Biotic Control over the Functioning of Ecosystems

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Changes in the abundance of species—especially those that influence water and nutrient dynamics, trophic interactions, or disturbance regime—affect the structure and functioning of ecosystems. Diversity is also functionally important, both because it increases the probability of including species that have strong ecosystem effects and because it can increase the efficiency of resource use. Differences in environmental sensitivity among functionally similar species give stability to ecosystem processes, whereas differences in sensitivity among functionally different species make ecosystems more vulnerable to change. Current global environmental changes that affect species composition and diversity are therefore profoundly altering the functioning of the biosphere.

The two most dramatic ecological trends of the past century are human-induced changes in biotic diversity and alterations to the structure and functioning of ecosystems (*1*). Ecosystem processes, such as productivity, nitrogen mineralization rate, and nitrate leaching, respond directly to human modification of ecosystems and to changes in atmospheric composition and climate (*2*). Changes in biota result from habitat conversion and land use change, reducing genetic and species diversity; and from the introduction of exotic species, leading to a homogenization of the global biota (*1*). In addition to the ethical, aesthetic, and economic concerns raised by this situation, we contend that these biotic changes will influence ecosystem processes sufficiently to alter the future state of the world's ecosystems and the services they provide to humanity. The current global extinction rate, which is 100 to 1000 times greater than prehuman levels (*3, 4*), and the loss of local diversity due to management practices have the potential to affect ecosystem processes strongly on both local and global scales. This article focuses on species, but there are also functionally important differences at other scales (*5*). For example, genetic diversity in crops improves resistance to disease and reduces the risk of large yield losses caused by epidemics (*6*). At large scales, the diversity and patterning of ecosystems in a landscape affect regional processes, such as nutrient transport from terrestrial to aquatic ecosystems across riparian zones (*7*).

Species differ in the rates and pathways by which they process resources, in their effects on the physical environment, and in their interactions with other species. Thus, changes in species composition are likely to alter ecosystem processes through changes in the functional traits of biota (Fig. 1). This can alter ecosystem processes, such as nitrogen uptake by vegetation, which in turn modifies community processes such as competition and herbivory, feeding back to further changes in community composition. Species-induced changes in ecosystem processes can also alter regional processes (Fig. 1) such as methane emissions from beaver ponds (*8*) or nutrient transfers to aquatic ecosystems (*7*), extending the impacts beyond the original zone of species change. Some species-induced changes in ecosystem and regional processes alter ecosystem services to humans, such as purity of water supplies (*9*) and forest productivity (*10*). Species diversity can influence these same processes (*11*), for two reasons. First, the number of species in a community is a measure of the probability of the presence of species with particularly important traits; second, greater diversity allows a greater range of traits to be represented in the ecosystem, providing opportunities for more efficient resource use in a variable environment.

Changes in species composition and diversity will affect the functioning of ecosystems most strongly when species differ in their effects on ecosystem processes or in their response to environmental change. In the first case, by definition a change in species composition or abundance must affect ecosystem functioning. In the second case, differential environmental sensitivity among functionally similar species gives stability (resistance and resilience) to ecosystem processes, whereas differences in sensitivity among functionally different species make ecosystems more vulnerable to change.

Species Traits

What species traits are most likely to affect ecosystem processes? Traits with profound effects are those that (i) modify the availability, capture, and use of soil resources such as water and nutrients, (ii) affect the feeding relationships (trophic structure) within a community, and (iii) influence the frequency, severity, and extent of disturbances such as fire (*12*).

Resource dynamics. The supplies of water, nutrients, and space are important "bottom-

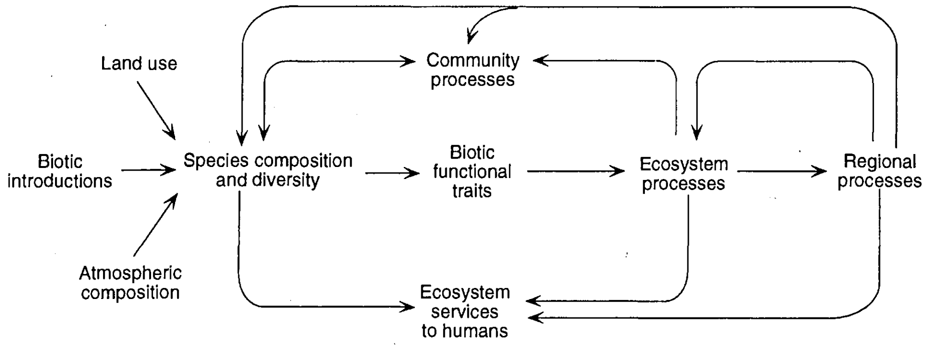

Fig. 1. Linkages involving species composition and diversity and ecosystem processes. Ecosystem processes include productivity and nutrient cycling. Regional processes include trace gas fluxes to the atmosphere and nutrient fluxes from terrestrial to aquatic systems. Community processes include competition and predation. Ecosystem services are the benefits derived by humans from ecological processes.

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up" controls of ecosystem structure and dynamics (*13*), so the introduction or loss of species that alter resource availability strongly affects ecosystem processes. A species could alter resource supply by tapping an otherwise unused source; examples are the introduction of mycorrhizal fungi into mine tailings, where they enhance phosphorus availability to their plant hosts (*14*); the introduction of nitrogen fixers in systems where they did not previously occur (*15*); or the introduction of deep-rooted species, such as *Tamarix* (salt cedar) into deserts (*16*) or *Eucalyptus* into mediterranean ecosystems (*17*), that tap previously inaccessible water and nutrient sources. These species shifts can have major implications for runoff to lakes and streams, salinization of reservoirs, or recovery of degraded ecosystems (*18*).

Organisms modify rates of element and energy transfer within ecosystems in species-specific ways (*19*). For example, there are substantial differences among plant species in litter quality (*20*), effects on soil temperature and moisture (*21*), and exudation of organic compounds from roots (*22*), all of which affect nutrient mineralization. Animals influence the resource base of the ecosystem by changing the distribution (*23*) or importation of nutrients; an example is nutrient import from oceans to streams by migratory salmon. Similarly, termites transport clay particles from subsoils to near the surface, increasing water and nutrient retention (*24*). Microbial functional groups that mediate nutrient cycling, including heterotrophs, nitrifiers, and denitrifiers, differ in their effects on nutrient availability and loss from ecosystems. However, less is known about how the composition of microbial communities within these broad guilds affects processes at the ecosystem level (*25*); there may be substantial overlap in function at the level of microbial species. Although nitrogen and phosphorus dynamics are sensitive to changes in microbial community composition and biomass, carbon cycling may be less so (*26*). In aquatic systems, groups of microbes of different sizes differ in their effects on nutrient and energy flow; small-bodied taxa retain nutrients and energy within the microbial community, whereas the larger plankton are consumed by grazers large enough to provide food to fish (*27*). Changes in microbial biota will have major ramifications for ecosystems in which only one or a few species fill a functional group, in which species-specific interactions control ecosystem dynamics (for example, mutualisms or pathogens), or in which microbes that are "strong controllers" are sensitive to disturbance (*25*).

Widespread changes in species composition that alter resource use can have regional-scale impacts. Simulations suggest that conversion of the Amazon basin from forest to pasture would cause a permanent warming and drying of South America, because the shallower roots of grasses access less water, leading to less evapotranspiration and greater energy dissipation as sensible heat (*28*).

Trophic structure. Some of the most dramatic changes in ecosystem processes have resulted from the introduction or loss of predators or diseases that have large "keystone" effects, which are effects that are substantially greater than would be expected from the biomass of the species (*9, 29*). For example, the introduction of exotic fish can radically alter the abundance of other fish or insects that eat zooplankton, which in turn graze on algae, the abundance of which determines water quality and use by people (*9, 29*). Removal by humans of elephants or other keystone mammalian herbivores leads to encroachment of woody plants into savannas (*30*). Such changes in the abundance of keystone herbivores may have contributed to past shifts in the distribution of biomes (*31*), which, in turn, influence climate (*32*). Microbial trophic dynamics in both soil and aquatic systems can also have large effects on the turnover and fate of nutrients. In soil, the grazing of microorganisms by protozoans often leads to higher rates of nutrient turnover and greater nitrogen and phosphorus availability to plants (*33*). Similarly, epidemic diseases, such as rinderpest in Africa, act as keystone species by modifying competitive interactions and community structure (*34*). A species that is innocuous in its home environment frequently becomes invasive in a new location, if introduced without its herbivores, diseases, and other natural control agents (*35*).

Disturbance regime. Animals or plants that alter the disturbance regime increase the importance of nonequilibrium processes, such as colonization, relative to equilibrium processes, such as competition (*5, 19*). For example, gophers and pigs disturb the soil, creating sites for seedling establishment and favoring early successional, short-lived species (*36*). Beavers in North America are "ecosystem engineers" (*19*) that alter hydrology, aeration, and carbon inputs to soil, influencing the production of greenhouse gases such as methane and CO_2 (*8*). Plants can reduce disturbance rates by stabilizing soils and reducing wind and soil erosion. Thus, even species that are uncommon in mid- and late succession can be critical to the long-term sustainability of an ecosystem (*12*). On the other hand, introduction of grasses into forest or shrubland ecosystems can increase the frequency of fire and cause a replacement of forest by savanna (*37*). Disturbances created by overgrazing can alter the albedo of the land surface and change regional patterns of temperature and precipitation. In one case, the reduced heating and convective uplift of the overlying air mass caused less advection of moisture from the Mediterranean and reduced precipitation (*38*). The increased drought amplified the regional reduction in biomass and production. In another case, the reduction in transpiration resulting from overgrazing in northern Mexico increased sensible heat flux, causing regional warming (*39*).

Indirect species effects. Species that by themselves have small effects on ecosystem processes can have large indirect effects if they influence the abundance of species with large direct ecosystem effects. Thus, a seed disperser or pollinator that has little direct effect on ecosystem processes may be essential for the persistence of a canopy species that has greater direct ecosystem impact (*40*). Unknown indirect effects are often cited by ecologists as justification for the importance of species diversity. However, there is currently no theoretical framework to predict when these indirect effects are most important.

Species Differences in Environmental Response

Species differences in response to environmental change can either provide stability or trigger dramatic functional changes, depending on the traits of the species involved. Species that are similar to one another in their effects on ecosystem processes but differ in their response to the environment provide stability, because any decrease in the abundance of one species will be compensated for by increases in other functionally similar species (*41, 42*). For example, in response to acidification of a lake, the biomass of various groups such as cladocerans, copepods, rotifers, and total zooplankton remained high despite the loss of component species from each group, owing to compensatory increases by other taxa (*43*). The more functionally similar species there are in a community—that is, the greater the diversity within a functional group—the greater will be its resilience in responding to environmental change, if those species differ in environmental responses (*41, 42*). For example, because of the presence of drought-tolerant species, diverse grasslands maintained higher productivity in response to drought than did grasslands whose diversity had been reduced by experimental addition of nutrients (*44*). In Western Australia, functionally similar *Acacia* species have different temperature thresholds for germination, and therefore different species colonize after fires of different intensities (*45*), thus ensuring the replacement of nitrogen after fire across a broad range of burn conditions. Conversely, the fewer species there are in any assemblage, the more likely it is that extinctions will alter ecosystem processes associated with that functional group (*46*). For example, overhunting of sea otters, the only major predator of sea urchins in the western Pacific, increased the abundance of urchins, which grazed down kelp and eliminated kelp forests over extensive areas (*47*). As time scales increase, an ecosystem will experience a wider range of conditions, increasing the importance of diversity among functionally similar species. Thus, genetic and species diversity per se are important to long-term maintenance of community and ecosystem structure and processes. This argues that no two species are ecologically redundant, even if they appear similar in their ecosystem effects under one particular set of environmental conditions.

In contrast to the buffering provided by ecologically similar species, species that differ in their response to the environment and in their effects on ecosystem processes can make ecosystems vulnerable to change. For example, rising concentrations of atmospheric CO_2 can reduce plant transpiration, resulting in increased magnitude or duration of soil moisture (*48*). This, in turn, can shift the competitive balance from grasses to shrubs, promoting shrub encroachment into grasslands and savannas and causing replacement of one biome by another. If extensive, shrub encroachment could reduce regional albedo and enhance regional warming. Similarly, model simulations suggest that forest expansion into tundra at the arctic treeline could have accounted for up to 50% of the high-latitude climate warming that occurred during the Holocene warming 6000 years before the present (*49*).

Impacts of Species Number

Recent experimental and observational studies reveal that biotic diversity can affect multiple ecosystem processes (*5*). In all cases, this dependence comes from diversity being a summary variable that measures the extent of differences in the traits represented in the ecosystem. Studies in Minnesota grasslands (*50*), greenhouses (*51*), and controlled environment chambers (*52*) show that either increased plant diversity, or the types of species represented at different levels of diversity, led to increased plant productivity. Other studies, including those with mixed-species agriculture, find that mixture yields are less than yields of the most productive monoculture but often exceed the average productivity of monocultures of the component species (*5, 53, 54*). In the Minnesota grassland study, greater plant diversity increased the uptake of limiting soil nitrogen and reduced leaching loss of nitrogen, which could, in the long term, help maintain soil fertility. This may occur because species have complementary patterns of resource acquisition or because higher diversity increases the probability of the presence of productive species (*11, 54*).

Higher diversity might increase the stability of ecosystem processes in at least three ways (*5, 41, 44*). First, a high diversity of trophic interactions in diverse ecosystems might provide alternative pathways of energy flow and therefore more stable energy flow among trophic levels (*5, 55*). Second, higher species diversity might reduce the susceptibility of ecosystems to invasion by species with novel ecosystem effects after disturbance (*56*). Third, higher diversity can reduce the spread of plant pathogens by increasing the average distance between individuals of a given species (*53*). For each process, there are simple, but mostly untested, mechanisms that cause the rates and intensities of various ecosystem processes to depend on species diversity.

However, in comparisons among natural ecosystems, there is often no clear relation between species diversity and function; for example, the high resistance of diverse Australian shrub communities to plant invasion (*57*) and high susceptibility to introduced pathogens (*58*) compares with the vulnerability of diverse South African shrublands to plant invasion (*59*). This suggests that factors other than diversity are also important and that we still have much to learn about the role of high levels of natural diversity. This highlights the need for carefully designed comparative and experimental studies of systems with high diversity (*60*).

Future Scenarios

Given the frequently strong effects of species composition and diversity on ecosystem processes seen in experimental studies, what can we expect in the future? Land use change currently has the largest effect on biodiversity (Fig. 2), but changes in atmospheric composition and climate will likely have increasing impacts. The current rapid rates of deforestation, urbanization, and overexploitation, whether through overgrazing or overfishing (*61*), strongly affect species composition and diversity. Areas in which there is substantial nitrogen deposition also exhibit reduced diversity (*62*).

Fig. 2. Many human activities drastically simplify the species richness of ecosystems. (**A**) shows an ancient hay meadow on the Lower Derwent Ings in North Yorkshire, England. "Ing" is a Viking word meaning flooded meadow. The Ings flood every winter, remain damp in the summer, receive no fertilizer or pesticide inputs, and are cropped for hay and grazed in traditional land use practices that have their origins in Viking Britain. The resulting seminatural ecosystems are extremely rich in plants, insects, and birds. They are also very easily destroyed and drastically simplified (**B**) by draining, ploughing, the elimination of winter flooding, and conversion to arable agriculture. Similar changes in land use are severely altering the biological diversity of ecosystems all over the world.

The effects of altered land use on diversity may depend on changes in atmospheric composition and climate. For example, habitat fragmentation may prevent species migration in response to climatic change (*32*), thus causing greater species loss than would either factor by itself.

General circulation models predict geographically variable changes in climate, with temperature increases being most pronounced at high latitudes and precipitation changing with more complex patterns (*63*). Because high-latitude ecosystems have low diversity, climatically mediated changes in species composition will likely have large ecosystem effects in these areas. Land use change will also be heterogeneous because population growth, demand for food, and the suitability of ecosystems to produce that food vary regionally (*64*). The combination of rapid land use change and high diversity in the tropics have made these areas particularly vulnerable to species loss, with largely unknown functional consequences. In regions where changes in both land use and climate are strong, such as in midcontinent regions, we expect to see the greatest changes in species composition, diversity, and ecosystem processes. Often areas that are hot spots for diversity, such as riparian corridors, are the areas that experience the greatest human impact and have the largest effects on landscape processes.

Recent research on biotic controls on ecosystem processes has only scratched the surface of the complex web of interactions that govern the functioning of the biosphere. Comparative studies, both manipulative and observational, are required to determine why some ecosystems are more resistant and resilient to interference than others.

Conclusions

Both types of species present and diversity per se have important influences on ecosystem processes and services. The apparent conflict between the perspectives that each species is important (*65*) and that there is ecological redundancy among species (*42*) is resolved when biotic composition is considered in terms of functional types of organisms and their environmental responses. Changes in the abundance of species that differ in ecosystem consequences should affect process rates or patterns, whereas the abundance of species with similar ecological effects should give stability (resistance and resilience) to ecosystems in the face of increasingly rapid human-induced environmental change. Loss of a keystone species or of all species in a major functional group will, by definition, have large ecosystem effects. Efforts to identify and protect such species and groups often yield demonstrable near-term benefits. Of increasing concern is the loss of species that have similar ecosystem effects but differ in their environmental responses. Loss of such species may reduce ecosystem resilience and the capacity to adjust to ever-increasing rates of environmental change. This latter role of diversity is not adequately represented in current international conventions, but it may be one of the most important mechanisms by which we sustain the long-term functioning of ecosystems and the services they provide to society.

Species effects on ecosystems occur at all scales, from local to global, and their effects may be intense or subtle. Ecologists are only now beginning to establish the theoretical, empirical, and experimental frameworks to understand and predict how changes in species composition affect ecosystem processes. In a world in which local and global species extinctions are accelerating and exotic species are entering communities at unprecedented rates, links between species and ecosystem processes are emerging as a problem of fundamental concern.

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Agricultural Intensification and Ecosystem Properties

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Expansion and intensification of cultivation are among the predominant global changes of this century. Intensification of agriculture by use of high-yielding crop varieties, fertilization, irrigation, and pesticides has contributed substantially to the tremendous increases in food production over the past 50 years. Land conversion and intensification, however, also alter the biotic interactions and patterns of resource availability in ecosystems and can have serious local, regional, and global environmental consequences. The use of ecologically based management strategies can increase the sustainability of agricultural production while reducing off-site consequences.

Expansion of agricultural land is widely recognized as one of the most significant human alterations to the global environment. The total area of cultivated land worldwide increased 466% from 1700 to 1980 (*1*). Whereas the rate of expansion has slowed in the last three decades, yields (food produced per area of land) have increased dramatically (*2*, *3*) and have outpaced global human population growth. This remarkable scientific and technological achievement is based largely on intensification of management on land already under agriculture, accomplished through the use of high-yielding crop varieties, chemical fertilizers and pesticides, irrigation, and mechanization. In the developing countries, this intensification fell under the general heading of "the Green Revolution," which began in the 1960s with the transfer and dissemination of high-yielding seed (*3*). Intensification and rise in crop yields have been evident in both developed and less-developed countries, and are demonstrated by the long-term yield pattern for corn and wheat in eastern Colorado (Fig. 1), where irrigated corn yields have increased by 400 to 500% since 1940, and wheat yields have increased up to 100%.

Concerns have developed, however, over the long-term sustainability and environmental consequences of the intensification of agricultural systems. It is now clear that agricultural intensification can have negative local consequences, such as increased erosion, lower soil fertility, and reduced biodiversity; negative regional consequences, such as pollution of ground water and eutrophication of rivers and lakes; and negative global consequences, including impacts on atmospheric constituents and climate. Concerns about the ability to maintain long-term intensive agriculture are also growing. In India, for instance, the intensive rice-wheat systems of the Punjab are beginning to show signs of serious decline associated with loss of soil quality and increased plant health problems (*4*); the growth in yields from intensive paddy rice in Asia is also in question (*5*).

At the same time that environmental concerns are increasing, so are concerns about feeding a rapidly growing human population and reducing hunger. Demographers predict that the population will grow to between 8 billion and 10 billion in the 21st century. Meanwhile, some 800 million people are malnourished today. Although malnutrition and hunger are currently more related to poverty and inequitable food access than to inadequate food production per se, many regions of the world, particularly parts of Africa, are not self-sufficient in food production (*6*). Thus, agricultural intensification remains a major target of research and development. Reconciliation of these two needs—increased world food production with greater protection of the environment for the future—is subsumed under the umbrella of "sustainable development" and presents a major challenge for science in the 21st century. Understanding how ecosystems are altered by intensive agriculture, and developing new strategies that take advantage of ecological interactions within agricultural systems (*7*), are crucial to the continuance of high-productivity agriculture in the future.

Biological Consequences of Agricultural Intensification

One key feature of agricultural intensification has been increasing specialization in the production process, resulting in reduction in the number of crop or livestock species, or both, that are maintained, often leading to monoculture (Fig. 2). The composition of the plant community, as determined by the farmer, may be described as the "planned diversity" of crop systems; ultimately, this crop diversity is critical not only in terms of production but because it is an important determinant of the total biodiversity. It influences the composition and abundance of the associated biota such as those of the pest complex and the soil invertebrates and microorganisms, which in turn affect plant and soil processes (*8*). In the following sections, we discuss the role of these biological components of the system and the ways they are altered by cultivation.

The pest complex. In both agricultural and natural ecosystems, herbivorous insects and microbial pathogens can have significant impacts on plant productivity. The reduction in plant species richness that accompanies agricultural intensification leads to changes in the community composition of the pest complex—herbivorous insects, their natural enemies (predators and para-

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