

Consequences of changing biodiversity

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Human alteration of the global environment has triggered the sixth major extinction event in the history of life and caused widespread changes in the global distribution of organisms. These changes in biodiversity alter ecosystem processes and change the resilience of ecosystems to environmental change. This has profound consequences for services that humans derive from ecosystems. The large ecological and societal consequences of changing biodiversity should be minimized to preserve options for future solutions to global environmental problems.

Humans have extensively altered the global environment, changing global biogeochemical cycles, transforming land and enhancing the mobility of biota. Fossil-fuel combustion and deforestation have increased the concentration of atmospheric carbon dioxide (CO₂) by 30% in the past three centuries (with more than half of this increase occurring in the past 40 years). We have more than doubled the concentration of methane and increased concentrations of other gases that contribute to climate warming. In the next century these greenhouse gases are likely to cause the most rapid climate change that the Earth has experienced since the end of the last glaciation 18,000 years ago and perhaps a much longer time. Industrial fixation of nitrogen for fertilizer and other human activities has more than doubled the rates of terrestrial fixation of gaseous nitrogen into biologically available forms. Run off of nutrients from agricultural and urban systems has increased several-fold in the developed river basins of the Earth, causing major ecological changes in estuaries and coastal zones. Humans have transformed 40–50% of the ice-free land surface, changing prairies, forests and wetlands into agricultural and urban systems. We dominate (directly or indirectly) about one-third of the net primary productivity on land and harvest fish that use 8% of ocean productivity. We use 54% of the available fresh water, with use projected to increase to 70% by 2050¹. Finally, the mobility of people has transported organisms across geographical barriers that long kept the biotic regions of the Earth separated, so that many of the ecologically important plant and animal species of many areas have been introduced in historic time^{2,3}.

Together these changes have altered the biological diversity of the Earth (Fig. 1). Many species have been eliminated from areas dominated by human influences. Even in

preserves, native species are often out-competed or consumed by organisms introduced from elsewhere. Extinction is a natural process, but it is occurring at an unnaturally rapid rate as a consequence of human activities. Already we have caused the extinction of 5–20% of the species in many groups of organisms (Fig. 2), and current rates of extinction are estimated to be 100–1,000 times greater than pre-human rates^{4,5}.

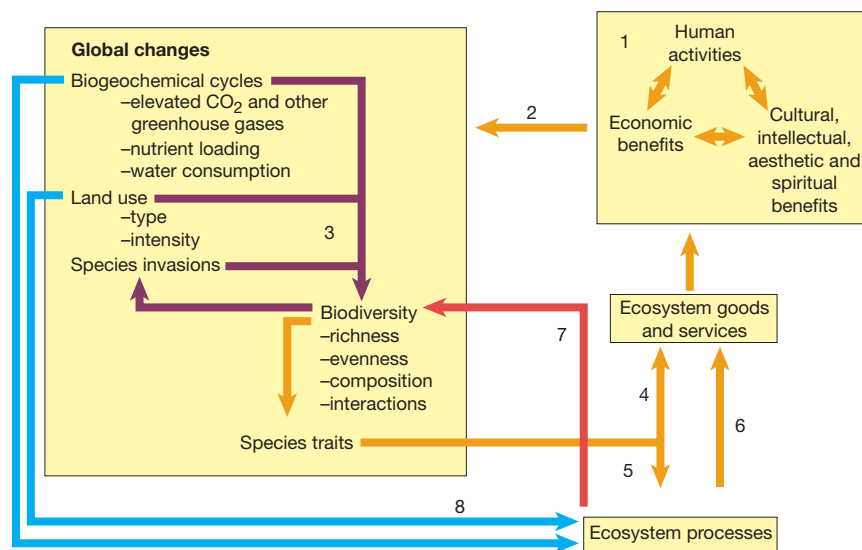
In the absence of major changes in policy and human behaviour, our effects on the environment will continue to alter biodiversity. Land-use change is projected to have the largest global impact on biodiversity by the year 2100, followed by climate change, nitrogen deposition, species introductions and changing concentrations of atmospheric CO₂ (ref. 6). Land-use change is expected to be of particular importance in the tropics, climatic change is likely to be important at high latitudes, and a multitude of interacting causes will affect other biomes (Fig. 3)⁶. What are the ecological and societal consequences of current and projected effects of human activity on biological diversity?

Ecosystem consequences of altered diversity

Diversity at all organizational levels, ranging from genetic diversity within populations to the diversity of ecosystems in landscapes, contributes to global biodiversity. Here we focus on species diversity, because the causes, patterns and consequences of changes in diversity at this level are relatively well documented. Species diversity has functional consequences because the number and kinds of species present determine the organismal traits that influence ecosystem processes. Species traits may mediate energy and material fluxes directly or may alter abiotic conditions (for example, limiting resources, disturbance and climate) that regulate process rates. The components of species diversity that determine this expression of traits include the number of species present (species richness), their relative abundances (species

Figure 1 The role of biodiversity in global change.

Human activities that are motivated by economic, cultural, intellectual, aesthetic and spiritual goals (1) are now causing environmental and ecological changes of global significance (2). By a variety of mechanisms, these global changes contribute to changing biodiversity, and changing biodiversity feeds back on susceptibility to species invasions (3, purple arrows; see text). Changes in biodiversity, through changes in species traits, can have direct consequences for ecosystem services and, as a result, human economic and social activities (4). In addition, changes in biodiversity can influence ecosystem



processes (5). Altered ecosystem processes can thereby influence ecosystem services that benefit humanity (6) and feedback to further alter biodiversity (7, red arrow). Global changes may also directly affect ecosystem processes (8, blue arrows). Depending on the circumstances, the direct effects of global change may be either stronger or weaker than effects mediated by changes in diversity. We argue that the costs of loss of biotic diversity, although traditionally considered to be 'outside the box' of human welfare, must be recognized in our accounting of the costs and benefits of human activities.

evenness), the particular species present (species composition), the interactions among species (non-additive effects), and the temporal and spatial variation in these properties. In addition to its effects on current functioning of ecosystems, species diversity influences the resilience and resistance of ecosystems to environmental change.

Species richness and evenness

Most theoretical and empirical work on the functional consequences of changing biodiversity has focused on the relationship between species richness and ecosystem functioning. Theoretical possibilities include positive linear and asymptotic relationships between richness and rates of ecosystem processes, or the lack of a simple statistical relationship⁷ (Box 1). In experiments, species richness correlates with rates of ecosystem processes most clearly at low numbers of species. We know much less about the impact of species richness in species-rich, natural ecosystems. Several studies using experimental species assemblages have shown that annual rates of primary productivity and nutrient retention increase with increasing plant species richness, but saturate at a rather low number of species^{8,9}. Arbuscular

mycorrhizal species richness also seems to enhance plant production in an asymptotic fashion, although phosphorus uptake was enhanced in a linear fashion from 1 to 14 species of fungi¹⁰. Microbial richness can lead to increased decomposition of organic matter¹¹. In contrast, no consistent statistical relationship has been observed between plant species richness of litter inputs and decomposition rate¹². Thus, in experimental communities (which typically focus on only one or two trophic levels), there seems to be no universal relationship between species richness and ecosystem functioning, perhaps because processes differ in their sensitivity to species richness compared with other components of diversity (such as evenness, composition or interactions). The absence of a simple relationship between species richness and ecosystem processes is likely when one or a few species have strong ecosystem effects.

Although the relationship of species richness to ecosystem functioning has attracted considerable theoretical and experimental attention because of the irreversibility of species extinction, human activities influence the relative abundances of species more frequently than the presence or absence of species. Changes in species evenness warrant increased attention, because they usually respond more rapidly to human activities than do changes in species richness and because they have important consequences to ecosystems long before a species is threatened by extinction.

Species composition

Particular species can have strong effects on ecosystem processes by directly mediating energy and material fluxes or by altering abiotic conditions that regulate the rates of these processes (Fig. 4)^{13,14}. Species' alteration of the availability of limiting resources, the disturbance regime, and the climate can have particularly strong effects on ecosystem processes. Such effects are most visible when introduced species alter previous patterns of ecosystem processes. For example, the introduction of the nitrogen-fixing tree *Myrica faya* to nitrogen-limited ecosystems in Hawaii led to a fivefold increase in nitrogen inputs to the ecosystem, which in turn changed most of the functional and structural properties of native forests¹⁵. Introduction of the deep-rooted salt cedar (*Tamarix* sp.) to the Mojave and Sonoran Deserts of North America increased the water and soil solutes

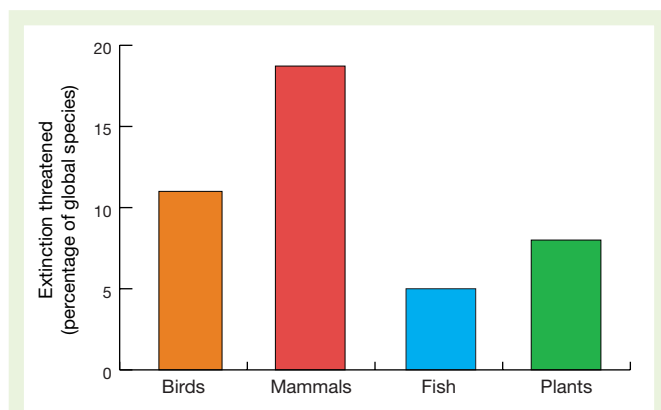


Figure 2 Proportion of the global number of species of birds, mammals, fish and plants that are currently threatened with extinction⁴.

Box 1

Species richness and ecosystem functioning

There has been substantial debate over both the form of the relationship between species richness and ecosystem processes and the mechanisms underlying these relationships⁶⁵. Theoretically, rates of ecosystem processes might increase linearly with species richness if all species contribute substantially and in unique ways to a given process — that is, have complementary niches. This relationship is likely to saturate as niche overlap, or ‘redundancy’, increases at higher levels of diversity⁶⁶. Several experiments indicate such an asymptotic relationship of ecosystem process rates with species richness. An asymptotic relationship between richness and process rates could, however, arise from a ‘sampling effect’ of increased probability of including a species with strong ecosystem effects, as species richness increases¹³. The sampling effect has at least two interpretations. It might be an important biological property of communities that influences process rates in natural ecosystems¹⁹, or it might be an artefact of species-richness experiments in which species are randomly assigned to treatments, rather than following community assembly rules that might occur in nature⁶⁷. Finally, ecosystem process rates may show no simple correlation with species richness. However, the lack of a simple statistical relationship between species richness and an ecosystem process may mask important functional relationships. This could occur, for example, if process rates depend strongly on the traits of certain species or if species interactions determine the species traits that are expressed (the ‘idiosyncratic hypothesis’)⁷. This mechanistic debate is important scientifically for understanding the functioning of ecosystems and effective management of their biotic resources. Regardless of the outcome of the debate, conserving biodiversity is essential because we rarely know *a priori* which species are critical to current functioning or provide resilience and resistance to environmental changes.

accessed by vegetation, enhanced productivity, and increased surface litter and salts. This inhibited the regeneration of many native species, leading to a general reduction in biodiversity¹⁶. The perennial tussock grass, *Agropyron cristatum*, which was widely introduced to the northern Great Plains of North America after the 1930s ‘dustbowl’, has substantially lower allocation to roots compared with native prairie grasses. Soil under *A. cristatum* has lower levels of available nitrogen and ~25% less total carbon than native prairie soil, so the introduction of this species resulted in an equivalent reduction of 480×10^{12} g carbon stored in soils¹⁷. Soil invertebrates, such as earthworms and termites, also alter turnover of organic matter and nutrient supply, thereby influencing the species composition of the aboveground flora and fauna¹⁸.

Species can also influence disturbance regime. For example, several species of nutritious but flammable grasses were introduced to the Hawaiian Islands to support cattle grazing. Some of these grasses spread into protected woodlands, where they caused a 300-fold increase in the extent of fire. Most of the woody plants, including some endangered species, are eliminated by fire, whereas grasses

rebound quickly¹⁹. Similar increases in the ecological role of fire resulting from grass invasions have been widely observed in the Americas, Australia and elsewhere in Oceania. The invasion of cheatgrass (*Bromus tectorum*) into western North America is one of the most extensive of these invasions. Cheatgrass has increased fire frequency by a factor of more than ten in the >40 million hectares ($1 \text{ ha} = 10^4 \text{ m}^2$) that it now dominates²⁰.

Species-induced changes in microclimate can be just as important as the direct impacts of environmental change. For example, in late-successional boreal forests, where soil temperatures have a strong influence on nutrient supply and productivity, the presence of moss, which reduces heat flux into the soil, contributes to the stability of permafrost (frozen soils) and the characteristically low rates of nutrient cycling²¹. As fire frequency increases in response to high-latitude warming, moss biomass declines, permafrost becomes less stable, the nutrient supply increases, and the species composition of forests is altered. Plant traits can also influence climate at larger scales. Simulations with general circulation models indicate that widespread replacement of deep-rooted tropical trees by shallow-

Figure 3 Scenarios of change in species diversity in selected biomes by the year 2100. The values are the projected change in diversity for each biome relative to the biome with greatest projected diversity change⁶. Biomes are: tropical forests (T), grasslands (G), Mediterranean (M), desert (D), north temperate forests (N), boreal forests (B) and arctic (A). Projected change in species diversity is calculated assuming three alternative scenarios of interactions among the causes of diversity change. Scenario 1 assumes no interaction among causes of diversity change, so that the total change in diversity is the sum of the changes caused by each driver of diversity change. Scenario 2 assumes that only the factor with the greatest impact on diversity influences diversity change. Scenario 3 assumes that factors causing change in biodiversity interact multiplicatively to determine diversity change. For scenarios 1 and 2, we show the relative importance of the major causes of projected change in diversity. These causes are climatic change, change in land use, introduction of exotic species, and changes in atmospheric CO₂ and/or nitrogen deposition (labelled ‘other’). The graph shows that all biomes are projected to experience substantial change in species diversity by 2100, that the most important causes of diversity change differ among biomes, and that the patterns of diversity change depend on assumptions about the nature of interactions among the causes of diversity change. Projected biodiversity change is most similar among biomes if causes of diversity change do not interact (scenario 1) and differ most strongly among biomes if the causes of biodiversity change interact multiplicatively (scenario 3).

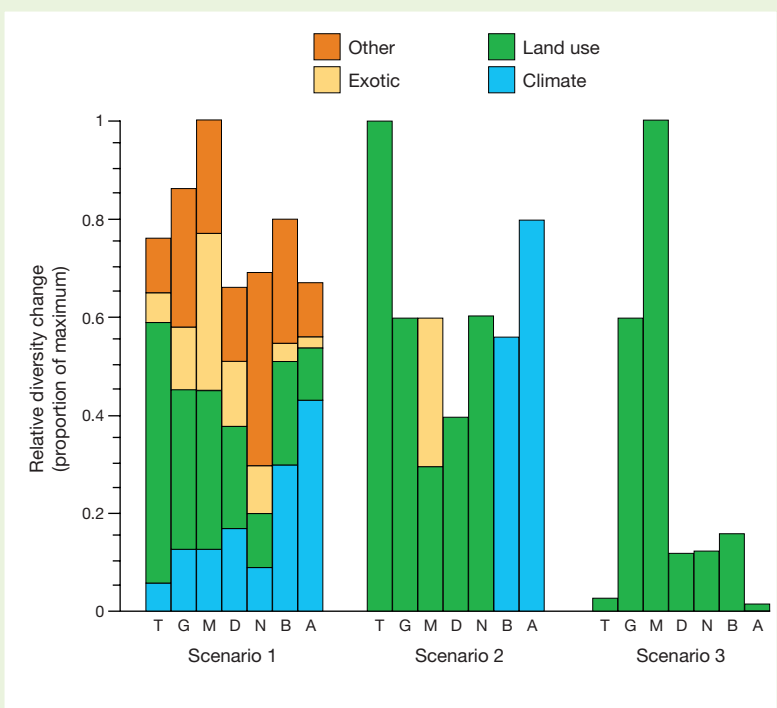
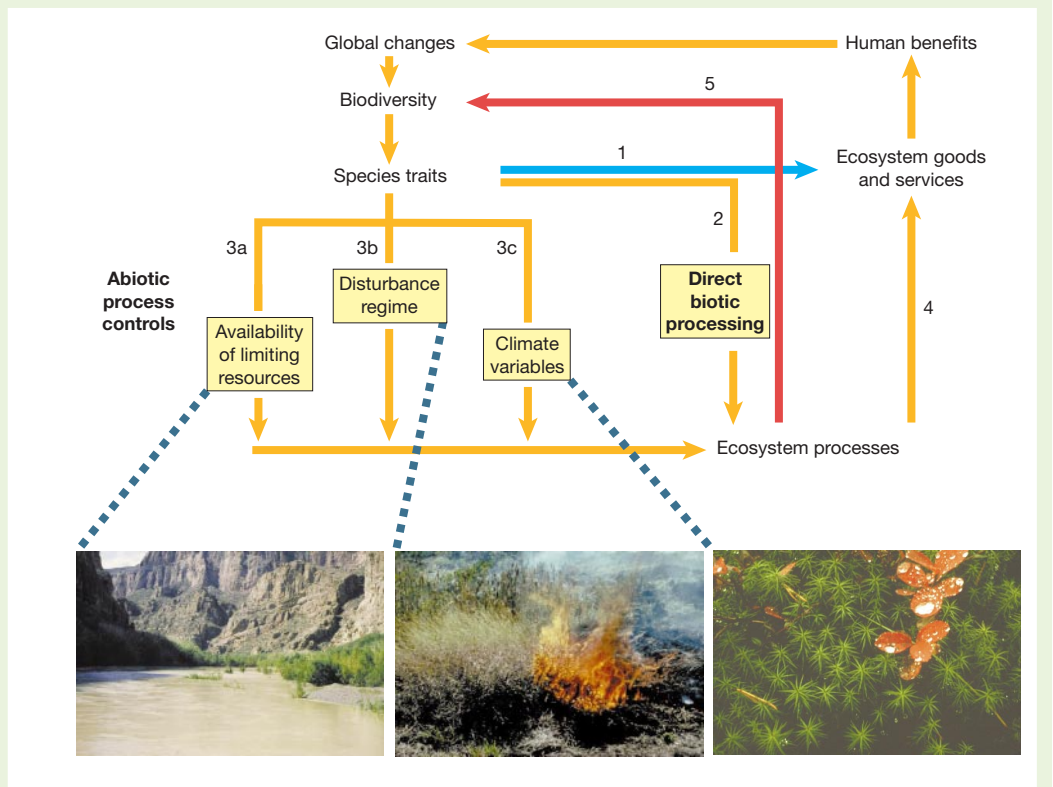


Figure 4 Mechanisms by which species traits affect ecosystem processes. Changes in biodiversity alter the functional traits of species in an ecosystem in ways that directly influence ecosystem goods and services (1) either positively (for example, increased agricultural or forestry production) or negatively (for example, loss of harvestable species or species with strong aesthetic/cultural value). Changes in species traits affect ecosystem processes directly through changes in biotic controls (2) and indirectly through changes in abiotic controls, such as availability of limiting resources (3a), disturbance regime (3b), or micro- or macroclimate variables (3c). Illustrations of these effects include: reduction in river flow due to invasion of deep-rooted desert trees (3a; photo by E. Zavaleta); increased fire frequency resulting from grass invasion that destroys native trees and shrubs in Hawaii (3b, photo by C. D'Antonio); and insulation of soils by mosses in arctic tundra, contributing to conditions that allow for permafrost (3c; photo by D. Hooper). Altered processes can then influence the availability of ecosystem goods and services directly (4) or indirectly by further altering biodiversity (5), resulting in loss of useful species or increases in noxious species.



rooted pasture grasses would reduce evapotranspiration and lead to a warmer, drier climate²². At high latitudes, the replacement of snow-covered tundra by a dark conifer canopy will probably increase energy absorption sufficiently to act as a powerful positive feedback to regional warming²³.

Species interactions

Most ecosystem processes are non-additive functions of the traits of two or more species, because interactions among species, rather than simple presence or absence of species, determine ecosystem characteristics (Fig. 5). Species interactions, including mutualism, trophic interactions (predation, parasitism and herbivory), and competition may affect ecosystem processes directly by modifying pathways of energy and material flow²⁴ or indirectly by modifying the abundances or traits of species with strong ecosystem effects²⁵.

Mutualistic species interactions contribute directly to many essential ecosystem processes. For example, nitrogen inputs to terrestrial ecosystems are mediated primarily by mutualistic associations between plants and nitrogen-fixing microorganisms. Mycorrhizal associations between plant roots and fungi greatly aid plant nutrient uptake from soil, increase primary production and speed succession²⁶. Highly integrated communities (consortia) of soil microorganisms, in which each species contributes a distinct set of enzymes, speeds the decomposition of organic matter²⁷. Many of these interactions have a high degree of specificity, which increases the probability that loss of a given species will have cascading effects on the rest of the system.

Trophic interactions can have large effects on ecosystem processes either by directly modifying fluxes of energy and materials, or by influencing the abundances of species that control those fluxes. When top predators are removed, prey populations sometimes explode and deplete their food resources, leading to a cascade of ecological effects. For example, removal of sea otters by Russian fur traders allowed a population explosion of sea urchins that

overgrazed kelp²⁸ (Fig. 6a). Recent over-fishing in the North Pacific may have triggered similar outbreaks of sea urchin, as killer whales moved closer to shore and switched to sea otters as an alternate prey²⁹. In the absence of dense populations of sea urchins, kelp provides the physical structure for diverse subtidal communities and attenuates waves that otherwise augment coastal erosion and storm damage³⁰. Removing bass from lakes that were fertilized with phosphorus caused an increase in minnows, which depleted the biomass of phytoplankton grazers and caused algal blooms³¹ (Fig. 6b). The algal blooms turned the lake from a net source to a net sink of CO₂. Thus, biotic change and altered nutrient cycles can interact to influence whole-system carbon balance. The zebra mussel (*Dreissena polymorpha*) is a bottom-dwelling invasive species that, through its filter feeding, markedly reduces phytoplankton while increasing water clarity and phosphorus availability³². Introduction of this species shifts the controlling interactions of the food web from the water column to the sediments. Trophic interactions are also important in terrestrial ecosystems. At the micro scale, predation on bacteria by protozoan grazers speeds nitrogen cycling near plant roots, enhancing nitrogen availability to plants³³. At the regional scale, an improvement in hunting technology at the end of the Pleistocene may have contributed to the loss of the Pleistocene megafauna and the widespread change from steppe grassland to tundra that occurred in Siberia 10,000–18,000 years ago³⁴. The resulting increase in mosses insulated the soil and led to cooler soils, less decomposition and greater sequestration of carbon in peat. Today, human harvest of animals continues to have a pronounced effect of the functioning of ecosystems.

Competition, mutualisms and trophic interactions frequently lead to secondary interactions among other species, often with strong ecosystem effects (Fig. 5). For example, soil microbial composition can modify the outcome of competition among plant species³⁵, and plants modify the microbial community of their

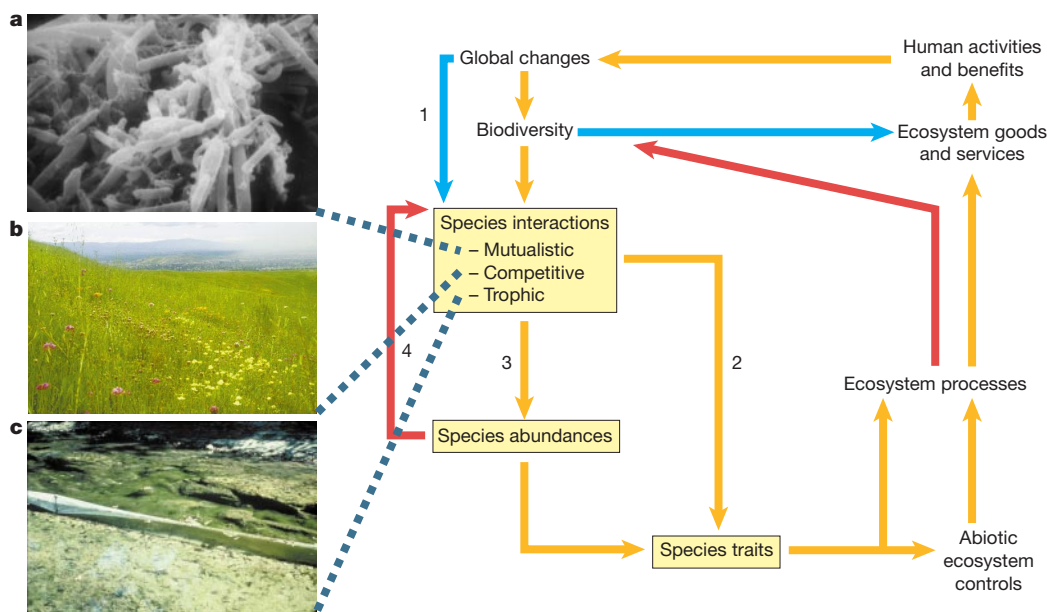


Figure 5 Mechanisms by which species interactions affect ecosystem processes. Global environmental change affects species interactions (mutualism, competition and trophic interactions) both directly (1) and through its effects on altered biodiversity. Species interactions may directly affect key traits (for example, the inhibition of microbial nitrogen fixation by plant secondary metabolites) in ecosystem processes (2) or may alter the abundances of species with key traits (3). Examples of these species interactions include (a) mutualistic consortia of microorganisms, each of which produces only some of the enzymes required to break down organic matter (photo by M. Klug), (b) altered abundances of native California forbs due to competition from introduced European grasses (photo by H. Reynolds), and (c) alteration of algal biomass due to presence or absence of grazing minnows⁸⁴ (photo by M. Power). Changes in species interactions and the resulting changes in community composition (3) may feedback to cause a cascade of further effects on species interactions (4).

neighbours, which, in turn, affects nitrogen supply and plant growth³⁶. Stream predatory invertebrates alter the behaviour of their prey, making them more vulnerable to fish predation, which leads to an increase in the weight gain of fish³⁷. In the terrestrial realm, grazers can reduce grass cover to the point that avian predators keep vole populations at low densities, allowing the persistence of *Erodium botrys*, a preferred food of voles³⁸. The presence of *E. botrys* increases leaching³⁹ and increases soil moisture⁴⁰, which often limits production and nutrient cycling in dry grasslands. These examples clearly indicate that all types of organisms — plants, animals and microorganisms — must be considered in understanding the effects of biodiversity on ecosystem functioning. Although each of these examples is unique to a particular ecosystem, the ubiquitous nature of species interactions with strong ecosystem effects makes these interactions a general feature of ecosystem functioning. In many cases, changes in these interactions alter the traits that are expressed by species and therefore the effects of species on ecosystem processes. Consequently, simply knowing that a species is present or absent is insufficient to predict its impact on ecosystems.

Many global changes alter the nature or timing of species interactions⁴¹. For example, the timing of plant flowering and the emergence of pollinating insects differ in their responses to warming, with potentially large effects on ecosystems and communities⁴². Plant–herbivore interactions in diverse communities are less likely to be disrupted by elevated CO₂ (ref. 43) than in simple systems involving one specialist herbivore and its host plant⁴⁴.

Resistance and resilience to change

The diversity–stability hypothesis suggests that diversity provides a general insurance policy that minimizes the chance of large ecosystem changes in response to global environmental change⁴⁵. Microbial microcosm experiments show less variability in ecosystem processes in communities with greater species richness⁴⁶, perhaps because every species has a slightly different response to its physical and biotic environment. The larger the number of functionally similar species

in a community, the greater is the probability that at least some of these species will survive stochastic or directional changes in environment and maintain the current properties of the ecosystem⁴⁷. This stability of processes has societal relevance. Many traditional farmers plant diverse crops, not to maximize productivity in a given year, but to decrease the chances of crop failure in a bad year⁴⁸. Even the loss of rare species may jeopardize the resilience of ecosystems. For example, in rangeland ecosystems, rare species that are functionally similar to abundant ones become more common when grazing reduces their abundant counterparts. This compensation in response to release from competition minimizes the changes in ecosystem properties⁴⁹.

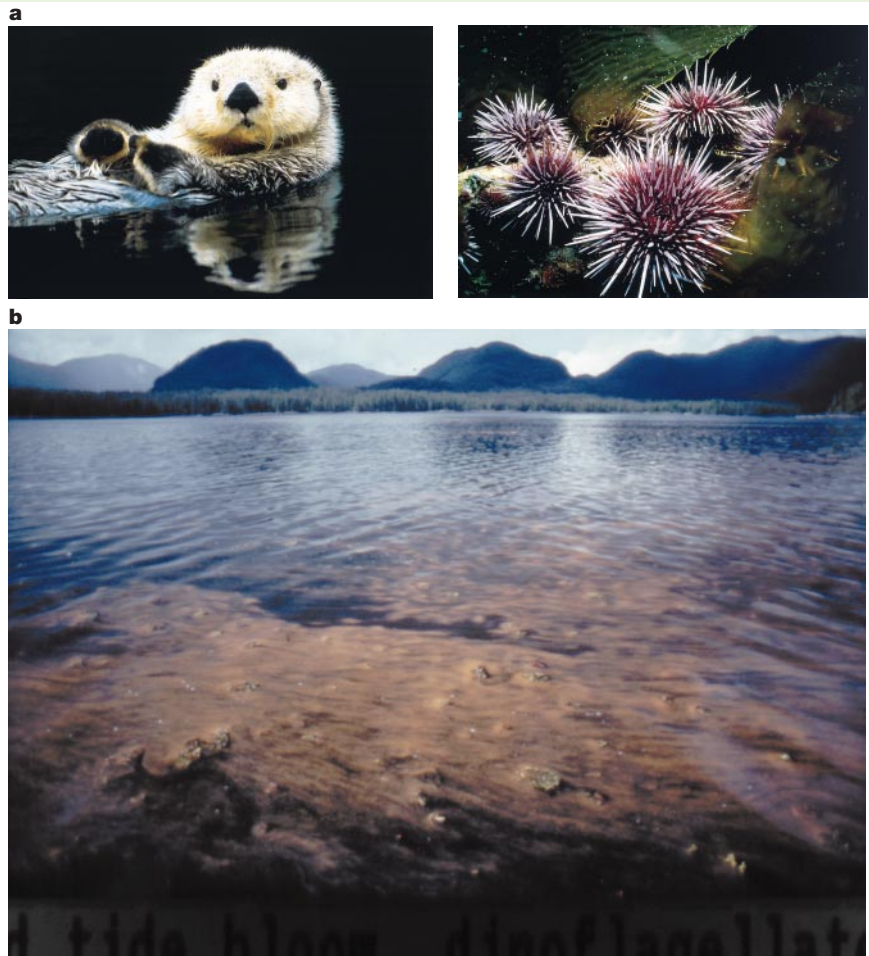
Species diversity also reduces the probability of outbreaks by ‘pest’ species by diluting the availability of their hosts. This decreases host-specific diseases⁵⁰, plant-feeding nematodes⁵¹ and consumption of preferred plant species⁵². In soils, microbial diversity decreases fungal diseases owing to competition and interference among microbes⁵³.

Resistance to invasions

Biodiversity can influence the ability of exotic species to invade communities through either the influence of traits of resident species or some cumulative effect of species richness. Early theoretical models and observations of invasions on islands indicated that species-poor communities would be more vulnerable to invasions because they offered more empty niches⁵⁴. However, studies of intact ecosystems find both negative⁵⁵ and positive⁵⁶ correlations between species richness and invasions. This occurs in part because the underlying factors that generate differences in diversity (for example, propagule supply, disturbance regime and soil fertility) cannot be controlled and may themselves be responsible for differences in invasibility⁵⁶. The diversity effects on invasibility are scale-dependent in some cases. For example, at the plot scale, where competitive interactions might exert their effect, increased plant diversity correlated with lower vulnerability to invasion in Central Plains grasslands of the United States. Across landscape scales, however, ecological factors that promote

Figure 6 Trophic interactions can affect ecosystem processes by influencing species' abundances.

a. Removal of sea otters by Russian fur traders caused an explosion in the population of sea urchins that overgrazed kelp. (Photographs courtesy of M. Sewell/Still Pictures and J. Rotman/BBC Natural History Unit.) **b.** Similarly, changes in the species balance and the abundance of fish can deplete phytoplankton grazers and cause algal blooms. (Photograph courtesy of J. Foott/BBC Natural History Unit.)



native plant diversity (for example, soil type and disturbance regime) also promote species invasions⁵⁷.

Experimental studies with plants⁵⁸ or soil microorganisms⁵⁹ often show that vulnerability to invasion is governed more strongly by the traits of resident and invading species than by species richness *per se*. Both competition and trophic interactions contribute to these effects of community composition on invasibility. For example, in its native range, the Argentine ant (*Linepithaema humile*) is attacked by species-specific parasitoids that modify its behaviour and reduce its ability to dominate food resources and competitively exclude other ant species⁶⁰. These parasitoids are absent from the introduced range of Argentine ants, which may explain their success at eliminating native ant communities in North America⁶¹. Observational and experimental studies together indicate that the effect of species diversity on vulnerability to invasion depends on the components of diversity involved (richness, evenness, composition and species interactions) and their interactions with other ecological factors such as disturbance regime, resource supply and rate of propagule arrival. Humans significantly affect all of these factors (Figs 1, 4), thereby dramatically increasing the incidence of invasions worldwide.

Societal consequences of altered diversity

Biodiversity and its links to ecosystem properties have cultural, intellectual, aesthetic and spiritual values that are important to society. In addition, changes in biodiversity that alter ecosystem functioning have economic impacts through the provision of ecosystem goods and services to society (Fig. 1 and Box 2). Changes in diversity can directly reduce sources of food, fuel, structural materials, medicinals or genetic resources. These changes can also alter the abundance of other species that control ecosystem processes, leading to further

changes in community composition and vulnerability to invasion. Introduction of exotic species or changes in community composition can affect ecosystem goods or services either by directly reducing abundances of useful species (by predation or competition), or by altering controls on critical ecosystem processes (Fig. 4).

These impacts can be wide-ranging and costly. For example, the introduction of deep-rooted species in arid regions reduces supplies and increases costs of water for human use. Marginal water losses to the invasive star thistle, *Centaurea solstitialis*, in the Sacramento River valley, California, have been valued at US\$16–56 million per year (J. D. Gerlach, unpublished results) (Fig. 7). In South Africa's Cape region, the presence of rapidly transpiring exotic pines raises the unit cost of water procurement by nearly 30% (ref. 62). Increased evapotranspiration due to the invasion of *Tamarix* in the United States costs an estimated \$65–180 million per year in reduced municipal and agricultural water supplies⁶³. In addition to raising water costs, the presence of sediment-trapping *Tamarix* stands has narrowed river channels and obstructed over-bank flows throughout the western United States, increasing flood damages by as much as \$50 million annually⁶³.

Those species changes that have greatest ecological impact frequently incur high societal costs. Changes in traits maintaining regional climate²² constitute an ecosystem service whose value in tropical forests has been estimated at \$220 ha⁻¹ yr⁻¹ (ref. 64). The loss or addition of species that alter disturbance regimes can also be costly. The increased fire frequency resulting from the cheatgrass invasion in the western United States has reduced rangeland values and air quality and led to increased expenditures on fire suppression⁶⁵. The disruption of key species interactions can also have large societal and ecological consequences. Large populations of passenger pigeons (*Ectopistes migratorius*) in the northeastern United States

may once have controlled Lyme tick-bearing mice by out-competing them for food⁶⁶. The loss of the passenger pigeon to nineteenth-century over-hunting may, therefore, have contributed to the rise of Lyme disease in humans in the twentieth century. The economic impacts of invasions of novel species are particularly well documented. The introduction and spread of single pests such as the golden apple snail (*Pomacea canaliculata*) and the European corn borer (*Ostrinia nubilalis*) have had major impacts on food production and farm incomes^{67,68}. Estimates of the overall cost of invasions by exotic species in the United States range widely from \$1.1 to \$137 billion annually^{69,70}. In Australia, plant invasions alone entail an annual cost of US\$2.1 billion⁷¹.

The provision of tangible ecosystem goods and services by natural systems depends not only on species' presence or absence but also on their abundance. Large populations of the white-footed mouse (*Peromyscus leucopus*) in the northeastern United States control outbreaks of gypsy moth (*Lymantria dispar*) but spread Lyme disease, whereas small populations of the mouse decrease the incidence of Lyme disease but allow gypsy moth defoliation⁷². An analysis of the costs of changes in biodiversity thus involves more than just analysis of extinctions and invasions. The loss of a species to extinction is of special societal concern, however, because it is irreversible. Future opportunities to learn and derive newly recognized benefits from an extinct species are lost forever. Preventing such a loss preserves an 'option value' for society — the value of attaining more knowledge about species and their contribution to human well being in order to make informed decisions in the future^{73,74}. For example, significant value (\$230–330 million) has been attributed to genetic information gained from preventing land conversion in Jalisco, Mexico, in an area containing a wild grass, teosinte (*Euchlaena mexicana*), that can be used to develop viral-resistant strains of perennial corn⁷³. If this land had been converted to agriculture or human settlements, the societal benefits of development would have come at the expense of an irreversible loss in genetic material that could be used for breeding viral resistance in one of the most widely consumed cereal crops in the world. The perceived costs of diversity loss in this situation might have been small — especially relative to the development benefits — whereas the actual (unrecognized) costs of losing genetic diversity would have been significant (Fig. 8). Decisions to preserve land to gain further information about the societal value of species diversity or ecosystem function typically involve a large degree of uncertainty, which often leads to myopic decisions regarding land use.

Figure 7 Water losses to the invasive, deep-rooted star thistle, *C. solstitialis*, provides an example of the financial impacts of introducing exotic species on ecosystem composition. (Photograph courtesy of P. Collins/A-Z Botanical Collection.)



Box 2

Ecosystem services

Ecosystem services are defined as the processes and conditions of natural ecosystems that support human activity and sustain human life. Such services include the maintenance of soil fertility, climate regulation and natural pest control, and provide flows of ecosystem goods such as food, timber and fresh water. They also provide intangible benefits such as aesthetic and cultural values⁸⁸. Ecosystem services are generated by the biodiversity present in natural ecosystems. Ecologists and economists have begun to quantify the impacts of changes in biodiversity on the delivery of ecosystem services and to attach monetary value to these changes. Techniques used to attach value to biodiversity change range from direct valuation based on market prices to estimates of what individuals are willing to pay to protect endangered wildlife⁸⁹. Although there are estimates of the global values of ecosystem services⁶⁴, valuation of the marginal losses that accompany specific biodiversity changes are most relevant to policy decisions. Predicting the value of such losses involves uncertainty, because ecological and societal systems interact in nonlinear ways and because human preferences change through time. Assumptions today about future values may underestimate the values placed on natural systems by future generations⁸⁹. Therefore, minimizing loss of biodiversity offers a conservative strategy for maintaining this value.

Global environmental changes have the potential to exacerbate the ecological and societal impacts of changes in biodiversity⁶. In many regions, land conversion forces declining populations towards the edges of their species range, where they become increasingly vulnerable to collapse if exposed to further human impact⁷⁵. Warming allows the poleward spread of exotics and pathogens, such as dengue- and malaria-transmitting mosquitoes (*Aedes* and *Anopheles* sp.)⁷⁶ and pests of key food crops, such as corn-boring insects⁶⁸. Warming can also exacerbate the impacts of water-consuming invasive plant species in water-scarce areas by increasing regional water losses. The *Tamarix*-invaded Colorado River in the United States currently has a mean annual flow that is 10% less than regional water allocations for human use⁷⁷. Warming by 4°C would reduce the flow of the Colorado River by more than 20%, further increasing the marginal costs of water losses to *Tamarix*⁷⁸. Similar impacts of global change in regions such as Sahelian Africa, which have less water and less well developed distribution mechanisms, might directly affect human survival. In many cases, accelerated biodiversity loss is already jeopardizing the livelihoods of traditional peoples⁷⁹.

The combination of irreversible species losses and positive feedbacks between biodiversity changes and ecosystem processes are likely to cause nonlinear cost increases to society in the future, particularly when thresholds of ecosystem resilience are exceeded⁸⁰. For example, *Imperata cylindrica*, an aggressive indigenous grass, colonizes forest lands of Asia that are cleared for slash-and-burn agriculture, forming a monoculture grassland with no vascular plant diversity and many fewer mammalian species than the native forest. The total area of *Imperata* in Asia is currently about 35 million ha (4% of land area)⁸¹. Once in place, *Imperata* is difficult and costly to remove and enhances fire, which promotes the spread of the grass. The annual cost of reversing this conversion in Indonesia, where 4% of the nation's area (8.6 million ha) is now in *Imperata* grasslands, would be over \$400 million if herbicides are used, and \$1.2 billion if labour is used to remove the grass manually. Farmers typically burn the fields because herbicides and labour are too expensive. Burning these grasslands, however, increases losses of soil nitrogen and carbon, which erode agricultural productivity, and enhances regeneration of *Imperata*. This positive feedback with nonlinear changes in land cover will probably continue in the future as lands are deforested

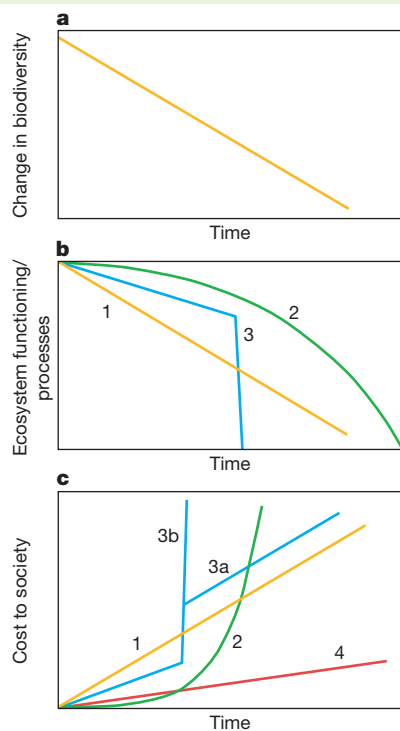


Figure 8 Ecosystem and societal consequences of changes in biodiversity. **a**, A linear change in biodiversity through time. **b**, This change might (1) induce a linear response in ecosystem processes, (2) have increasingly large impacts on ecosystem functioning, yielding exponential ecosystem change through time, or (3) exhibit abrupt thresholds owing to the loss of a keystone species, the loss of the last member of a key functional group, or the addition of a new species trait. **c**, Even if ecosystem response to diversity changes is linear, associated societal costs through time may respond nonlinearly. Departures from a linear increase (1) in societal costs over time might include larger cost increases (2) associated with each additional unit of change in ecosystem processes, yielding an exponential cost curve through time. Reductions of resource supply below threshold levels may induce step increases in societal costs (3a), such as reductions in water supply below the point where all consumers have access to enough for desired uses. If changes in resource supply or ecosystem processes exceed thresholds for supporting large segments of society, stepwise cost increases may be unmeasurable or essentially infinite (3b). The perceived ecological changes and societal costs of diversity change may be small (4). Actual, unrecognized costs may be far higher (lines 1, 2 and 3) and discovered only later as lost option values. Conservation of biodiversity can help avoid such negative ecological and economic ‘surprises’.

for timber and agricultural purposes, causing further declines in regional biodiversity.

Uncertainty related to positive feedbacks and nonlinear changes in land cover and biodiversity make social adaptation to change more difficult and costly (Fig. 8). It may be more important from an economic perspective to understand the nature and timing of rapid or nonlinear changes in societal costs caused by loss of biodiversity and associated ecosystem services than it is to predict average consequences of current trends of species decline. By analogy, economic models of ecological ‘surprises’ in response to climatic change show that the information about the nonlinearities in damage from warming is worth up to six times more than information about current trends in damage levels⁸². In the *Imperata* example, the costs of replacing the original ecosystem goods and services from the forest — including timber products, fire stability and soil nutrients — rise sharply as *Imperata* spreads. If these nonlinearities in the ecological and economic effects of this conversion had been anticipated, policies could have been implemented to encourage agroforestry instead of rice production or to reduce migration and settlement in

the most vulnerable areas⁸³.

In sum, these examples indicate a tight coupling between altered species diversity, ecosystem function and societal costs. A pressing task for ecologists, land managers and environmental policy makers is to determine where and when such tight couplings exist. Policies to safeguard ecosystem services must be able to respond dynamically to new knowledge, the rapidly changing global environment, and evolving societal needs. Nonlinearity, uncertainty and irreversibility call for a more aggressive approach to mitigating changes in biodiversity than is now being pursued so that future options are not foreclosed.

Conclusion

We are in the midst of one of the largest experiments in the history of the Earth. Human effects on climate, biogeochemical cycles, land use and mobility of organisms have changed the local and global diversity of the planet, with important ecosystem and societal consequences (Fig. 1). The most important causes of altered biodiversity are factors that can be regulated by changes in policy: emissions of greenhouse gases, land-use change and species introductions. In the past, the international community has moved to reduce detrimental human impacts with unambiguous societal consequences. For example, the Montreal Protocol prohibited release of chlorofluorocarbons in response to evidence that these chemicals caused loss of ozone and increased levels of cancer-producing UV-B radiation. Strong evidence for changes in biodiversity and its ecosystem and societal consequences calls for similar international actions. We urge the following blueprint for action.

- The scientific community should intensify its efforts to identify the causes of nonlinearities and thresholds in the response of ecosystem and social processes to changes in biodiversity.
- The scientific community and informed citizens should become engaged in conveying to the public, policy-makers and land managers the enormity and irreversibility of current rapid changes in biodiversity. Despite convincing scientific evidence, there is a general lack of public awareness that change in biodiversity is a global change with important ecological and societal impacts and that these changes are not amenable to mitigation after they have occurred.
- Managers should consider the ecological and social consequences of biodiversity change at all stages in land-use planning. For example, environmental impact assessments should consider both the current costs of ecosystem services that will be lost and the risk of nonlinear future change. Managed landscapes can support a large proportion of regional biodiversity with proper planning, management and adaptive responses.
- Scientists and other citizens should collaborate with governmental organizations, from local to national levels, in developing and implementing policies and regulations that reduce environmental deterioration and changes in biodiversity. For example, more stringent restrictions on the import of biotic materials could curb the rate of biotic invasions, and improved land and watershed management could reduce their rates of spread.
- A new international body that would be comparable to the Intergovernmental Panel on Climate Change (IPCC) should assess changes in biodiversity and their consequences as an integral component of the assessment of the societal impacts of global change.
- International bodies should establish and implement agreements such as the Convention on Biological Diversity that institute mechanisms for reducing activities that drive the changes in biodiversity. These activities include fossil-fuel emissions, land-use change and biotic introductions. □

1. Postel, S. L., Daily, G. C. & Ehrlich, P. R. Human appropriation of renewable fresh water. *Science* **271**, 785–788 (1996).
2. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of Earth’s ecosystems. *Science* **277**, 494–499 (1997).
3. Kattenberg, A. et al. in *Climate Change 1995. The Science of Climate Change* (ed. Houghton, J. T.) 285–357 (Cambridge Univ. Press, Cambridge, 1996).

4. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* **269**, 347–350 (1995).
5. Lawton, J. H. & May, R. M. *Extinction Rates* (Oxford Univ. Press, Oxford, 1995).
6. Sala, O. E. *et al.* Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1776 (2000).
7. Lawton, J. H. What do species do in ecosystems? *Oikos* **71**, 367–374 (1994).
8. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
9. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127 (1999).
10. van der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
11. Saloniemi, P. O. Metabolic capabilities of forest soil microbial populations with reduced species diversity. *Soil Biol. Biochem.* **13**, 1–10 (1981).
12. Wardle, D. A., Bonner, K. I. & Nicholson, K. S. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**, 247–258 (1997).
13. Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305 (1997).
14. Tilman, D. *et al.* The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302 (1997).
15. Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D. & Matson, P. A. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**, 802–804 (1987).
16. Berry, W. L. Characteristics of salts secreted by *Tamarix aphylla*. *Am. J. Bot.* **57**, 1226–1230 (1970).
17. Christian, J. M. & Wilson, S. D. Long-term impacts of an introduced grass in the northern Great Plains. *Ecology* **80**, 2397–2407 (1999).
18. Lavelle, P., Bignell, D. & Lepage, M. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* **33**, 159–193 (1997).
19. D'Antonio, C. M. & Vitousek, P. M. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23**, 63–87 (1992).
20. Whisenant, S. *Changing Fire Frequencies on Idaho's Snake River Plains: Ecological Management Implications 4–10* (US Forest Service General Technical Report INT-276, Washington, 1990).
21. Van Cleve, K., Chapin, F. S. III, Dryness, C. T. & Viereck, L. A. Element cycling in taiga forest: state-factor control. *BioScience* **41**, 78–88 (1991).
22. Shukla, J., Nobre, C. & Sellers, P. Amazon deforestation and climate change. *Science* **247**, 1322–1325 (1990).
23. Foley, J. A., Kutzbach, J. E., Coe, M. T. & Levis, S. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature* **371**, 52–54 (1994).
24. de Ruiter, P. C., Neutel, A. & Moore, J. C. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260 (1995).
25. Power, M. E. *et al.* Challenges in the quest for keystones. *BioScience* **46**, 609 (1996).
26. Read, D. J. Mycorrhizas in ecosystems. *Experientia* **47**, 376–391 (1991).
27. Paerl, H. W. & Pinckney, J. L. A mini-review of microbial consortia: their roles in aquatic production and biogeochemical cycling. *Microbial Ecol.* **31**, 225–247 (1996).
28. Estes, J. A. & Palmisano, J. F. Sea otters: their role in structuring nearshore communities. *Science* **185**, 1058–1060 (1974).
29. Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476 (1998).
30. Mork, M. The effect of kelp in wave damping. *Sarsia* **80**, 323–327 (1996).
31. Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F. & Pace, M. L. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* **277**, 248–251 (1997).
32. Caraco, N. F. *et al.* Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology* **78**, 588–602 (1997).
33. Clarholm, M. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* **17**, 181–187 (1985).
34. Zimov, S. A. *et al.* Steppe-tundra transition: an herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* **146**, 765–794 (1995).
35. Chanway, C. P., Turkington, R. & Holl, F. B. Ecological implications of specificity between plants and rhizosphere micro-organisms. *Adv. Ecol. Res.* **21**, 121–169 (1991).
36. Lawley, R. A., Newman, E. I. & Campbell, R. Abundance of endomycorrhizas and root-surface microorganisms on three grasses grown separately and in mixtures. *Soil Biol. Biochem.* **14**, 237–240 (1982).
37. Soluck, D. A. & Richardson, J. S. The role of stoneflies in enhancing growth of trout: a test of the importance of predator–predator facilitation within a stream community. *Oikos* **80**, 214–219 (1997).
38. Rice, K. J. Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology* **68**, 1113–1115 (1987).
39. Shock, C. C., Jones, M. B., Williams, W. A. & Center, D. M. Competition of S and N by associations of three annual range species in lysimeters. *Plant Soil* **81**, 311–321 (1984).
40. Gordon, D. R. & Rice, K. J. Partitioning of space and water between two California annual grassland species. *Am. J. Bot.* **79**, 967–976 (1992).
41. Jifon, J. L., Friend, A. L. & Berrang, P. C. Species mixture and soil-resource availability affect the root growth response of tree seedlings to elevated atmospheric CO₂. *Can. J. For. Res.* **25**, 824–832 (1995).
42. Harrington, R., Woivod, I. & Sparks, T. Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150 (1999).
43. Diaz, S., Fraser, L. H., Grime, J. P. & Falczuk, V. The impact of elevated CO₂ on plant–herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia* **117**, 177–186 (1998).
44. Lindroth, R. L. In *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch, G. W. & Mooney, H. A.) 105–120 (Academic Press, San Diego, 1996).
45. McNaughton, S. J. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.* **111**, 515–525 (1977).
46. Naem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
47. Chapin, F. S. III & Shaver, G. R. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66**, 564–576 (1985).
48. Altieri, M. A. In *Agroecology* (eds Carrol, C. R., Vandermeer, J. H. & Rosset, P. M.) 551–564 (McGraw Hill, New York, 1990).
49. Walker, B., Kinzig, A. & Langridge, J. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**, 95–113 (1999).
50. Burdon, J. J. The structure of pathogen populations in natural plant communities. *Annu. Rev. Phytopathol.* **31**, 305–323 (1993).
51. Wasilewska, L. Differences in development of soil nematode communities in single- and multi-species grass experimental treatments. *Appl. Soil Ecol.* **2**, 53–64 (1995).
52. Bertness, M. D. & Leonard, G. H. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**, 1976–1989 (1997).
53. Nitta, T. Diversity of root fungal floras: its implications for soil-borne diseases and crop growth. *Jap. Agric. Res. Quart.* **25**, 6–11 (1991).
54. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
55. Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92 (1997).
56. Levine, J. M. & D'Antonio, C. M. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26 (1999).
57. Stohlgren, T. J. *et al.* Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* **69**, 25–46 (1999).
58. Lavorel, S., Prieur-Richard, A.-H. & Grigulis, K. Invasibility and diversity of plant communities: from patterns to processes. *Diversity Distrib.* **5**, 41–49 (1999).
59. McGrady-Steed, J., Harris, P. M. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165 (1997).
60. Orr, M. R. & Seike, S. H. Parasitoids deter foraging by Argentine ants (*Linepithema humile*) in their native habitat in Brazil. *Oecologia* **117**, 420–425 (1998).
61. Holway, D. A. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**, 238–251 (1999).
62. Van Wilgen, B. W., Cowling, R. M. & Burgers, C. J. Valuation of ecosystem services: a case study from South African fynbos ecosystems. *BioScience* **46**, 184–189 (1996).
63. Zavaleta, E. S. In *Invasive Species in a Changing World* (eds Hobbs, R. J. & Mooney, H. A.) (Island, Washington DC, in the press).
64. Costanza, R. *et al.* The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260 (1997).
65. Stewart, G. & Hull, A. C. Cheatgrass (*Bromus tectorum* L.) — an ecological intruder in southern Idaho. *Ecology* **30**, 58–74 (1949).
66. Blockstein, D. E. Letter to the editor. *Science* **279**, 1831 (1998).
67. Naylor, R. L. Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* **25**, 443–448 (1996).
68. Porter, J. H., Parry, M. L. & Carter, T. R. The potential effects of climatic change on agricultural insect pests. *Agric. For. Meteorol.* **57**, 221–240 (1991).
69. Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**, 53–65 (2000).
70. USOT Assessment. *Harmful Non-indigenous Species in the United States* (US Government Printing Office, Washington, 1993).
71. Thorp, J. *The National Weeds Strategy: A Strategic Approach to Weed Problems of National Significance* (Agriculture and Resource Management Council of Australia and New Zealand, Canberra, 1997).
72. Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M. & Wolff, J. O. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* **279**, 1023–1026 (1998).
73. Fisher, A. C. & Hanemann, W. M. Option value and the extinction of species. *Adv. Appl. Micro-Econ.* **4**, 169–190 (1986).
74. Naylor, R. L. In *Invasive Species in a Changing World* (eds Hobbs, R. & Mooney, H. A.) (Island, Washington DC, in the press).
75. Channell, R. & Lomolino, M. V. Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84–86 (2000).
76. Bryan, J. H., Foley, D. H. & Sutherst, R. W. Malaria transmission and climate change in Australia. *Med. J. Aust.* **164**, 345–347 (1996).
77. Morrison, J. I. *The Sustainable Use of Water in the Lower Colorado River Basin* (Pacific Institute and the Global Water Policy Project, Oakland, 1996).
78. Zavaleta, E. S. The emergence of waterfowl conservation among Yup'ik hunters in the Yukon-Kuskokwim Delta, Alaska. *Hum. Ecol.* **27**, 231–266 (2000).
79. Warren, D. M. & Pinkston, J. In *Linking Social and Ecological Systems* (eds Berkes, F. & Folke, C.) 158–189 (Cambridge Univ. Press, Cambridge, 1998).
80. Schlesinger, W. H. *et al.* Biological feedbacks in global desertification. *Science* **247**, 1043–1048 (1990).
81. Garrity, D. P. *et al.* The *Imperata* grasslands of tropical Asia: area, distribution, and typology. *Agrofor. Syst.* **36**, 1–29 (1997).
82. Peck, S. C. & Teisberg, T. J. In *Assessing Surprises and Nonlinearities in Greenhouse Warming* (eds Darmstadter, J. & Toman, M. A.) 80–83 (Resources for the Future, Washington, 1993).
83. Tomich, T. P., Kuusipalo, J., Menz, K. & Byron, N. *Imperata* economics and policy. *Agrofor. Syst.* **36**, 233–261 (1997).
84. Power, M. E., Matthews, W. J. & Steward, A. J. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* **66**, 1448–1456 (1985).
85. Johnson, K. G., Vogt, K. A., Clark, H. J., Schmitz, O. J. & Vogt, D. J. Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* **11**, 372–377 (1996).
86. Vitousek, P. M. & Hooper, D. U. In *Biodiversity and Ecosystem Function* (eds Schulze, E.-D. & Mooney, H. A.) 3–14 (Springer, Berlin, 1993).
87. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460 (1997).
88. Daily, G. C. *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington DC, 1997).
89. Goulder, L. H. & Kennedy, D. In *Nature's Services: Societal Dependence on Natural Ecosystems* (ed. Daily, G. C.) 23–48 (Island, Washington DC, 1997).

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