive on dead roots and is usually sufficient to prevent immediate mobilization of critical nutrients (Vitousek and Matson 1985). In much of the temperate forest region, where forests are rarely clear-felled, wet and dryfall from air pollution acidifies soils and increases N and S pools. As a result, leaching of cations (Ca, Mg, K) is accelerated and seepage water is enriched in nitrogen (Schulze 1989). Even without atmospheric deposition, monocultures of evergreen species may acidify soils (Last and Watling 1991), although this depends on the type of soil, the species of evergreens (Speirs *et al.* 1986), and the presence of species that may cycle calcium or other elements from deeper soil horizons (Thomas 1959; Attiwell and Adam 1993).

6.1.3.4 Water distribution, balance and quality

Human impacts on biodiversity. Fragmentation of forests causes increased desiccation of canopies into the interior of remaining forests (Saunders *et al.* 1991; Chen *et al.* 1995).

As a result, epiphyte cover is reduced and less precipitation is intercepted by the canopy. Outbreaks of insect defoliators occur more regularly, causing a weakening of the surviving trees which reduces their flower and seed production, which in turn limits the number of vertebrates and invertebrates present. Replacement of deciduous forests with extensive plantations of evergreens increases stream-flow (Swift *et al.* 1975). A closed forest canopy along stream channels prevents the development of an algae-based food chain in the aquatic system (Triska *et al.* 1982). Where forests are frequently cut or where agricultural lands are intermixed with forests, surface and subsoil runoff to streams increases. The runoff carries with it soil, minerals, and often pesticide residues that degrade the stream habitat and reduce species diversity. As a result, spawning habitat for salmon, striped bass and other commercial and sport fisheries has been lost throughout much of the temperate forest region, and surviving populations of fish and other aquatic animals often carry high residues of pesticides.

Ecosystem consequences of impacts. Reduction in the leaf area of forests, and conversion to agricultural or urban development, greatly impact the way in which solar energy is dissipated. At full leaf area, a forest may transpire the equivalent of 3–5 mm water per day. Agricultural crops do not develop a full canopy until mid growing season and are harvested before the end of the normal growing season so that the total surface of foliage available for interception and evaporation is much reduced compared to forested conditions. Urban landscapes transpire or evaporate even less water. Peak storm flow increases following forest disturbance, causing flood damage downstream (Waring and Schlesinger 1985). The shorter stature of vegetation in fields and woodlands that replaces mature forests tends to make the surrounding area warmer (Kelliher *et al.* 1993). A major impact of forest removal is upon streams. Loss of shade increases water temperatures, and harvesting activities reduce the periodic addition to streams of large woody debris that creates pools and enhances the processing of dissolved and particulate organic matter. Increased erosion fills channels and allows silt to accumulate over gravels in which spawning fish lay their eggs. Acidification and pesticide residues further limit the ability of stream organisms to process organic matter and to remove harmful materials.

6.1.3.5 Feedbacks to atmospheric properties

Human impacts on biodiversity. Fragmented landscapes composed of deciduous woodlands, evergreen forests, fields and urban areas, absorb solar radiation differently from a uniform cover of vegetation. With generally less surface area in forest canopy, evaporative cooling is reduced and the meso-scale climate becomes less stable (Pielke *et al.* 1991). Dust and haze created by air pollutants

reduce incident solar radiation. Conversion to plantations of conifers increases the production of hydrocarbons by the vegetation (Chameides *et al.* 1988).

Ecosystem consequences of impacts. The presence of forest cover increases the surface area of exchange for the deposition of aerosols by up to 20 times that of bare ground while the loss of the forest canopy and its epiphyte community allows wider distribution of the aerosol load (Lindberg *et al.* 1986). Haze generated by compounds produced by trees or by human activities diffuses light and increases the efficiency of photosynthesis by plants. The concomitant reduction in solar radiation heats surfaces less and reduces respiration so that net ecosystem carbon balances may not be changed as much as otherwise predicted (Hollinger *et al.* 1994). Evergreen forests reflect less solar energy than deciduous forests (Goward *et al.* 1994). As a result, when separate blocks of deciduous and evergreen forests are present, heat islands develop, which increase afternoon thunderstorm activity (Nicholls *et al.* 1995). Snow that accumulates under evergreen forests will not reflect as much solar radiation as that deposited under deciduous canopies. The presence of snow may also lengthen the start of the growing season by delaying soil warming.

6.1.3.6 Landscape and waterscape structure

Human impacts on biodiversity. Agriculture, urbanization, road building and surface mining throughout temperate forest ecosystems have substantially altered landscape structure and diversity. The building of roads introduces corridors for the transportation of plants, insects and pathogens. Road construction also increases hillslope erosion, which reduces landscape diversity. The removal of forests along the floodplains reduces the capacity of the land to store water, which leads to more rapid runoff and excessive flooding when dam capacities are exceeded. The simplification and instability of floodplain vegetation are increased when unstable slopes are present in upper drainages. In total, the overall diversity of habitats is reduced across a drainage area when forests are fragmented or converted to other uses.

Ecosystem consequences of impacts. The net effect of reduced forest cover is accelerated transfer of soil, organic matter and water into streams, lakes and reservoirs, and because water carries high concentrations of nutrients, eutrophication of waterways results. The general effect is degradation and simplification of aquatic systems. Pollution, and the introduction of nonnative plants, insects and pathogens, make native forests less resilient and thus more sensitive to periodic disturbance and sustained nutrient losses. As a result, the productive capacity of the landscape may be degraded, and in extreme cases prevented from supporting forests (Schulze and Ulrich 1991).

6.1.3.7 Biotic linkages and species interactions

Human impacts on biodiversity. With increased commerce between continents, many insects and pathogens have been introduced into forests without co-evolved biotic controls. For example, virulent pathogens such as Dutch elm disease (*Graphium ulmi*) and chestnut blight (*Endothia parasitica*) have largely removed their respective host trees from the landscape in the eastern US. Gypsy moth (*Lymantria dispar*) and other introduced insects have also caused extensive damage. In addition, invasive plants such as Kudzu (*Pueraria lobata*), a nitrogen-fixing vine, have taken over many areas in the Southeastern USA and restricted the regeneration of forests. When European livestock were introduced into the New Zealand forests they destroyed much of the native vegetation, which was ill-adapted to browsing, and caused excessive compaction of the soil (Veblen and Stewart 1982). Air pollution has greatly reduced the epiphytic component of forest canopies (Hawksworth and Rose 1970) as has the conversion of old-growth forests to younger age classes (Sollins *et al.* 1980). More locally, where road systems are well developed, organisms are readily transported across natural boundaries, often without their biotic controlling agents. Pesticide applications to farmland and forests accumulate in food chains and are particularly harmful to raptors (Carson 1962), and reduction in forest cover, combined with bounty hunting and trapping, has caused the extinction of many large carnivores such as wolves, bears and mountain lions. Keystone species such as beaver and coyote have also been lost. Selective management of forests for particular sizes and types of trees has great consequence for the diversity of all species, as do policies for fire suppression, waste deposition and air pollution. The reduction in the area of forests, together with loss of tree species, has an especially hard impact on bird populations. Birds that migrate between temperate and tropical forests are most affected because they are losing habitat in both biomes (Wilcove 1990). Reduction in bird populations allows defoliating insects to reach epidemic population levels more frequently and thus further endangers the survival of some species of trees (Crawford and Jennings 1989; Mason *et al.* 1983).

Ecosystem consequences of impacts. Continual reduction in forest cover accentuates pollution, erosion and species extinction. Forests managed on short rotations limit diversity: fire protection, on the other hand, may lead to equally unstable conditions where multiple age classes of trees provide excessive accumulation of fuel. Thinning and salvage logging have an important role to play in such situations. Management may also ameliorate the effects of acid rain by liming soils and surface waters and by judicious tree harvesting, careful road construction, and expansion of land conservation policies. Some opportunities for organic matter recycling from urban areas

and agricultural fields into forests may buffer trends, but heavy metal concentrations and excessive applications of fertilizer lead to more polluted streams and ground water. Policies that favour fire protection often result in a change in species composition and a more fire-prone situation than normal. On the other hand, short cutting cycles or selective harvesting of the largest trees reduces habitat niches for many species of vertebrates and invertebrates while increasing the availability of forage for a few species of ungulates (Turner *et al.* 1994). Birds, butterflies and other species that migrate between temperate and tropical forests are particularly sensitive because losses of habitat are occurring in both types of forests. The loss of keystone animals such as beaver and coypu from most of the temperate forests has reduced the area of wetlands and the availability of habitat for fish, birds and other animals. Loss of large carnivores allows populations of ungulates to oscillate more widely, resulting in selective removal of more palatable deciduous shrubs and trees unless hunting pressures are increased accordingly. If headwater forests, floodplain woods and adjacent wetlands can be protected in corridors, some buffering may be provided against erosion and the eutrophication of water bodies, even with expanded use of other lands.

6.1.3.8 Microbial activities

Human impacts on biodiversity. Most temperate forest ecosystems have a large capacity to store nitrogen, but chronic additions may lead to saturation (Aber *et al.* 1994). Deposition of heavy metals in sewage sludge or from atmospheric sources represents an increasing problem near urban areas. Increases in the evergreen component of forests changes the quality of litter for microbial activity, while removal of the litter for bedding, as was done in Europe for centuries, leads to impoverished substrates. Atmospheric additions of S and N encourage microbial activity that converts these elements to gases. At the same time, other functional groups of microbes may be lost, such as N-fixing bacteria and many fungi adapted to low levels of nutrients.

Ecosystem consequences of impacts. Increased enrichment with nitrogen and sulphur may not enhance microbial decomposition if the carbon substrate is inappropriate, particularly if symbiotic fungi (mycorrhizae) become less active on the roots of trees and other plants. On the other hand, denitrification and trace gas production of sulphur compounds is enhanced (Aber *et al.* 1994) unless heavy metal concentrations are sufficient to limit microbial activity. Loss of earthworms due to compaction and acidification reduces mixing and will further limit decomposition rates. Global increases in atmospheric CO₂, however, may result in more carbon being allocated by plants to mycorrhizal fungi, which should enhance nutrient mobilization in the rooting zone. Concomitant changes in

climate may completely alter forest composition and distribution (Neilson and Marks 1994).

6.1.3.9 Summary and relevance to human activities

The dominant effect of human activity on temperate forest ecosystems has been their conversion to agricultural use. Large plantations of single species of conifers and hardwoods, combined with more frequent harvesting, exert a major impact on ecosystem functioning and biodiversity. In the last half-century, air pollution has changed the properties of the atmosphere and precipitation, and this has resulted in the removal of some species, alterations in nutrient cycling, and the creation of ecosystems more susceptible to outbreaks of insects and diseases. Loss of some keystone species and the introduction of others further destabilize temperate forest ecosystems. The full impact of changes in the chemical composition of the atmosphere induced by human activity is not known but if climatic conditions change rapidly, as they are predicted to do, we would expect forests composed of long-lived trees, typically with infrequent seed production, to be particularly vulnerable, along with the complex food chains they support. As a result, we predict largely negative consequences on biodiversity, net primary production, and net ecosystem production with rapid climate change.

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6.1.4 Arid and semi-arid lands

6.1.4.1 Introduction

In arid lands, water availability (precipitation vs. evaporative demand) imposes severe constraints on biological activity. Precipitation is characterized by unpredictability in time and space as well as by low total amounts (Noy-Meir 1973). Semi-arid ecosystems differ from true arid areas in structure and in the rate and regulation of ecosystem processes. We differentiate between these two, and highlight cases of conversion from semi-arid to arid lands (desertification; Verstraete and

Schwartz 1991). Biodiversity, reflected in species richness, is moderately high in semi-arid regions and declines with increasing aridity for most taxa (Shmida 1985; Pianka and Schall 1981; O'Brien 1993). Certain taxa are diverse relative to other biomes (e.g. predatory arthropods, ants and termites, grasshoppers, snakes and lizards, rodents, annual plants), but there is substantial variation in the richness of particular taxa among the deserts of different continental areas. The abundance and activity of desert organisms are 'pulsed' in correspondence with episodes of high moisture availability (Noy-Meir 1973; Louw and Seely 1982); while the prevalence of dormancy, cryptobiosis, aestivation and other modes of escaping harsh conditions means that most of the biodiversity of arid regions can be impossible to census or sample during most time periods.

6.1.4.2 Productive capacity, biomass, decomposition and nutrient cycling

Human impacts on biodiversity. Human activity has caused changes in the biodiversity of arid lands primarily through the use of arid and semi-arid systems for grazing of livestock. Introductions of domestic and game animals have altered the character and the magnitude of animal consumption (Oesterheld *et al.* 1992), and these have been accompanied by creation of water points, introduction of non-native plants, and removal of predators and of burrowing and herbivorous animals seen as threats to livestock. Plant species diversity decreases when the local extinction of grazing- or trampling-sensitive species exceeds the establishment of new grazing-tolerant or weedy species (Westoby *et al.* 1989; Milchunas and Lauenroth 1993); after a time lag, loss of native plant species may result in a loss of animal taxa (Jones 1981; Jepson-Innes and Bock 1989; Heske and Campbell 1991). In some regions the intensive cultivation of irrigated croplands has eliminated large portions of native ecosystems (Jackson *et al.* 1991).

Ecosystem consequences of impacts. In North America and Africa, semi-arid grasslands have often been converted to shrublands by grazing and by the dispersal of shrub seeds by livestock (e.g. Peinetti *et al.* 1993), leading to a different structure and display of biomass as well as altered species composition (Schlesinger *et al.* 1990). Production will be reduced if grazers remove leaf area and cause an increase in the proportion of water lost to evaporation, rather than being used by plants. However, net primary productivity or NPP (the amount of plant material produced by photosynthesis per unit area over a time period) is not necessarily changed by changes in plant species composition induced by grazing (Milchunas and Lauenroth 1993). Decreases in NPP are most pronounced where there has been no long evolutionary history of intense grazing (Milchunas and Lauenroth 1993). Some semi-arid and arid ecosystems comprise diverse assemblages of different plant

growth forms, physiologies and life histories, which form distinct guilds with respect to water use because of correlations among morphological, phenological and physiological traits (e.g. Golluscio and Sala 1993). Where the members of a guild (e.g. perennial grasses using shallow water during the hot season) respond similarly to a disturbance (e.g. are all grazing-sensitive), the elimination of that functional group will have direct influences on the structure and functioning of the ecosystem. In addition, the importance of macro-organisms in determining microbial populations (Gallardo and Schlesinger 1992) means that removal of plants or alteration of the distribution and abundance of plant roots will alter the pool and rates of activity of decomposers, thus altering rates of decomposition as well as of organic matter inputs. Termites and nest- or burrow-building mammals provide micro-environments that enhance decomposition and nutrient cycling. Their removal by humans has the potential to slow decomposition and increase the chances of loss or transport of nutrients from the surface (Whitford 1991).

Conversion of semi-arid or arid lands to agriculture (usually by irrigation) may increase local NPP values, but the effects on biodiversity are severe. Native plant communities are displaced, and are notoriously difficult to restore after cessation of cultivation (Jackson *et al.* 1991). In India the birds of semi-arid regions have proved especially likely to disappear following cultivation and fragmentation of native habitats (Daniels *et al.* 1990). It is not clear how human activities have altered the role that fire plays in semi-arid regions. In some places fires may have maintained semi-desert grassland, suggesting that grazing (causing the reduction of fuel loads) and fire suppression have contributed to the conversion of grasslands to shrublands. However, in other systems the perennial grasses appear to be more sensitive to fire than the woody plants (Wright 1980), and there is no clear guideline for the use of fire in maintaining grassland or manipulating species composition (Bock and Bock 1992).

6.1.4.3 Soil structure and nutrient pools

Human impacts on biodiversity. Introduction of hoofed livestock to regions lacking a recent evolutionary history of ungulate grazing (e.g. Australia, southwestern North America) has been the primary human effect on the biodiversity of semi-arid regions. This has been accompanied by reduction of populations of native burrowing herbivores (e.g. North American prairie dogs, Australian marsupials), thus reducing the soil-disturbing activities of these animals.

Ecosystem consequences of impacts. The introduction of large hoofed animals to regions previously lacking them has caused changes in the compaction of soil, reducing infiltration (Roundy *et al.* 1992), while also churning up dry surface soil and increasing its vulnerability to erosion.

Vegetation influences the 'roughness' of the surface, which in turn influences the movement and erosive power of wind and water (e.g. Abrahams *et al.* 1994); thus the activities of livestock (or humans) have direct influences on the rates of erosion of surface layers. Erosion and transport of surface soil particles will in turn influence the transport and loss of mineral nutrients from the site (Schlesinger *et al.* 1990). The soil-binding properties of plant roots are especially critical in dunes, where species that can stabilize sediments serve a critical role in determining ecosystem structure (e.g. Klopatek and Stock 1994). Harvesting or loss of these species may shift a stable substrate (offering habitat for plant and animal populations) to a much harsher migrating dune system. Disruption of a microbial 'crust' on the soil surface (e.g. by hooves) alters inputs of nitrogen by these N-fixers (see 6.1.4.8). Burrowing animals (termites, ants, rodents, marsupials) create and reinforce heterogeneity in soil structure and nutrients (Whitford 1993).

6.1.4.4 Water distribution, balance and quality

Human impacts on biodiversity. Human and livestock activity have altered plant species composition and vegetation cover in many regions, both by reducing native vegetation and by introducing non-native species, either deliberately or accidentally. Aquatic habitats (riparian zones, springs) have been especially vulnerable to invasions of non-native plants. Populations of burrowing organisms have also been reduced. Road construction and other activities have altered drainage patterns, with resulting changes in water distribution and hydrologic regimes: these changes then impact the distribution and behaviour of organisms.

Ecosystem consequences of impacts. Vegetation cover modulates the impact energy of raindrops, reducing the amount of sediment dislodged and transported during heavy storms (Wood *et al.* 1987; Rogers and Schumm 1991). Rooted plants provide root channels which in turn enhance deep percolation of water into the soil profile (e.g. Greene 1992), and the nature of the plant canopy influences the proportion of rainfall that is intercepted and that falls either as throughfall or stem-flow (West and Gifford 1976; Navar and Bryan 1990; Tromble 1987). Deep roots of shrubs, and transpirational losses, are a strong influence on soil water content in the lower parts of the soil profile and thus on the depth of carbonate deposition, leading potentially to alterations in the effective rooting depth of the soil (Schlesinger *et al.* 1987). Removal of shrubs would then be expected to have potentially strong effects on soil moisture content and other characteristics. On the other hand, Dugas and Mayeux (1991) and Carlson *et al.* (1990) found that increased herbaceous cover following shrub removal resulted in little net change in water distribution or in total evapotranspiration from dry rangeland sites over the short term. Introduction of phreatophytic (deep-rooted)

plants, especially the genus *Tamarix*, has dramatically altered hydrology in some riparian systems (Blackburn *et al.* 1982), even leading to the elimination of surface water from previous spring sites due to its high evapotranspiration). Reduction in populations of termites (small burrowing animals) has a dramatic influence on infiltration and surface runoff (Elkins *et al.* 1986).

6.1.4.5 Feedbacks to atmospheric properties

Human impacts on biodiversity. At the global scale, human activity is expressed primarily through direct and indirect alterations of vegetation cover and disturbance of the soil surface.

Ecosystem consequences of impacts. Vegetation cover is negatively associated with albedo. Arid lands are significant determinants of the Earth's overall albedo (Otterman 1989) and thus of its global radiation balance. Arid lands are also significant contributors of dust, and reductions in vegetation cover caused by grazing or other human activity (e.g. roads) increase these contributions (Pewe 1981; Pye 1987). While it has been proposed that arid-zone termites contribute substantial amounts of methane to the atmosphere, recent work suggests that arid regions are actually a significant sink for methane (Striegl *et al.* 1992). Conversion of semi-arid grassland to shrubland or woodland may increase carbon storage, affecting the global carbon cycle (McPherson *et al.* 1993).

6.1.4.6 Landscape structure

Human impacts on biodiversity. Human alterations to semi-arid landscapes are generally to facilitate grazing by livestock: they include fencing of pastures or paddocks, creation of new water points for animals, and construction of roads or trails for transport. Human and livestock activity often creates gradients of disturbance or of alteration (a 'variegated' landscape), rather than the conspicuously patchy or fragmented nature of landscapes in other ecosystem types (McIntyre and Barrett 1992).

Ecosystem consequences of impacts. Creation of new watering points has perhaps increased local rates of NPP. Conversely, disruption of normal drainage patterns (e.g. by road construction or by diversion of water) alters the hydrology of intermittent streams and playas, and decreases the productivity of vegetation dependent on that water flow (Schlesinger and Jones 1984).

6.1.4.7 Biotic linkages and species interactions

Human impacts on biodiversity. Importation of non-native plants for improvement of forage or as weeds in some regions has reduced local plant diversity by replacing native species. Humans have attempted direct removals of plant species considered to be undesirable forage species (e.g. large-scale removals of native shrubs in southwestern US rangelands). Populations of some tree species in semi-

arid regions have been depleted by heavy use for fuel or other purposes. Populations of native mammals have been reduced either intentionally, when these are viewed as competitors for forage or as possible predators of livestock, or indirectly, e.g. through the effects of insecticide use on bat populations.

Ecosystem consequences of impacts. Alteration of native to non-native grass cover has apparently reduced populations of native ants and other consumers in Arizona (Whitford, pers. comm.). There is also some evidence that declining bat populations in the southwestern states of the USA have led to decreased frequency of effective pollination in some bat-pollinated monocarpic species of *Agave* (Howell and Roth 1981). Many biotic interactions in arid lands are less direct, however, resulting from the modification or modulation of the harsh environment by one species in such a fashion as to facilitate the occurrence or reproduction of other organisms. Among plants this facilitation is described as the 'nurse plant' phenomenon. The regeneration of one species under another might create a cyclic replacement or successional series (McAuliffe 1988; Yeaton and Esler 1990; Gutierrez *et al.* 1993): there are many reports that the presence of one plant species creates a specific environment that facilitates the establishment of other particular species (e.g. Montaña 1992; Silvertown and Wilson 1994). The loss of large woody species for use as fuel or as carving material has been suggested as a negative influence on the persistence of many typical species of desert plants (e.g. Franco and Nobel 1989). Introductions of large animals (as game or livestock) have often established wild or feral populations (horses, camels, oryx) that affect native vegetation and compete with native herbivores.

6.1.4.8 Microbial activities

Human impacts on biodiversity. The most prominent and conspicuous arena of microbial activity is the formation of crusts on the soil surface by algae, cyanobacteria and lichens (Isichei 1990; West 1990). Introduction of hooved grazers has reduced the prevalence and development of these crusts in many regions (West 1990).

Ecosystem consequences of impacts. Microbial crusts play significant roles in nitrogen cycling and in stabilizing the soil surface against erosion (Eldridge and Greene 1994). In some cases these microbes secrete polysaccharides that absorb water, increasing the effective infiltration of precipitation; in other cases the secretions are actually hydrophobic, reducing soil wetting. Reductions in soil crusts are assumed to have reduced nitrogen fixation, increased soil erosion, and altered local infiltration of moisture.

6.1.4.9 Summary and relevance to human activities

Human alterations of biodiversity in desert regions have been mediated chiefly by the management of semi-arid and

arid regions for livestock use and by the importation of non-native plants. Arid regions are a reservoir of genetic variation useful for the development of new crops and new varieties of existing crops better suited to agriculture in marginal environments (e.g. Glenn *et al.* 1991). Because biological activity plays such an important role in moderating the harsh environment of arid regions, alteration of biodiversity is expected to have negative feedbacks on the remaining biological components of the system. These feedbacks lead to the formation of alternative stable states of the system, with stronger control by abiotic forces (Schlesinger *et al.* 1990), and the necessity for management strategies focused on transitions between states (Westoby *et al.* 1989).

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ungulates graze seasonally in grasslands with a high proportion of nutritious species. These plant species assemblages are more likely to occur in grasslands of higher diversity, and therefore support more herbivores (Ben-Shahar and Coe 1992). Diverse natural grasslands seem to be more resilient to drought-induced changes in productivity than simplified systems developed through long-term fertilization (Frank and McNaughton 1991; Tilman and Downing 1994). Changes in biodiversity in Australian and South American savannahs have affected biogeochemical cycles leading to habitat and landscape deterioration. The planting of exotic grasses with high production capacity is frequently followed by a reduction in yield and quality of forage due to slower mineralization of humic material and turnover of nitrogen in plant residues with high lignin:nitrogen ratios, and the gradual loss of nitrogen from animal excreta (Holmes and Mott 1993; Klink *et al.* 1993).

6.1.5.4 Soil structure and nutrients

Introduction of African grasses into South American and Australian savannahs increases biomass production per unit area, allowing larger numbers of cattle to be grazed per unit of land. Higher cattle density reduces soil permeability and vegetation cover, and leads to increased runoff and erosion (Mott *et al.* 1979; Seiny-Boukar 1992). Grazing-intolerant native grasses are being replaced by faster growing, invasive grasses (Mott *et al.* 1979; Holmes and Mott 1993). In dry years overgrazing destroys the grassland allowing the penetration of woody weeds, and resulting in extended erosion (Winter 1990). Exclusion of large herbivores in East Africa reduced overgrazing and resulted in tree regeneration and a significant increase in soil fertility (Hatto and Smart 1984), while introduction of legumes improved nitrogen availability in Australian grasslands (Henzell 1968; Myers and Robbins 1991). Higher palatability of legumes, and patchy distribution in pasture, leads to increased trampling and soil deterioration strongly affecting pasture productivity in the short term (Mott *et al.* 1979).

6.1.5.5 Water distribution, balance and quality

Large-scale agricultural utilization of savannahs either changes the composition of primary producers (native grasses are substituted by alien grasses and legumes for intensified cattle production), or eliminates the plant cover for planting of cash crops (soybean, peanuts, sugar cane, etc.). In both cases savannah soils require a heavy input of fertilizers leading to long-term impacts on water quality (pollution of underground water resources and rivers) (Mott *et al.* 1979; Gillard *et al.* 1989; Seiny-Boukar *et al.* 1992).

6.1.5.6 Atmospheric properties

Periodic burning of savannah landscapes reduces tree/grass ratios (Medina and Silva 1990) and has implications for

atmospheric chemistry (Lobert *et al.* 1990). There are potential strong feedbacks between the species composition of grasslands and nitrogen cycling. Grass species differ in below-ground biomass accumulation and tissue-nitrogen and lignin concentrations, and these factors affect nitrogen mineralization rates (Wedin and Tilman 1990). Grass species also differ in their nitrogen requirements depending on their mode of photosynthetic C4 pathway. Malate formers seem to require less nitrogen and have lower tissue-nitrogen concentration, while aspartate formers require more nitrogen and are more palatable (Huntley 1982). The relative proportion of these photosynthetic types may therefore affect nitrogen losses through fire and the rate of nitrogen mineralization in soils. Changes in soil nitrogen availability modify substantially the relative proportion of malate and aspartate formers in South African grasslands (Medina and Huber 1992). The rapid transition from *miombo* woodland and savannah to maize-based agriculture in southern Africa results in an almost complete loss of ecosystem carbon pools. Clearing of the *miombo* and establishment of maize-based agriculture on a sandy alfisol resulted in a decline in total soil organic carbon from 28 to 9 Mg/ha (Woomer 1993).

6.1.5.7 Landscape and waterscape structure

Habitat heterogeneity determined by the co-occurrence of trees and grasses in savannahs is considered to be a key factor for the maintenance of their biodiversity (Gillard *et al.* 1989; Holmes and Mott 1993). Utilization of savannah lands for grazing has modified their original fire regimes. Natural savannah fires have a low frequency because they depend on the occurrence of dry electrical storms, but fire frequency has been increased under human influence in order to prevent excessive fuel accumulation and to provide green forage for cattle during the dry season. As a result, tree/grass ratios have changed markedly. Trees are more sensitive to fire than grasses, because the latter accumulate most of their biomass and nutrient resources below ground. High fire frequency reduces the number of tree species, and the numbers of individuals per species in most savannah sites (San José and Fariñas 1991; Dauguet and Menaut 1992).

6.1.5.8 Biotic linkages and species interactions

The co-occurrence of trees and grasses in savannahs results in patchiness of resource availability. Changes in tree/grass ratios significantly modify rates of biogeochemical and energy cycling as a result of the contrasting characteristics of the two components with respect to light interception and nutrient requirements (Kellman 1979; Georgiadis 1989; Ben-Shahar 1991; Isichei and Muoghalu 1992; Belsky *et al.* 1993; Mordelet *et al.* 1993). The recent human population explosion in Africa, and the migratory constraints imposed by political boundaries, increased the occupation of land with a consequent restriction of the

ranges of wild animals. Most of the formerly wooded southern section of the Murchison Falls National Park (Uganda), c. 2600 km², has been converted from woodland into grassland (Hatton and Smart 1984). Numbers of elephants in Tsavo National Park increased dramatically after the Second World War as a result of the enforcement of anti-poaching activities, and the consequent overpopulation of elephants resulted in habitat deterioration, particularly along waterways. Under the influence of elephants and fire the dry *Commiphora-Acacia* bush has been destroyed over large areas and replaced by grassland (Laws 1970; Owen-Smith 1988). In the same area, a long-term experiment excluding herbivory by large ungulates resulted in a marked tree regeneration, and a pronounced increase in soil fertility (Hatton and Smart 1984).

Vegetation-herbivore interactions are highly varied. In eastern Africa herbivory patchiness can be associated with nutritional quality of the forage, but also grazing animals can modify plant nutritional properties through their influence on soil nutrient availability and plant species composition (McNaughton 1985; Georgiades and McNaughton 1990). Although savannahs of northern Australia and South America evolved in conjunction with herbivore pressure, their herbivore megafauna disappeared in the Pleistocene (Martin 1973). Europeans introduced several medium- and large-sized herbivore species, in numbers comparable to those of native herbivores elsewhere. In Australia, due to the lack of predators and pathogens, the density of feral populations of introduced herbivores is much larger than in their original habitats, and the high density of herbivores has led to ecosystem deterioration (Freeland 1990). Mutualistic relationships in Australian ecosystems have frequently evolved presumably in response to low resource availability. Australasian woody plants produce copious quantities of nectar, and this has had a pronounced effect on the fauna. Forty-two percent of the honey-eater species of the family Meliphagidae occur in Australia, and most of the rest are found in New Guinea (Braithwaite 1990). The potential damage for tree reproduction following reductions in honey-eaters' diversity is large. Pasture improvement and tree clearances have produced substantial reductions in the number and frequency of native herbaceous species, but also of bird species and soil invertebrates (Greenslade 1992). Thinning of bird populations has been associated with the spread of eucalyptus dieback (rural dieback) caused by more intensive defoliation by insect herbivores.

6.1.5.9 Microbial activities

Mycorrhizae play an important role in nutrient uptake, and possibly also water uptake, by vascular plants. C₄ plants in nutrient-poor soils appear to be more dependent on mycorrhizal symbiosis than are C₃ plants (Hetrick *et al.*

1990), both at the seedling stage and during regrowth from rhizomes. Mycorrhizal abundance in grasslands is generally inversely related to soil fertility and positively related to the ratio of plant to soil nutrient contents (McNaughton and Osterheld 1990). Therefore, mycorrhizal associations are thought to stabilize ecosystem nutrient fluxes. The semi-arid savannahs in Botswana (rainfall 500 mm) have been degraded by overgrazing, so restoration depends on the probability of inoculation of seedlings' roots (Veenendaal *et al.* 1992). Populations of mycorrhizae in the soil can be managed by the introduction of spores of species differing in their host selectivity and efficiency in phosphorus uptake capacity (Dodd *et al.* 1990). Changes in ecological conditions leading to modifications in the mycorrhizal fungi may result in disturbances of the phosphorus availability for native grasses. Introduction of legumes improves nitrogen supply to the vegetation through symbiotic nitrogen fixation (Henzell 1968). Plant growth in eastern African grasslands induced by rainfall events is accompanied by strong pulses of microbial activity, and the concentration of large herbivores attracted by the green foliage. Therefore, soil microbial activity is closely correlated with patterns of herbivore use and intensity of herbivory in natural grasslands of eastern Africa (Ruess and Seagle 1994).

6.1.5.10 Summary and relevance to human activities

Savannah ecosystems have been profoundly modified throughout human history. Most modifications are related to overpopulation and mismanagement of natural resources. Reductions in landscape, community, and species diversity have affected ecosystem functioning as expressed by habitat deterioration and diminished capacity of savannah environments to support human populations. Erosion, pollution of water sources, reductions in soil fertility and diminished carrying capacity for herbivores are some of the ecological consequences relevant for the continued use of these environments. Restoration of ecosystem functioning through the recovery of biodiversity is an essential step in the planning of sustainable use of savannahs.

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- between species but also between biogeographic provinces of major plant species (Bryant *et al.* 1989, 1994). Tissue chemistry controls decomposition and nutrient availability, palatability and flammability (Bryant and Chapin 1986; Pastor and Mladenoff 1992; Pastor and Naiman 1992) and is correlated with life form, growth rates and longevity (Chapin 1986; Bryant and Chapin 1986).

6.1.6.2 Human-induced impacts and threats to biodiversity

Increased atmospheric loadings of radiatively active gases, with consequent warming of the climate, and logging are the two human activities with great consequences for changes in biodiversity and ecosystem properties in boreal regions over the next several decades. Initially, these societal impacts will alter the diversity of tree species. Because of the couplings between tree species, food web structure, nutrient cycling and the atmosphere, these changes in tree species composition ramify throughout the ecosystem and biome. The probability of climate warming and increased logging over the next several decades is high, but the ecosystem effects of these impacts are greatly conditioned by the functional group affected and local conditions. Human-induced changes in biodiversity in boreal regions therefore introduce high variance in ecosystem properties at local and regional scales.

6.1.6.3 Productive capacity, biomass and decomposition

Human impacts on biodiversity. Global warming will cause differential migration of tree species northward from the boreal zone into the tundra, and from grasslands and northern hardwood areas into areas currently occupied by boreal trees (Pastor and Post 1988; Davis and Zabinski 1992; Pastor and Johnston 1992). Logging in the boreal forest generally consists of clear-cutting or plantation establishment. Clear-cutting alone perpetuates early successional forests dominated by shade-intolerant hardwoods, but with generally high species richness, while plantations consist mainly of monocultures of conifers (Mladenoff and Pastor 1993; Haila 1994).

Ecosystem consequences of impacts. As the climate warms, the differential migration of tree species changes productivity, biomass and decomposition (Payette *et al.* 1985; Pastor and Post 1988; Bonan *et al.* 1990; MacDonald *et al.* 1993). The direction of change depends on the local distribution of soil types. On sandy soils in mid-continental regions south of the permafrost line, drought stress will increase and the boreal forest will be replaced by a jack pine-oak savanna of low productivity and slow decomposition. On clay soils that can retain water, the boreal forest will be replaced by northern hardwoods of higher productivity and decomposition rates (Pastor and Post 1988). In far northern regions, the local distribution of permafrost affects how ecosystems respond to climate warming because of differential sorting of species (Bonan

6.1.6 Boreal forests

6.1.6.1 Introduction

The boreal forest is a circumpolar biome covering approximately $13 \times 10^6 \text{ km}^2$ in upland forest and $2.6 \times 10^6 \text{ km}^2$ in peatland in North America and Eurasia (Olson *et al.* 1983; Shugart *et al.* 1992; Apps *et al.* 1993). Although ecosystems in this biome are generally species-poor, many species respond to and affect resource availability, food supply for herbivores, and disturbance regimes in very different ways (Bryant and Chapin 1986; Payette 1992; Pastor and Mladenoff 1992). Functional diversity is therefore high, but each functional group is represented by only a few species. These strong feedbacks between species life traits, resources and disturbance regimes may in turn cause cyclic fluctuations in populations of animals (Hansson 1979; Haukioja *et al.* 1983). Plant tissue chemistry integrates biodiversity with ecosystem properties. Tissue chemistry varies not only