Chapter 11

Biodiversity Regulation of Ecosystem Services

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Main Messages

Biodiversity, including the number, abundance, and composition of genotypes, populations, species, functional types, communities, and landscape units, strongly influences the provision of ecosystem services and therefore human well-being (*high certainty*). Processes frequently affected by changes in biodiversity include pollination, seed dispersal, climate regulation, carbon sequestration, agricultural pest and disease control, and human health regulation. Also, by affecting ecosystem processes such as primary production, nutrient and water cycling, and soil formation and retention, biodiversity indirectly supports the production of food, fiber, potable water, shelter, and medicines.

Species composition is often more important than the number of species in affecting ecosystem processes (*high certainty***).** Thus, conserving or restoring the composition of communities, rather than simply maximizing species numbers, is critical to maintaining ecosystem services. Changes in species composition can occur directly by species introductions or removals, or indirectly by altered resource supply due to abiotic drivers (such as climate) or human drivers (such as irrigation, eutrophication, or pesticides).

Although a reduction in the number of species may initially have small effects, even minor losses may reduce the capacity of ecosystems for adjustment to changing environments (*medium certainty*). Therefore, a large number of resident species, including those that are rare, may act as "insurance" that buffers ecosystem processes in the face of changes in the physical and biological environment (such as changes in precipitation, temperature, or pathogens).

Productivity, nutrient retention, and resistance to invasions and diseases tend to increase with increasing species number in experimental ecosystems that have been reduced to a small number of species (10 or fewer). This is known with *high certainty* for experimental herbaceous ecosystems and with *low certainty* for natural ecosystems, especially those dominated by long-lived species. In natural ecosystems these direct effects of biodiversity loss may often be masked by other environmental changes that are caused by the factors that resulted in the loss of biodiversity (such as eutrophication or climate change). Nevertheless, human activities that cause severe reductions in species number can directly impair these ecosystem services.

Preserving interactions among species is critical for maintaining long-term production of food and fiber on land and in the sea (*high certainty*). The production of food and fiber depends on the ability of the organisms involved to successfully complete their life cycles. For most plant species, this requires interactions with pollinators, seed disseminators, herbivores, or symbionts. Therefore, land use practices that disrupt these interactions will have a negative impact on these ecosystem services.

Intended or accidental changes in the composition of ecological communities can lead to disproportionately large, irreversible, and often negative alterations of ecosystem processes, causing large monetary and cultural losses (*high certainty*). In addition to direct interactions, the maintenance of ecosystem processes depends on indirect interactions, whose disruption can lead to unexpected consequences. These consequences can occur very quickly; for example, in a wide range of terrestrial, marine, and freshwater ecosystems, the introduction of exotic species by humans has altered local community interactions. Alternatively, these consequences may be manifest only after a long time. For example, the intraspecific genetic diversity of certain plant species decreases when the populations of their animal pollinators or dispersers are reduced.

Invasion by exotic species, facilitated by global trade, is a major threat to the biotic integrity of communities and the functioning of ecosystems. Empirical evidence suggests that areas of high species richness (such as hot spots) are more susceptible to invasion than species-poor areas. On the other hand, within a given habitat the preservation of its natural species pool appears to decrease its susceptibility to invasions. On the basis of our present theoretical knowledge, however, we still cannot predict with accuracy whether a certain organism will become a serious invader in a given ecosystem.

The extinction of local populations, or their reduction to the point that they become functionally extinct, can have dramatic consequences in terms of regulating and supporting ecosystem services. Local extinctions have received little attention compared with global extinctions, despite the fact that the former may have more dramatic ecosystem consequences than the latter. Before becoming extinct, species become rare and their ranges contract. Therefore their influence on ecosystem processes decreases, even if local populations persist for a long time, well before the species becomes globally extinct. We do not have sufficient knowledge to predict all the consequences of these local extinctions. However, because they tend to be biased toward particular organisms that depend on prevailing land uses and types, rather than occurring at random, we can anticipate some of the most obvious impacts.

The properties of species are more important than species number in influencing climate regulation (*medium certainty*). Climate regulation is influenced by species properties via effects on sequestration of carbon, fire regime, and water and energy exchange. The traits of dominant plant species, such as size and leaf area, and the spatial arrangement of landscape units are particularly important in climate regulation. The functional characteristics of dominant species are thus a key element determining the success of mitigation practices such as afforestation, reforestation, slowed-down deforestation, and biofuel plantations.

The diversity of landscape units also influences ecosystem services (*high certainty***).** The spatial arrangement of habitat loss, in addition to its amount, determines the effects of habitat loss on ecosystem services. This is because the effects of habitat loss on remaining habitat fragments are greater on the edges than in their cores. Thus, fragmentation of habitat has disproportionately large effects on ecosystem services. These effects are best documented in the case of carbon sequestration and pollination in the tropics.

Maintenance of genetic and species diversity and of spatial heterogeneity in low-input agricultural systems reduces the risk of crop failure in a variable environment and reduces the potential impacts of pests and pathogens (*high to medium certainty*). Agroforestry systems, crop rotations, intercropping, and conservation tillage provide opportunities to protect crops and animals from pests and diseases while maintaining yields without heavy investment in artificial chemicals.

Global change drivers that affect biodiversity indirectly also affect biodiversity-dependent ecosystem processes and services. Among these global change drivers, a major threat to biodiversity-dependent human well-being is large-scale land use change, especially the intensification and extensification associated with large-scale industrial agriculture *(high certainty).* This threat is most obvious for those human groups that are already vulnerable because their livelihoods rely strongly on the use of natural and seminatural ecosystems. These include subsistence farmers, the rural poor, and traditional societies.

A considerable amount of new research is needed to understand the role of different components of biodiversity in the provision of ecosystem

services. Although the available evidence clearly points to the key importance of the maintenance of the genetic, species, and landscape diversity of ecosystems in order to preserve the ecosystem services they provide, important knowledge gaps remain to be filled. These are particularly obvious in the case of high-diversity ecosystems, ecosystems dominated by long-lived plants, and trophic levels other than plants.
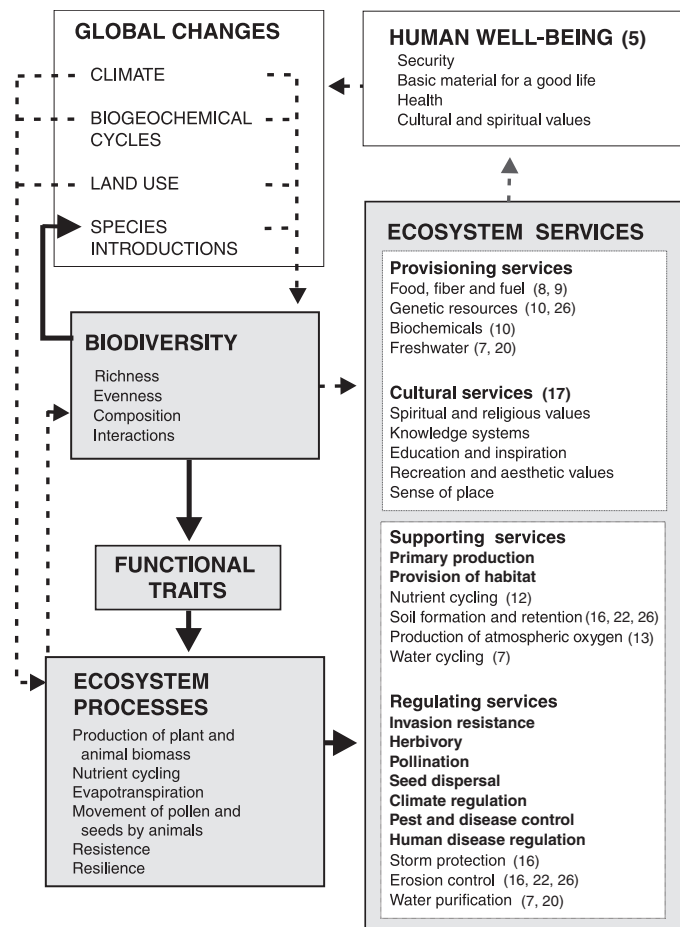
11.1 Introduction

Biodiversity refers to the number, abundance, and composition of the genotypes, populations, species, functional types, communities, and landscape units in a given system. Biodiversity is both a response variable that is affected by changes in climate, resource availability, and disturbance (see Chapter 4) and a factor with the potential to influence the rate, magnitude, and direction of ecosystem processes. This chapter focuses on this second aspect—the effects of biodiversity on ecosystem processes and the ecosystem services that humans obtain from them.

Ecosystem services are broadly defined as the benefits provided by ecosystems to humans; they contribute to making human life both possible and worth living (Daily 1997; MA 2003). Biodiversity affects numerous ecosystem services, both indirectly and directly. Some ecosystem processes confer direct benefits on humanity, but many of them confer benefits primarily via indirect interactions.

This chapter focuses on regulating and supporting ecosystem services (see Chapter 1) that result from interactions between two or more species or genotypes. The regulating ecosystem services addressed in this chapter include pollination, seed dispersal, climate regulation, carbon sequestration, and pest and disease control. (See Figure 11.1.) Biodiversity also provides supporting ecosystem services, which are necessary for the production of all other—more direct—ecosystem services. For example, by influencing primary production and nutrient and water cycling, biodiversity indirectly supports the production of food, fiber, and shelter. The enormous value of biodiversity per se and its importance in the provision of cultural ecosystem services are described in detail in Chapters 4, 10, and 17. Here the focus is on how biodiversity affects the quantity and temporal stability of the supply of those services.

Consideration of all components of biodiversity—genotypes, species, functional traits and types, communities, and landscape units—is essential in order to understand its role in ecosystem processes and thus in the provision of ecosystem services. Although traditionally the focus has been mainly on species number, there is now broad consensus that functional diversity—the value, range, and relative abundance of organismal traits present in a community—is the most important component of biodiversity influencing ecosystem functioning (Díaz and Cabido 2001; Loreau et al. 2001; Hooper et al. 2005). Recent scientific literature on the functional role of biodiversity has generated conflicting results that are sometimes difficult to interpret. However, some basic points of agreement have emerged that are relevant to land use and conservation policies.

Most of the current evidence and theory described early in this chapter deal with direct interactions among terrestrial plants. Although a growing number of studies incorporate other ecosystem processes, most of what we know about biodiversity effects on ecosystem functioning refers specifically to the production of plant biomass (the tissues formed using the solar energy captured by photosynthetic plants). However, there is growing empirical evidence suggesting that the influence of interactions between

Figure 11.1. Biodiversity as Response Variable Affected by Global Change Drivers and as Factor Modifying Ecosystem Processes and Services and Human Well-being (modified from Chapin et al. 2000). Solid arrows indicate the links that are the focus of this chapter. Regulating services are the benefits obtained from the regulation of ecosystem processes. Supporting services are those that are necessary for the production of all other services. Ecosystem services in bold are developed in detail in this chapter. Other services are not addressed here because the role of biodiversity in regulating them in ecosystem processes is minor or uncertain, or because they are developed in detail elsewhere in this volume (relevant chapter number is indicated in parentheses).

plants and microorganisms and between plants and animals as well as the influence of indirect interactions on ecosystem properties are both important and widespread. Because these intertrophic and indirect interactions have received much less attention in the literature, they are emphasized in this chapter. The effects of terrestrial biodiversity on ecosystem services is discussed first, followed by a similar discussion of the effects of marine biodiversity on ecosystem processes provided by oceans and coastal areas, a topic whose importance has been recognized only recently.

Two major aspects of ecosystem functioning form the focus of this analysis: resource dynamics at given point in time (which includes processes such as primary and secondary production, nutrient cycling, and water dynamics) and long-term stability of such processes in the face of environmental variability or directional change.

11.2 Terrestrial Biodiversity Effects on Supporting Services

Region-to-region differences in ecosystem processes are driven mostly by climate, resource availability, and disturbance—not by differences in species richness. In most ecosystems, changes in the number of species are the consequence of changes in major abiotic and disturbance factors, so that the ecosystem effect of species richness (number of species) per se is expected to be both comparatively small and very difficult to isolate. For example, variation in primary productivity depends strongly on temperature and precipitation at the global scale and on soil resources and disturbance regime at the region-to-landscape-to-local scales. Factors that increase productivity, such as nutrient addition, often lead to lower species richness because more productive species outcompete less productive ones. In nature, therefore, high species diversity and high productivity are often not positively correlated (Grime 1979, 2001; Gough et al. 1994; Waide et al. 1999).

When elaborating management recommendations, it is extremely important to bear these considerations in mind and to interpret the conclusions of experiments within the right context. Here again, if taken uncritically, results from synthetic assemblages may lead to misleading recommendations to land managers (see also Fridley 2001; Schmid 2002; Hodgson et al. 2005).

Similarly, artificial increases of species richness in naturally species-poor areas (such as moorlands, boreal forests, or desert shrublands) may not result in any substantial "improvement" in ecosystem services. In natural ecosystems, low species richness does not necessarily imply impaired ecosystem properties and services. In most synthetic-community experiments, the assemblage of experimental communities occurs by random draws of species from a species pool decided by the experimenter, and the abundances of different species are artificially even, at least at the initial stages. This strongly differs from the process of community assembly that occurs in nature, in which the local assemblage is the product of a "filtering" process exerted by the environment on the regional species pool (Zobel 1997; Díaz et al. 1998).

Extinction in natural ecosystems similarly tends to be biased to certain organisms (Vitousek et al. 1997; Grime 2002; see also Chapter 4) rather than being a random process. In most natural assemblages, any unused resources are likely to be quickly used by members of the species pool, even in communities with low species richness (Zobel 1997; Hodgson et al. 1998). Some low-species-richness combinations in synthetic communities, on the other hand, are artificially maintained and could not persist in nature (Hodgson et al. 1998; Lepš 2005). This does not necessarily invalidate the results of experiments based on artificial assemblages; however, it is crucial to understand that low species richness in these experiments and in real ecosystems stem from different causes. Low diversity in nature tends to occur at either very high or very low productivity and to result from different processes in each situation. Most often, it results from strong abiotic constraints at low productivity and high biotic constraints at high productivity (see, e.g., Huston 1999; Pärtel et al. 2000).

Nevertheless, biodiversity can directly affect supporting services such as primary productivity, soil formation, and nutrient cycling, which in turn influence provisioning services such as genetic resources and production of food, timber, fuel, and fiber. The mechanisms by which that happens, and the empirical evidence accumulated to date are discussed in the remainder of this section.

In general, the most important component of plant biodiversity influencing ecosystem services is functional composition. And, other things being equal, a greater number of resident species should result in greater production, higher nutrient retention, and enhanced resistance to invasion, at least in experimental studies using a low number of resident species. There is also some indication that a high number of species within each functional type (a group of organisms that responds to the environment or affects ecosystem processes in a similar way) should lead to more stability in the face of perturbations than a low number of species, although direct experimental evidence of this is limited.

Productivity of agroecosystems may not increase if individual agricultural fields are planted with higher species richness, because under intensive modern agriculture a single strain of a single crop species is likely to give the highest yield or the highest profit in a given field (Swift and Anderson 1993). The situation may be different, however, in agroecosystems managed using approaches that incorporate biodiversity (such as the "agricultural diversification" or "integrated pest management" paradigms described later), where species composition and resource levels are under much looser control by the land managers, and thus recruitment from the natural species pool plays a more relevant role (Swift and Anderson 1993; Fridley 2001).

In high-biodiversity agriculture, a larger number of species may provide "ecological insurance" against crop failures, which is especially important to poor farmers disconnected from market insurance systems. (See Chapters 6 and 26.) Changes in species numbers may have only subtle short-term effects in some ecosystems but may directly influence their capacity for long-term adjustment in the face of a changing environment.

Major changes in species composition due to direct introduction or removal of species, or caused indirectly by changing relative abundances via altered resource supply (such as irrigation or eutrophication), can shift the functional trait composition of ecosystems and therefore deeply modify their derived services. Therefore, the preservation of the integrity, in terms of size and composition, of the regional species pool is a key factor in maintaining the rate, magnitude, and long-term persistence of those ecosystem processes that support ecosystem services. The regional species pool is defined as the set of species occurring in a certain region that is capable of coexisting in the target community.

11.2.1 Ecosystem Resource Dynamics, with Emphasis on Primary Production

The relationship between plant species richness and ecosystem production (including both total biomass achieved and the rate at which that biomass is achieved—that is, productivity) and the efficiency of resource use is probably the single most tested—and most debated—aspect of the relationship between biodiversity and ecosystem functioning. One important source of controversy among authors stems from the different results that emerge from studies at different spatial scales, where the controlling processes may differ (Fridley 2001; Loreau et al. 2001; Hooper et al. 2005). Specifically, some studies have focused on the relationship between species richness within a single habitat, whereas others have compared patterns among different habitats. For example, when ecosystems developed in different habitats are compared, soil fertility is a strong determinant of primary production and plant species diversity.

Two synthesis articles published in the last few years provide a good overview of the state of the art in this topic (Loreau et al. 2001; Hooper et al. 2005). Some of the main empirical findings and underlying theoretical issues related to the role of biodiversity in regulation ecosystem resource dynamics in general, and to primary production in particular, are summarized here.

Experimental manipulation of species richness in greenhouse (Naeem et al. 1995; Symstad et al. 1998) and large-scale field

experiments (Tilman et al. 1996, 1997a, 2001; Hector et al. 1999, 2001) has shown a positive relationship between plant species richness and primary production, especially at low number of species (see Schläpfer and Schmid 1999; Schwartz et al. 2000; Hector 2002; Schmid et al. 2002; Tilman et al. 2002b). (See Table 11.1.)

In some experimental studies, total plant biomass has experimentally been shown to be greater, on average, and levels of soil nitrate—the limiting resource—lower (less leaching) at higher levels of plant species richness (Tilman et al. 1996, 1997a). Tilman et al. (2001) found that both species richness and functional type composition were significant controllers of productivity, and that no low-richness plot was as productive as many higher-richness combinations of species were. However, other experimental studies have found that ecosystem processes are more strongly linked to plant species and functional type composition than to species richness (Hooper and Vitousek 1997; Tilman et al. 1997a; Wardle et al. 1997a, 1999; Crawley et al. 1999; Lavorel et al. 1999; Kenkel et al. 2000; Paine 2002; Hooper and Dukes 2004). The influence of plant species richness or composition on soil processes such as decomposition and microbial activity is less well understood (Wardle et al. 2004).

For forest ecosystems, most data come from observational field surveys that compare natural, managed, or old forest plantations with different tree species richness. Single-species tree stands and adjacent two-species stands have been the most studied (reviewed by Cannell et al. 1992; Kelty et al. 1992). In general, two-species forests are more productive than stands dominated by a single species, but they are not necessarily more productive than the best monoculture.

Inhibitory and enhancing effects are also common. In the United Kingdom, for example, studies of two-species combinations of a pool of four species have shown that mixtures that con-

Table 11.1. Main Components of Biodiversity Involved in Supporting and Regulating Ecosystem Services Addressed in This Chapter. Bullets indicate importance and/or degree or certainty (•••> ••> •). The mechanisms and shape of the relation between the provision of ecosystem services and diversity remain highly speculative in many cases. In the cases of most saturating curves, the level at which diversity effects saturate for different ecosystem services is poorly known. Biodiversity also contributes to provisioning and cultural ecosystem services in important ways.

Ecosystem Services	Main Components of Biodiversity Involved	Mechanisms That Produce the Effect	How the Provisioning of Service Scales to Diversity
Supporting services			
Amount of primary production	••• functional composition of plant assemblage	faster-growing, bigger, more efficient, more locally adapted plants will produce more biomass	complex relationship; processes depend on identity of dominant species, not species richness
		in low-diversity systems, coexisting plants with very different (complementary) resource use strategies will take up more resources	saturating curve
	•• species richness of plant assemblage	a larger species pool is more likely to contain groups of complementary species and individual species that are highly productive, both of which should lead to higher productivity of the community	saturating curve
Stability of primary production	••• genetic diversity	large genetic variability within a crop species buffers production against losses due to diseases and environmental change	saturating curve
	••• species richness	polycultures (more than one species cultivated together) maintain production over a broader range of conditions	saturating curve
	••• functional composition of plant assemblage	life history, resource use strategy, and regeneration strategy of dominant plants determine resistance and resilience of ecosystem functioning against perturbations	complex relationship; stability depends on identity of dominant species, not species richness saturating curve; subordinate species can totally or partially compensate for functions of dominants
Provision of habitat	••• habitat diversity, including spatial distribution, size and shape of landscape units	connectivity, landscape heterogeneity, and large landscape units are necessary for migrating species and species that need large foraging areas	complex relationship, likely to be different for different kinds of organisms
	••• functional composition of vegetation	some vertebrates need a complex vegetation structure for breeding and roosting	complex relationship; stability depends on identity of dominant species, not species richness
	•• species richness	the more species at each trophic level, the more species herbivores, predators, and/or pathogens are provided a resource base	saturating curve
Regulating services			
Invasion resistance	••• species composition	some key native species are very competitive or can act as biological controls to the establishment and naturalization of aliens	complex relationship; processes depend on identity of dominant species, not species richness
	••• arrangement of landscape units	landscape corridors (e.g., roads, rivers, extensive crops) can facilitate the spread of aliens	complex relationship; size and nature of suitable corridors likely to be different for different organisms
	•• species richness and diversity	all else being equal, species-rich communities are more likely to contain highly competitive species and fewer vacant niches, and therefore to be more resistant to invasions	decreasing curve, often exponential decay to zero in experimental studies

Table 11.1. *continued*

Ecosystem Services	Main Components of Biodiversity Involved	Mechanisms That Produce the Effect	How the Provisioning of Service Scales to Diversity
Pollination	••• functional composition of pollinator assemblage	loss of specialized pollinators leads to a reduction of number and quality of fruits produced and plant genetic impoverishment	complex relationship; processes depend on identity of dominant species, not species richness
	•• species richness of pollinator assemblage	lower pollinator species richness leads to a reduction of number and quality of fruits produced and plant genetic impoverishment	linear relationship for co-evolved pollination systems; saturating curve or linear relationship for generalist pollination systems
	•• arrangement and size of landscape units	large landscape units and/or connectivity among them maintain plant genetic pool and number and quality of fruits	saturating curve
Climate regulation	••• arrangement and size of landscape units	size and spatial arrangement of landscape units over large areas influence local-to-regional climate, by lateral movement of air masses of different temperature and moisture	threshold for effect is patch size (landscape diversity) of about 10 km diameter, depending on wind speed and topography
	•• functional composition of vegetation	height, structural diversity, architecture, and leaf seasonal patterns modify albedo, heat absorption, and mechanical turbulence, thus changing local atmospheric temperature and air circulation patterns	linear relationship between albedo and heating; albedo depends on structural diversity and on the plant functional types that dominate the canopy
Carbon sequestration	••• arrangement and size of landscape units	carbon loss is higher at forest edges; as forest fragments decline in size, a larger proportion of the total landscape is losing carbon	nonlinear relationship; as patches get larger, changes in carbon sequestration should saturate (the edges become a smaller proportion of total area); conversely, as patches get smaller, carbon loss increases exponentially with degree of fragmentation
	•• functional composition of vegetation	fast-growing, fast-decomposing, short-leaved, small-sized plants retain less carbon in their biomass than slow-growing, slow-decomposing, long-leaved, large-statured plants	saturating relationship with plant size; linear relationship with surface area of landscape units; note that the diversity has to do with the column to the left; in some cases the shape of this relationship is not related to diversity
	• species richness of vegetation	high species richness can slow down the spread of pests and pathogens, which are important agents of disturbance and carbon loss from ecosystems	saturating curve
Pest and disease control in agricultural systems	••• genetic diversity of crops	reduces density of hosts for specialist pests, and thus their ability to spread	saturating curve, but substantial effects are achieved with only a few species
	•• high richness of crop, weed, and invertebrate species	similar to genetic diversity, but also increases habitat for natural enemies of pest species	saturating curve in general, but some weed or invertebrate species may lead to a complex relationship
	•• spatial distribution of landscape units	natural vegetation patches intermingled with crops are the habitat of many natural enemies against insect pests	saturating curve as the size and number of natural vegetation patches increase; saturation point likely to be different for different groups of natural enemies

tain the pine *Pinus sylvestris* are always more productive than any monospecific stand due to the nursing effect of pines on other species with no detriment to itself, whereas mixtures of Norway spruce (*Picea abies*) and alder (*Alnus glutinosa*) have lower productivity than monospecific stands of either species (Brown 1992). These results suggest that, for temperate forests, species identity and combination might be more important than tree species richness per se. Forest productivity seems to be improved in two-species stands when there is complementarity in resource use (for instance, early and late successional species, shade-tolerant and shade-intolerant species, or different duration of the growing season).

Few studies have compared primary production of forests over a wide range of species richness. The Forest Inventory and Analysis database in the United States shows a positive correlation between tree species richness and stand productivity (Caspersen and Pacala 2001). However, the lack of environmental description

hinders the interpretation of this association, especially because for two-species mixtures it is known that whether mixtures are more productive than pure stands depends on site conditions. In the western Mediterranean basin, productivity has also been compared across a range of forests with different tree species richness (Vilà et al. 2003). Here, monospecific pine forests have lower wood production than mixed (two- to five-species) forests. However, the species-rich forests are associated with humid climates, certain bedrock types, and early successional stages, which may be the cause of higher productivity.

The production of leaf litter may be greater in forests with two or more tree species than in monospecific forests, but whether there was a positive effect beyond two-species mixtures depended on the species and functional identity of the dominant tree species (Vilà et al. 2004). Similarly, the effect of tree species interactions on decomposition, a key process in nutrient cycling, seems to be species- and mixture-specific (Fyles and Fyles 1993),

depending on the leaf litter quality of the trees and the associated microbial detritivore community (Blair et al. 1990; Wardle et al. 1997). Species-specific effects do not necessarily contradict the possibility of diversity effects. However, the lack of long-term monitoring with a reasonable number of species limits the ability to assess the relative importance of composition versus number of tree species. Therefore, general conclusions about the causal links between species richness and ecosystem processes in forests cannot yet be made.

On the other hand, an increasing number of reports indicate that the functional components of biodiversity (value, range, and relative abundance of plant traits) play an important role in ecosystem resource dynamics. Significant associations of ecosystem processes with plant functional composition and richness have been found more consistently than associations with species richness (Díaz and Cabido 2001). Considerable evidence, both from experiments and from nonmanipulative field studies of plant communities, shows that not all species are equally important to ecosystem functioning. Some are particularly crucial due to their traits or relative abundance.

In particular, the relative distribution of plant biomass among species is highly inequitable in most communities, with a minority of species (dominants) contributing most of the total biomass. The traits of the dominant plant species are usually the key drivers of an ecosystem's processing of matter and energy (see Hobbie 1992; Aerts 1995; Chapin et al. 1996; Aerts and Chapin 2000; Lavorel and Garnier 2002 for reviews). Therefore, at any given time the relative roles of species and functional type richness in ecosystem functioning tend to be small compared with the effect of the most dominant species. In these situations, the loss or introduction of dominant plant species may lead to much more important shifts in ecosystem functioning than those of other plant species, irrespective of changes in species richness (Lepš et al. 1982; Hooper and Vitousek 1997; McGrady-Steed et al. 1997; Wardle et al. 1997a; Mikola 1998; Symstad et al. 1998; Grime et al. 2000).

Even in situations where the average effect of the loss of randomly chosen plant species is a decrease in ecosystem productivity and nutrient use, large variations in ecosystem processes exist depending on which species or functional types are lost. The literature on invasive species provides dramatic examples of major ecosystem changes brought about by very small changes in species richness, usually the addition of a single species. (See Table 11.2.)

Biodiversity can influence ecosystem processes via at least two qualitatively different but not mutually exclusive mechanisms. One is the "niche complementarity effect" or "niche differentiation effect." Because the range of functional types is likely correlated with species number, species-rich communities may achieve more efficient resource use in a spatially or temporally variable environment than in species-poor communities (Tilman 1999; Loreau 2000). Complementary interactions, which are caused by differences among species in their resource and environmental needs, allow combinations of species to obtain more resources and produce more biomass than could any single species. Typical examples of resource-use complementarity are plant species with shallow and deep roots, warm-season and cool-season grasses, and diurnal and nocturnal pollinators or predators. In species-poor situations, increasing species richness would add novel traits, which will allow a more complete use of available resources. Positive interactions between species, such as facilitation and mutualism (increased availability of nitrogen to grasses as a consequence of the presence of nitrogen-fixing legumes, for example), may also enhance biomass production.

The second mechanism that can explain the positive effects of species diversity on ecosystem processes is the "sampling effect"

(Aarssen 1997; Huston 1997; Tilman et al. 1997b), also called the "selection probability effect" (Loreau 1998): the greater the number of species initially present in an ecosystem, the higher the probability of including a species that performs particularly well under these conditions. Because any given species has a greater chance of being present at higher species richness, communities with higher number of species would be more likely to contain "better-performing" species (bigger, faster-growing, more tolerant to the prevailing conditions, more likely to have facilitative effects on other species, and so on) and thus to function "better" than species-poor communities. The sampling effect emphasizes the effects of a single dominant species and its greater chance of being present ("sampled") in communities with more species.

The niche complementarity effect and the sampling effect are not mutually exclusive, and their relative importance varies among ecosystems, depending on the environmental conditions. For example, the niche complementarity effect should be most relevant in areas of high spatial heterogeneity of environmental conditions and resource availability, whereas the sampling effect should be most relevant in small habitat patches, in early successional communities, and in areas with high resource availability (Fridley 2001). Differences among species are central to both mechanisms (Díaz and Cabido 2001). This is because the traits of the dominant plants have a strong influence on local ecosystem functioning (sampling effect) and because the greater the differences among coexisting species in terms of traits, the more likely they are to be complementary (rather than overlapping) in their resource use (niche complementarity effect).

Most biodiversity studies have focused on plant biomass, in part because of its importance in the production of food and fiber. However, much less is known about biodiversity effects on other important ecosystem processes, such as nutrient cycling, secondary production, or water dynamics. Another difficulty in generalizing from past biodiversity studies is that most empirical findings and theoretical developments are derived from a focus on herbaceous plant communities, where results are expressed rapidly. Further progress in the understanding of the role of biodiversity on ecosystem processes and services will depend on widening the scope of investigation toward other ecosystem processes, vegetation types, and trophic levels.

11.2.2 Ecosystem Stability, with Emphasis on Primary Production

For continued delivery of ecosystem services, both rate and magnitude of ecosystem processes and their stability over long periods of time, especially in the face of environmental variability, matter. Stability of an ecosystem is defined as its capacity to persist in the same state. Ecosystem stability is often divided into two components: resistance and resilience. Resistance is the capacity of a system to remain in the same state in the face of perturbation. Resilience is the rate at which a system returns to its former state after being displaced from it by a perturbation (Lepš et al. 1982). Temporal variability in community composition, including that associated with the invasion by non-native species, is an inverse measure of resistance.

Ecological theory predicts a positive relationship between species richness and the stability of ecosystems. Species-rich communities should have greater interspecific variation in responses to perturbation or environmental variation, and therefore variation in ecosystem services should be less than in species-poor communities (Tilman 1996; Doak et al. 1998; Yachi and Loreau 1999; Lehman and Tilman 2000). In addition, when species compete, the number of feedback loops in a competitive community in-

Table 11.2. Ecological Surprises Caused by Complex Interactions. Voluntary or involuntary introductions of species often trigger unexpected alterations in the normal provision of ecosystem services by terrestrial, freshwater, and marine ecosystems. Thus the introductions or deletions can have consequences opposite the intended management goals and can affect ecosystem services negatively. In all cases, the community and ecosystem alterations have been the consequence of indirect interactions among three or more species.

Study Case	Nature of the Interaction Involved	Ecosystem-service Consequences	Source
Introductions			
Top predators			
Introduction of brown trout (*Salmo trutta*) in New Zealand for angling	trophic cascade, predator increases primary producers by decreasing herbivores	negative — increased eutrophication	Flecker and Townsend 1994
Introduction of bass (*Cichla ocellaris*) in Gatun Lake, Panama	trophic cascade, top predator decreases control by predators of mosquito larvae	negative — decreased control of malaria vector	Zaret and Paine 1973
Introduction of pine marten (*Martes martes*) in the Balearic Islands, Spain	predator of frugivorous lizards (main seed dispersers)	negative — decreased diversity of frugivorous lizards due to extinction of native lizards on some islands; changes in dominant shrub (*Cneorum tricoccon*) distribution because marten replaced the frugivorous-dispersing role	Riera et al. 2002
Introduction of Artic fox (*Alopex lagopus*) in the Aleutian archipelago	predator of seabirds that transport large quantities of nutrient-rich guano from productive ocean waters to land	negative — reduced transport of nutrient from ocean to land; reduced soil fertility, nutrient status of plants, primary productivity and induced compositional shifts from productive grass-sedge to less productive shrub-forb communities	Croll et al. 2005
Intraguild predators			
Potential egg parasitoid (*Anastatus kashmirensis*) to control gypsy moth (*Lymantria dispar*)	hyperparasitism (parasitoids that may use parasitoids as hosts)	negative — disruption of biological control of pests; introduced parasitoid poses risk of hyperparasitism to other pest-regulating native parasitoids	Weseloh et al. 1979; see other examples in Rosenheim et al. 1995
Gambusia and *Lepomis* fish in rice fields to combat mosquitoes	intraguild predator (adult fish feed on juveniles as well as on mosquito larvae)	opposed to goal — decreased control of disease vector (mosquito)	Blaustein 1992
Intraguild preys			
Opposum shrimp (*Mysis relicta*) in Canadian lakes to increase fish production	intraguild prey depletes shared zooplankton preys	opposed to goal — decreased salmonid fish production	Lasenby et al. 1986
Apparent competitors			
Rats (*Rattus* spp) and cats (*Felis catus*) in Steward Island, New Zealand	rats induce high cat densities and increase predation on endangered flightless parrot (*Strigops habroptilus*)	negative — reduced diversity	Karl and Best 1982 see Müller and Bordeur (2002) for more examples
Herbivores			
Zebra mussel (*Dreissena polymorpha*) in Great Lakes, United States	zebra mussel reduces phytoplankton and outcompetes native bivalves	negative — reduced diversity positive — increased water quality	Benson and Boydstun 1995 Lodge 2001
Mutualists			
Myna bird (*Acridotheres tristis*) for worm pest control in Hawaiian sugarcane plantations	myna engages in the dispersal of the exotic woody weed *Lantana camara*	negative — increased invasion by *Lantana* produced impenetrable thorny thickets, reduced agricultural crops and pasture carrying capacity, and sometimes increased fire risk; displaces habitat of native birds	Pimentel et al. 2000
Ecosystem engineers			
Earthworm (*Pontoscolex corethrurus*) in Amazonian tropical forests converted to pasture	dramatically reduces soil macroporosity and gas exchange capacity	negative — reduced soil macrofaunal diversity and increased soil methane emissions	Chauvel et al. 1999
C4 perennial grasses *Schizachyrium condesatum, Melinis minutiflora* in Hawaii for pasture improvement	increases fuel loads, fuel distribution, and flammability	negative — increased fire frequency affecting fire-sensitive plants; reduced plant diversity; positive feedback for further invasion of flammable exotic species on burned areas	D'Antonio and Vitousek 1992
N-fixing firetree (*Myrica faya*) in Hawaii	increases soil N levels in newly formed N-poor volcanic soils	negative — increased fertility, increased invasion by other exotics, reduced regeneration of native *Metrosideros* tree, alteration of successional patterns	Vitousek et al. 1987 *(continues over)*

creases with species richness. Community biomass is stabilized because a decline in abundance of one species allows its competitors to increase, partially compensating for the initial decrease. In total, theoretical analyses suggest that increased species richness should slightly destabilize the production by individual species but more greatly stabilize production by the entire community (May 1973; Doak et al. 1998; Lehman and Tilman 2000).

Experimental manipulations provide weak evidence to support these theoretical predictions. In well-controlled laboratory experiments, species–rich communities were more resistant to perturbation (Naeem and Li 1997; McGrady-Steed et al. 1997). Also, African comparative field data suggested that greater species richness led to greater ecosystem stability (McNaughton 1993). Year-to-year variation in total community biomass (an inverse

Table 11.2. *continued*

Study Case	Nature of the Interaction Involved	Ecosystem-service Consequences	Source
Deletions/harvesting			
Top predators			
Sea otter (*Enhydra lutris*) harvesting near extinction in southern California	cascading effects produce reductions of kelp forests and the kelp-dependent community	negative — loss of biodiversity of kelp habitat users	Dayton et al. 1998
Pollution-induced reductions in predators of nematodes in forest soils	heavy metal bioaccumulation produces reductions in nematophagous predators and increases herbivorous nematodes	negative — disruption of forest soil food webs and increases in belowground herbivory; decrease in forest productivity	Parmelee 1995
Intraguild predators			
Declining populations of coyote (*Canis latrans*) in southern California	releases in raccoons (*Procyon lotor*) and feral house cats	negative — threat to native bird populations	Crooks and Soulé 1999
Overharvesting of seals and sea lions in Alaska	diet shifts of killer whales increased predation on sea otters	negative — conflict with other restoration programs; failure of reintroduction of sea otters to restore kelp forest ecosystems	Estes et al. 1998
Keystone predators			
Harvesting of triggerfish (*Balistaphus*) in Kenyan coral reefs	triggerfish declines release sea urchins, which outcompete herbivorous fish	negative — increased bioerosion of coral substrates; reduced calcium carbonate deposition	McClannahan and Shafir 1990
Herbivores			
Voluntary removal of sheep and cattle in Santa Cruz Is., United States, for restoration	release of the exotic plant component from top-down control	opposite to goal — explosive increases in exotic herbs and forbs and little recovery of native plant species	Zavaleta et al. 2000
Overfishing in the Caribbean, reducing herbivorous and predatory fish and reducing fish biomass	lack of fish grazers allowed macroalgae to outcompete coral following disturbances	negative — coral cover was reduced from 52% to 3%, and macroalgae increased from 4% to 92%	Hughes 1994
Ecosystem engineers			
Voluntary removal of exotic tamarisk (*Tamariscus* sp.) for restoration of riparian habitats in Mediterranean deserts	long-established tamarisk has replaced riparian vegetation and serves as habitat to endangered birds	opposite to goal — reduction in biodiversity; structural changes in riparian habitats	Zavaleta et al. 2000

measure of resistance) in a Minnesota grassland in the United States was greater in plots with lower species richness (Tilman 1996). However, these grassland plots differed in species richness mainly because of different rates of nitrogen addition, not because of direct experimental control of species richness (e.g., Givnish 1994; Huston 1997); therefore, additional field experiments are required to confirm these findings.

The evidence for a positive effect of biodiversity on stability is stronger in the case of resistance and weaker in the case of resilience (Schmid et al. 2002). Both components of ecosystem stability are strongly influenced by key traits of the dominant species, which explains why the effect of species life history on the stability characteristics of an ecosystem usually outweighs the effects of species richness (Lepš et al. 1982; Sankaran and McNaughton 1999; Osbornová et al. 1990; Grime et al. 2000).

In addition, there can be trade-offs between the traits that favor resistance and those that favor resilience (Lepš et al. 1982; McGillivray et al. 1995). For example, the dominance of short-lived, fast-growing, nutrient-demanding plants, with high output of persistent seeds, leads to high resilience and low resistance. These systems, such as annual grasslands, change very easily in the face of a perturbation but return to their initial condition relatively quickly. On the other hand, communities dominated by long-lived, slow-growing, stress-tolerant plants that allocate much energy to storage and defense tend to be more resistant and less resilient. These systems, such as mature forests in relatively dry climates, are resistant to environmental perturbations, but when

they are finally displaced away from their initial condition, they recover very slowly. Management alternatives that simultaneously try to maximize both resistance and resilience are therefore not likely to succeed.

Although the resistance/resilience characteristics of an ecosystem can be explained to a large extent by the functional traits of the most abundant species, less abundant species also contribute to the long-term preservation of ecosystem functioning. For example, subordinate and rare plants, despite their often negligible role in resource dynamics, can be crucially important in maintaining species richness of higher trophic levels (species further up the food chain) (Lepš et al. 1998; Lepš 2005). Subordinate and rare species can increase in abundance under changing environmental conditions, providing a source of colonizers or acting as positive or negative "filters" to the establishment of other species (Grime 1998; Fukami and Morin 2003; Magurran and Henderson 2003). The key role of some less abundant species, often mediated by complex and indirect interactions, is addressed in more detail later in the chapter.

The presence of multiple species, abundant or rare, within each functional type increases functional redundancy and may have important implications for ecosystem stability (Walker 1995; Grime 1998; Walker et al. 1999; Hooper et al. 2005). Functional redundancy occurs when several species in a community carry out the same process, such as nitrogen fixation. It is important because the larger the number of functionally similar species in a community, the greater the probability that at least some species will sur-

vive changes in the environment and maintain the functional properties of the ecosystem (Walker 1992; Chapin et al. 1996; Naeem and Li 1997). If there is no functional redundancy (that is, species richness is low in any given functional type), the loss of a single species could result in the elimination of an entire functional type (for instance, all the nitrogen-fixers, all the woody deciduous species, all the scavengers, or all the nocturnal pollinators), which would have a larger impact on ecosystem functioning than randomly deleting the same number of species from a variety of functional types.

Direct empirical support for this idea is still scarce, but species assigned to the same functional type have been reported to differ in their tolerances to frost (Gurvich et al. 2002), warming (Chapin et al. 1996), drought (Buckland et al. 1997), disturbance (Cowling et al. 1994; Walker et al. 1999), and changes in soil and atmosphere composition (Dormann and Woodin 2002). This suggests that the effect of species loss should depend on the number and composition of the species remaining, with the largest changes occurring when the last member of a functional type is lost. Thus the effect of species loss on stability cannot always be easily predicted (Díaz et al. 2003).

11.3 Terrestrial Biodiversity Effects on Regulating Services

11.3.1 Invasion Resistance

Invasions of species beyond their native range constitute a global driver of change of major concern for the conservation of natural and managed areas. Invasive species threaten biodiversity (Wilcove et al. 1998), change ecosystem functioning (Levine et al. 2003), and have economic costs (OTA 1993; Pimentel et al. 2000). For example, the economic costs of invasive exotic (alien) species in the United States are estimated in the tens of billions of dollars, the majority of which is due to crop losses and the application of herbicides and pesticides to reduce exotic weeds and pests. In addition, millions of dollars are spent annually in the United States to control numerous invasive species, including purple loosestrife (*Lythrum salicaria,* $45 million), Australian Melaleuca tree (*Melaleuca quenquenervia,* $3–6 million), feral pigs (*Sus scrofa,* $500,000), brown tree snake (*Boiga irregularis,* $4.6 million), fire ant (*Solenopsis invicta,* $200 million), gypsy moth (*Lymantria dispar,* $11 million), Dutch elm disease (*Ophiostoma ulmi,* $100 million), and aquatic weeds (several species, $100 million) (Pimentel et al. 2000).

Invasive species can have important negative impacts on ecosystem services and human well-being (OTA 1993; Pimentel et al. 2000): weeds and pests reduce agricultural yields; invasive eels reduce freshwater fisheries; invasive termites damage homes and other infrastructure; aquatic weeds clog waterways used for transportation and recreation; invasive mussels clog water pipes, threatening the flow of water used in such tasks as cooling power plants; invasive grasses increase fire frequency and intensity, threatening homes and other infrastructure. Conversion of native communities to invasive-dominated communities also has aesthetic and cultural impacts.

Trends in species introductions (Levine and D'Antonio 2003; Padilla and Williams 2004; Ruiz et al. 2000; Ribera Siguan 2003) and modeling predictions (Sala et al. 2000) strongly suggest that biological invasions will continue to increase in number and impact. In addition, human impacts on environmental characteristics required by native species (via eutrophication, pollution, nonsustainable harvesting, and so on) suggest that biotic resistance to invasions may decrease and that the number of communities dominated by invasive species will increase.

Invasibility—the overall susceptibility to invasion—depends on a region's climate and environmental properties and on the interaction between the invader and the recipient community (Lonsdale 1999; Hooper et al. 2005). The presence and abundance of invaders in an ecosystem are functions of both invasibility of the system and of the supply of invading species or propagules. Here we focus on the resistance to invasions that may be afforded by species already present in a community—biotic resistance (Elton 1958). Biotic resistance is defined as the ability of resident species to inhibit the establishment, growth, survival, and reproduction of invasive species. Biotic resistance may vary from habitat to habitat and over time due to changes in the identity, composition, and diversity of the species in the community.

In general, the available evidence and theoretical predictions suggest that higher species richness and functional type richness can increase the resistance of a community against invasion by exotic species. In addition, some individual species may be particularly important in conferring invasion resistance to a community. Therefore, all else being equal, maintaining native species assemblages should diminish the ability of exotic species to become invasive, and it is most likely that the loss of biodiversity from a particular habitat will decrease the invasion resistance of this habitat.

The location on the landscape where exotic species are most likely to invade can also be predicted. Numerous studies have found a positive correlation between native and exotic species richness across habitats (Rejmánek 1996; Levine et al. 2002; Stadler et al. 2000; Lonsdale 1999; Stohlgren 2003 and references therein), where high native species richness is not the cause of high richness of exotic species. Rather, these studies suggest that the factors that promote the richness and coexistence of native species, such as benign climate, intermediate levels of disturbance, and habitat heterogeneity, also promote the richness and coexistence of exotic species (Levine and D'Antonio 1999; Byers and Noonburg 2003). These results have major conservation implications, because they suggest that hot spots for diversity are particularly at risk of invasion by introduced species, and that the loss of native species (from communities of low or high native species richness) is expected to increase invasibility.

A number of mutually compatible mechanisms have been proposed to explain the effect of biodiversity on invasion resistance (Mack et al. 2000). For all hypothesized mechanisms, it is the traits of the resident species, not merely the species richness, that determine the invasibility of a system (Foster et al. 2002; Prieur-Richard et al. 2002; Dunstan and Johnson 2004).

One proposed mechanism for high species richness inhibiting invasibility is the "niche hypothesis," which suggests that communities that are relatively impoverished in numbers of native species cannot provide biological resistance to exotic species because there are unused resources in the system (sometimes referred to as a vacant niche). Diverse communities will resist invaders because they reduce resource availability and increase competition. Consistent with the niche hypothesis, the loss of biodiversity has been shown to reduce invasion resistance in experiments in which biodiversity and community composition have been manipulated while holding the habitat conditions constant (e.g. Stachowicz et al. 1999; Dukes 2002; Naeem et al. 2000; Hector et al. 2001; Kennedy et al. 2002; Fargione et al. 2003; van Ruijven et al. 2003).

Several types of biodiversity loss decrease invasion resistance, including losses of species richness, of functional richness, and of particular species. Loss of biodiversity may reduce competition

and provide increased space and resources for invading species. For example, reduced species richness in a grassland experiment led to increases in resource availability (both light and soil nitrogen) and caused higher levels of invasion (Knops et al. 1999). Invasion resistance in diverse stands has been associated with the closeness of neighbors (Kennedy et al. 2002) and with increasing temporal stability (reducing fluctuations of open space, for example) (Stachowicz et al. 1999). At this local scale, species invasion seems limited not only by species richness, but also the richness of functional types (grasses, herbs, and shrubs) (Symstad 2000). Overall, these studies suggest invading species can be most successful when they make use of resources that are incompletely used by the resident community (for example, brown trout) (Fargione et al. 2003).

The loss of biodiversity is most likely to result in unused resources in habitats that already have low functional redundancy, and for communities, such as oceanic or habitat islands, in which functional redundancy is also limited at the regional species pool level (that is, few species can disperse there naturally) (Rejmánek 1996). Thus, certain communities are susceptible to invasion because of a lack of competition from endemic species occupying one or more niches—a lack of biotic resistance. For example, the higher success of invasion by vertebrates in oceanic islands compared with corresponding continental areas is partially explained by the lack of native vertebrates that could act as predators or competitors (Brown 1989). Some stressful environments may have low species richness and in some cases low functional redundancy, but invasion is constrained by environmental conditions.

Natural enemies (pathogens, parasites, and herbivores) are important agents of biotic resistance to invasion. Invaders benefit from escaping their specialized natural enemies left behind in their region of origin, but they may be inhibited by the accumulation of natural enemies in the invaded range (Maron and Vilà 2001). Naturalized plant species that have accumulated more pathogen species native to their new habitat are less frequently listed as noxious weeds, whereas naturalized plant species that escape a greater proportion of their native pathogen species are more frequently listed as this, implying that associations with these pathogens help keep them from becoming pests in their native range (Mitchell and Power 2003).

It has also been shown that invasive animal species have fewer parasites in invaded than in native ranges (Torchin et al. 2003). Many invasive animal species have become pests only after losing their native parasites, which suggests a possible role for parasite species richness in controlling invasive species.

Similarly, invasive species may be successful because they accumulate fewer root pathogens than rare species (Klironomos 2002). In the Netherlands, weeds invading across an experimental gradient of plant species richness were found to be significantly reduced by the presence of a plant species, *Leucanthemum vulgare,* that acted as a host to parasitic nematodes, which then acted to control invading weeds (van Ruijven et al. 2003). Generalist native herbivores can also reduce the growth, seed set, and survival of introduced plants, but the evidence that they hinder the spread of invasive exotic plants is scarce (Maron and Vilà 2001). The natural enemies hypothesis is an integral part of the conceptual basis for biological control, in that specialized enemies are identified and introduced to control pests. Numerous examples of successful biological control demonstrate the importance of natural enemies in controlling invasive species (Hajek 2004; see also Chapter 10).

There is a general consensus that invasions flourish in areas disturbed by human activities (Hobbs and Huenneke 1992). Disturbances can be defined as events that create available space for the germination of propagules, increase the availability of resources, and reduce competition with colonizing species, such as changes in land use resulting in soil erosion or changes in water courses. Temporary increases in the availability of resources can reduce competition and increase the establishment and expansion of plant populations (Davis et al. 2000; Davis and Pelsor 2001). The ability of a biotic community to resist invaders may thus depend on its susceptibility to disturbances that create resource pulses.

Disturbance-induced invasions are more common when the disturbance in question does not have a long evolutionary history in an area. For example, livestock tends to favor invasion by exotic plants in areas where large herbivores have only recently been introduced (Milchunas et al. 1988; Díaz et al. 1999). There is some theoretical and empirical evidence suggesting that increased species and functional type richness can increase invasion resistance by decreasing both average resource availability and resource fluctuations (Prieur-Richard and Lavorel 2000). In addition, disturbances may interact with each other, with the highest rates of invasion occurring after multiple disturbances (such as biomass removal, fire, or soil disturbance) (Petryna et al. 2002).

Impacts of invasive species include altering the local environment in directions that are more favorable for them but less favorable to native species. Specifically, invading species may alter geomorphic processes (soil erosion rates, for instance, or sediment accretion), biogeochemical cycling, hydrological cycles, or fire or light regimes (Macdonald et al. 1996; Levine et al. 2003). For example, invading trees in the fynbos of upland South Africa reduce stream flow from mountain catchment areas, altering the hydrological regime of the whole area. In the fynbos biome, there are over 1500 threatened plant species and over 50% are threatened by the spread of introduced trees and shrubs, which prevent germination and growth of native species (Le Maitre 1996). Similarly, in Great Britain (Usher 1987), in the mixed oak (*Quercus petraea*) and holly (*Ilex aquifolium*) woodlands, the introduced species *Rhododendron ponticum* is thought to inhibit woodland regeneration both by casting a dense shade and by forming an impenetrable leaf litter layer on the ground.

Many invasive species also enhance the frequency and intensity of fires, to which many native species are not adapted. For example, numerous invasive grasses produce a great deal of flammable standing dead material and many resprout quickly after fires, giving them a competitive advantage over native species (D'Antonio and Vitousek 1992). However, some invasive species may have positive effects on native species. For example, some native species may benefit from preying upon invasive species, such as the endangered Hawaiian hawk (*Buteo solitarius*), which benefits from preying on the now-established invasive rat (*Rattus norvegicus*) (Klavitter et al. 2003).

Another hypothesis is that invasive species may exhibit positive feedbacks on subsequent invaders, either through mutualistic interactions or by modifying ecosystem properties (Simberloff and Von Holle 1999; D'Antonio and Vitousek 1992). For example, although it is thought that native species benefit more from the presence of mycorrhizal fungi than exotic plants do and that plant invaders will often be non-mycorrhizal (Klironomos 2002; Bever 2003), the intentional introduction of "improved" ectomycorrhizal fungi to increase crop or forest plantation production has altered the invasibility of many systems. These fungi may form mutualisms with invasive species and replace indigenous flora and fungi (Richardson et al. 2000). Another example of an established invader promoting subsequent invasions via mutualistic interac-

tions is introduced honeybees that provide reliable pollination to invading plants.

Although we have focused on the inhibitory effects of native species on invaders, it is also possible that some native species may benefit invaders. For example, generalist herbivores disperse the seeds of the exotic plants they consume over long distances, having more of a facilitating than an inhibiting effect on exotic plant invasion (Maron and Vilà 2001), especially in regions with a short evolutionary history of grazing by ungulates.

11.3.2 Direct and Indirect Interactions between Species

Many ecosystem processes and the services they provide depend on obligate or facultative interactions among species. Direct interactions between plants and fungi, plants and animals, and indirect interactions involving more than two species are essential for ecosystem processes such as transfer of pollen and many seeds, transfer of plant biomass production to decomposers or herbivores, construction of habitat complexity, or the spread or suppression of plant, animal and human pathogens. Because of this, interactions between different trophic levels are among the most important processes by which biodiversity regulates the provision of ecosystem services, as illustrated in Figure 11.1 (see also Chapin et al. 2000a). Although experimental evidence is growing (e.g. van der Putten et al. 2001; Haddad et al. 2001), most of the examples come from the dramatic community and ecosystem effects of the introduction or removal of only one or a small number of species. There is clearly still insufficient information to determine whether there are general principles that describe how biotic linkages between different trophic levels and indirect interactions affect various ecosystem processes. Nevertheless, the available studies suggest that the integrity of these interactions is important for maintaining ecosystem processes and that threats to them via habitat destruction and fragmentation (see Box 11.1) are likely to result in losses of ecosystem service.

11.3.2.1 Interactions between Plants and Symbiotic Microorganisms

The interactions between plants and symbiotic microorganisms, such as mycorrhizal fungi, endophytic fungi, and nitrogen-fixing microorganisms, can greatly influence ecosystem processes and have considerable impacts in the provision of ecosystem services by natural and agricultural ecosystems. These interactions are complex and can tip the balance between different plant-community members, with various consequences for the provision of plant-related ecosystem services.

The effects of mycorrhizal fungi on plant communities are both profound and widespread. Arbuscular mycorrhizal fungi form symbiotic relationships with approximately 80% of the land plants on Earth (Smith and Read 1997), in which the mycorrhizal fungus receives benefits from the plant in the form of carbon and provides various benefits to the plant, such as phosphorus absorption (Jakobsen et al. 2002) and resistance to pathogens (Klironomos 2000).

The abundance, species composition, and richness of AMF communities influence the productivity, composition, and species richness of plant communities. This is because AMF have different effects on different plant species, ranging from mutualism to parasitism (Sanders 1993; van der Heijden et al. 1998a; Moora et al. 2004; Rillig 2004), and therefore benefit some species more than others (Grime et al. 1987; Gange et al. 1993; Hartnett et al. 1993; Moora and Zobel 1996; Wilson et al. 2001; van der Heijden et al. 2003). It is likely that AMF enhances plant species di-

versity when they favor less abundant species, but decreases in plant diversity are likely when AMF favor dominant plant species (Urcelay and Díaz 2003).

The presence and species composition of the AMF community can even alter the relationship between plant species richness and productivity. In the absence of AMF, the relationship between plant species richness and productivity is positive and linear, whereas in the presence of AMF, the relationship is positive but asymptotic (Klironomos et al. 2000). The effects of different AMF species can also differ considerably.

Increasing AMF species richness can result in more-efficient exploitation of soil phosphorus and an increase in the size of the plant nutrient pool. Van der Heijden et al. (1998b) found that increased AMF species richness led to a significant increase in the amount of soil phosphorus captured by the plant community.

Much less is known about the effects of the richness and composition of ectomycorrhizal fungi communities on ecosystem processes (Dahlberg 2001). EMF are common in nutrient-limited forest ecosystems and can play a critical role in tree nutrition and carbon balance, supplying soil resources to their plant host in exchange for sugars (Smith and Read 1997). The effects of EMF on plants appear to be species-specific, such that the loss of EMF species richness could, in theory, reduce plant species richness and productivity (e.g., Timonen et al. 1997; Baxter and Dighton 2001). However, no relationship has been found between ecosystem productivity and EMF species richness (Gehring et al. 1998), although more research is clearly needed before general conclusions can be drawn.

Based on the limited available evidence, it is likely that other fungal groups also play important functional roles. For example, systemic fungal endophytes (fungi that live inside aboveground plant tissues and receive nutrition and protection from the host) change the performance, herbivore resistance, biomass allocation, and final biomass of plant individuals and may thus also have a considerable effect on competitive interactions among plants (Clay and Holah 1999; Matthews and Clay 2001; Pan and Clay 2002). The presence of fungal endophytes may also inhibit the activity of other microbial organisms like AMF (Chu-Chou et al. 1992; Guo et al. 1992) or soil invertebrates (Bernard et al. 1997), with possible indirect effects on plant community diversity or productivity. Toxic alkaloids in the leaf litter of endophyte-infected plants could inhibit decomposition, slowing rates of nutrient cycling (Bush et al. 1997). Pathogenic fungi in the root zone may influence plant distribution and competition by favoring certain species (de Rooij-van der Goes et al. 1998; Packer and Clay 2000). There are currently no results from biodiversity-ecosystem functioning experiments explicitly considering endophytes and soil fungal pathogens, but the complex relationships described above suggest that fungal diversity may play an important role in the structure and functioning of ecosystems.

Ecosystem productivity and carbon accumulation may be enhanced by nitrogen-fixing microorganisms. These include both nitrogen-fixing bacteria in symbiotic relationships with plants (especially, but not exclusively, legumes), and free-living microorganisms. As in the case of AMF, not only the presence but also the identity of the symbiotic nitrogen-fixing bacteria is important, since different genotypes may have different effects on host plant species (Thrall et al. 2000).

The input of nitrogen to soils from nitrogen-fixing plants is crucial in the productivity and successional dynamics of many natural ecosystems and can have important positive and negative impacts on ecosystem services (Walker and Vitousek 1991; Doyle 1994; Fridley 2001). Some of the positive effects of biodiversity on plant biomass production have been attributed, at least in part,
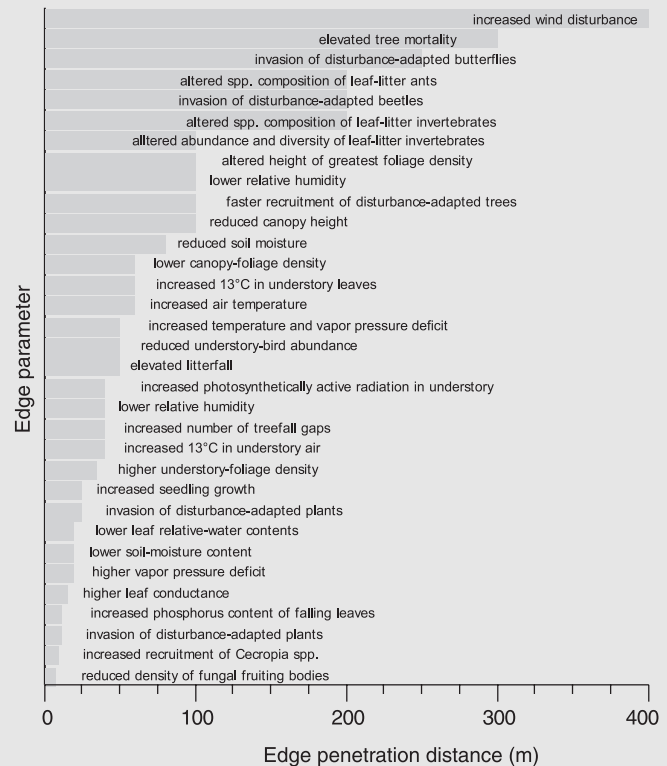
BOX 11.1

Impacts of Habitat Fragmentation on the Links between Biodiversity and Ecosystem Processes

Throughout the world, habitat fragmentation is one of the most critical threats to biodiversity and ecosystem services, such as pollination, seed dispersal, herbivory, and carbon sequestration (Dirzo 2001a; Laurance et al. 2002; Dirzo and Raven 2003). In the tropics, for example, millions of hectares of forest are destroyed each year (Whitmore 1997; Achard et al. 2002), typically leaving small islands of forest surrounded by a sea of pastures, crops, and scrubby regrowth. In other areas, such as the eastern United States and much of Europe, forests have been fragmented for centuries. Hence, the fragmented landscape is rapidly becoming one of the most ubiquitous features of our planet.

Habitat fragments are ecologically different from intact habitat, and they are often biologically depauperate. This occurs for several reasons. First, habitat destruction is often nonrandom. Humans tend to clear areas overlaying productive, well-drained soils and to avoid areas with steep or strongly dissected topography. Consequently, habitat remnants are often confined to areas with poor soils, rugged topography, and low species richness. Second, because they are limited in area, habitat fragments contain only a fraction of the habitat diversity found in a particular area (Wilcox 1980). Third, small fragments usually have higher local extinction rates than large fragments because they contain smaller, more vulnerable populations (MacArthur and Wilson 1967; Stratford and Stouffer 1999). Fourth, habitat fragments are influenced by edge effects, which are ecological changes associated with the artificial, abrupt margins of habitat fragments (Janzen 1986; Laurance et al. 2002; Hobbs and Yates 2003). Edge effects can be remarkably varied, altering physical gradients, species distributions, and many ecological and ecosystem processes. (See Figure.) Fifth, fragments that are isolated tend to support fewer species than do those that are near other habitat areas (MacArthur and Wilson 1967; Lomolino 1984).

By altering species richness, relative abundance, and composition, habitat fragmentation also indirectly affects many ecosystem processes. Smaller fragments often become hyper-disturbed, leading to progressive changes in floristic composition (Laurance 1997; Hobbs and Yates 2003).

Distances to Which Various Edge Effects Penetrate the Interiors of Fragmented Rainforests in Central Amazonia. Some edge effects, such as microclimatic alterations like higher vapor pressure deficits and lower soil-moisture content, penetrate only limited distances (<50 m) into forest fragments. Other edge effects, however, such as elevated wind disturbance, can penetrate hundreds of meters into fragments. As a result, even large fragments can be substantially altered by wind disturbance.

to the presence of nitrogen-fixing legumes in the assemblages (e.g. Hector et al. 1999). Nitrogen-fixing symbiotic relationship is at the very basis of intercropping (Vandermeer 1989) and renders high economic profit in many semi-natural pasture and agroforesty ecosystems. However, the invasion by trees with nitrogen-fixing symbiotic microorganisms has had dramatic consequences in some naturally nutrient-poor ecosystems (such as the firetree, *Myrica faya,* in Hawaii, where a nitrogen-fixing tree was previously absent).

11.3.2.2 Interactions between Plants and Animals

The provision of ecosystem services by plants and animals is inextricably linked. This is because animals interact with plants directly by eating them or by moving their pollen and seeds across the landscape. This has short-term consequences on ecosystem processes and also long-term evolutionary consequences (such as evolution of plant chemical defenses and floral and fruit structures). Major ecosystem services are supported by the direct interactions between plants and animals, such as herbivory, pollination, and seed dispersal. Animals and plants can also influence each other indirectly by changing each other's habitat and resource availability (such as the provision of nesting sites by plants to animals or the increased availability of soil nutrients to plants due to physical disturbance caused by animals).

11.3.2.2.1 Herbivory

Herbivory—the consumption of plant tissues or fluids by animals—is ubiquitous in ecosystems and often has a dramatic impact on ecosystem processes. This section describes the ecosystem effects of the interactions between wild herbivores and plants. The ecosystem effects of domestic herbivores are addressed in Chapters 8 and 22.

The consequences of herbivory for ecosystem services and human well-being go far beyond its widely recognized role in terms of impact on the production of plant biomass (such as food, wood, and fiber). This is because herbivores consume an important portion of the world's primary production, and in many cases they stimulate plant biomass production and nutrient cycling and favor stability (by decreasing the amount of standing dead biomass, for instance, and thus the probability of high-temperature fires). Herbivory has also played a key role in the development of plant functional biodiversity over evolutionary time (Dirzo 2001b).

Herbivory tends to be an antagonistic interaction in which plant performance (yield, reproduction, and survival) is often negatively affected. However, we now know that the impacts of herbivory move along a gradient from negative, neutral (compensation), and even positive (overcompensation) effects on plants (Strauss and Agrawal 1999). For example, mammals may speed

New trees regenerating near forest edges tend to be disturbance-loving pioneer and secondary species rather than old-growth, forest-interior species (Viana et al. 1997; Laurance et al. 1998b). Large canopy and emergent trees, which contain a high proportion of forest biomass, are particularly vulnerable to fragmentation (Laurance et al. 2000). As the biomass from the dead trees decomposes, it is converted into greenhouse gases such as carbon dioxide and methane. This loss of living biomass is not offset by increased numbers of lianas and small successional trees in fragments (Laurance et al. 2001), which have lower wood densities and therefore store less carbon than the old-growth species they replace (Nascimento and Laurance 2004). In fragmented forests worldwide, millions of tons of atmospheric carbon emissions may be released each year by this process. Edge-related losses of biomass increase sharply once fragments fall below 100–400 hectares in area, depending on fragment shape (Laurance et al. 1998b).

In addition to reduced carbon storage, the rate of carbon cycling is also altered in fragmented habitats. In undisturbed forests, carbon can be stored for very long periods in large trees, some of which can live for more than 1,000 years (Chambers et al. 1998). In forest fragments, however, the residence times for carbon will decrease as smaller, short-lived plants replace large old-growth trees (Nascimento and Laurance 2004). The dynamics of this cycle can have major effects on carbon storage in vegetation and soils and on the rate of input of organic material into tropical rivers and streams (Wissmar et al. 1981).

There is limited understanding of the ecosystem consequences of the effects of fragmentation on complex interspecific interactions. Many species can be negatively affected by secondary or "ripple effects" in fragmented habitats (Terborgh et al. 1997). For example, plants that rely on specialized pollinators can experience reduced fecundity in fragments if their key pollinators disappear (Aizen and Feinsinger 1994), although exotic pollinator species can sometimes compensate for the loss of native pollinators (Hobbs and Yates 2003). Moreover, the loss of seed dispersers has dramatically affected the life cycle of plants worldwide (Chapman and Chapman 1996; Terborgh and Wright 1994; Wright and Duber 2001), and scientists have shown that in areas affected by fragmentation or with heavy poaching, the number of seeds dispersed decreases (e.g., Wright and Duber 2001; Wright et al. 2000). Reduced dispersal may in turn decrease the genetic diversity of plant populations, since seeds are one of the main vectors of gene flow between populations (Pacheco and Simonetti 2000). Small, fragmented plant populations may show increased inbreeding, reduced genetic fitness, and increased susceptibility to environmental stress (Heschel and Paige 1995).

In addition, the rapid loss of large predators (wolves, bears, and tigers, for example) in many fragmented landscapes can lead to a phenomenon known as mesopredator release (Soulé et al. 1988), in which medium-sized omnivores (coyotes, raccoons, coatis, and opossums, for instance) that were formerly controlled by the large predators undergo population explosions. These omnivores may then decimate vulnerable species, such as nesting birds (Crooks and Soulé 1999) and large-seeded trees (Asquith et al. 1997).

In summary, from the point of view of biodiversity-mediated ecosystem services, habitat fragments are not simply reduced versions of nonfragmented habitats. Rather, they are often fundamentally altered in terms of their species composition and ecosystem functioning. By reducing biodiversity, habitat fragmentation affects a number of regulating processes, such as herbivory, pollination, seed dispersal, and carbon storage. When fragmented, forests may have a diminished capacity to provide natural products such as certain fruits, fibers, game, and pharmaceuticals; they may experience drastically altered fire regimes that can affect local communities, livestock, and croplands; and they may have a reduced capacity for capturing and storing atmospheric carbon in its living vegetation.

up biomass production by plants by removing dead parts or by eliminating apical dominance leading to the proliferation of secondary branches. This gradient of herbivore impacts and plant responses, together with the lack of information for most ecosystems, makes it difficult to understand the role of herbivores in ecosystem processes or the effect of their biodiversity on that role (e.g., van der Putten et al. 2001; Wardle et al. 2003). However, as this section illustrates, although negative impacts on plants are common, ecosystem services and even biodiversity maintenance depend on this biotic interaction.

Approximately 50% of the total species richness is accounted for by phytophagous insects and their food plants (Strong et al. 1984; Heywood and Watson 1995). Most of this biodiversity is concentrated in the tropics (Dirzo and Raven 2003), where herbivory rates, largely by insects, are also higher (Coley and Barone 1996).

The loss of herbivores can affect species throughout the community in ways that can be difficult to predict. In both tropical and nontropical ecosystems, herbivory by mammalian vertebrates can be high, and it appears that, regardless of species richness, removal of large herbivores can have profound effects on ecosystem diversity and functioning, including terrestrial, marine, and freshwater ecosystems (Pimm 1980). In the tropics, for instance, loss of mammalian herbivores resulting from hunting and habitat deterioration may reduce herbivory and seed dispersal, resulting in patches with high density and low species richness of seedlings. The high density and low species richness of these patches increases the abundance of insect herbivores and their parasites (Chapman and Chapman 1996; Dirzo 2001b; Wright 2003). The consequences of species loss depend on both the magnitude and type of animals that are removed and also on the potential for the remaining animals to ecologically compensate in the absence of those lost. In most systems, current knowledge is insufficient to predict the effect of herbivore loss reliably.

In grasslands and rangelands where native or domestic ungulates have been present over evolutionary time, these herbivores assist with nutrient cycling and buffer against disturbances. Herbivores open up the vegetation by eating and trampling it. Also, their feces and urine decompose faster than plant litter. As a consequence, nutrients, especially nitrogen, are recycled faster. In areas where ungulates have been present over evolutionary time, the loss or voluntary suppression of grazing leads to considerable accumulation of standing and dead biomass. In some areas, this increases fire frequency and intensity, with negative consequences for plant and soil communities (Collins et al. 1998; Perevolovsky and Seligman 1998). Biomass accumulation has also been reported to favor rodent outbreaks, because the tall, dense canopy provides a refuge from predators (Noy-Meir 1988).

In addition, herbivores can change the characteristics of their host plants over ecological and evolutionary time. Herbivory has

selected for adaptive responses by plants, including physical and chemical traits, such as the omnipresent plant secondary metabolites (tannins, alkaloids, cardiac glycosides, non-protein amino acids, and so on). These traits have in turn selected for adaptive responses by animals, including detoxification mechanisms. Such adaptive and counter-adaptive responses lead to coevolutionary changes that, beyond their academic importance, have important practical ramifications in terms of, for example, biological control and pharmacology (see Chapter 10).

The role of herbivores in supporting ecosystem services related to the maintenance of genetic resources and food production has been underestimated. The high economic losses of crops caused by insect pests would suggest, at first glance, that herbivory reduces ecosystem services, particularly if considering only the economic value. This interaction can have direct ecological and economic benefits, however, when herbivores operate as effective control agents of potential weeds (reviewed later in this section).

In addition, the impacts of herbivores on wild plants have led to the evolution of defensive mechanisms, particularly secondary plant metabolites, which are of great actual or potential importance for humans. For instance, about 25% of the currently prescribed drugs have their origin in defensive plant secondary compounds (Dirzo and Raven 2003), which in turn are believed to have arisen as a result of the interactions between plants and herbivores over evolutionary time.

The potential benefit of many other metabolites, still poorly investigated, is considerable. For example, the metabolite dihydromethyldihydroxypyrrolydine (DMDP) is produced in the foliage of the tropical liana *Omphalea diandra.* This and other related species in the genus are strongly protected against phytophagous insects, except the highly specialized caterpillars of the moth *Urania fulgens,* which, in turn, sequester the metabolite in their bodies. Remarkably, this metabolite plays some role in blocking the activity of HIV, has negative effects on bruchid beetles that attack stored grains in the tropics, and has shown some activity against cancer and diabetes (Dirzo and Smith 1995).

11.3.2.2.2 Pollination

Pollination, the transfer of pollen between flowers, without which many plants cannot achieve sexual reproduction, is an interaction between animals and plants that is essential for the provision of plant-derived ecosystem services. Worldwide, there is increasing realization of the extent to which both wild plant communities and agricultural systems depend on pollination services (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998). (See Box 11.2.)

Because many fruits and vegetables require pollinators, pollination services are critical to the production of a considerable portion of the vitamins and minerals in the human diet. When agroecosystems are managed in a way that reduces a diverse assemblage of native pollinators, crops are at risk of suffering yield losses (Kremen et al. 2002).

Estimates of the annual monetary value of pollination vary widely, from $120 billion per year for all pollination ecosystem services (Costanza et al. 1997), to $200 billion per year for the role of pollination in global agriculture alone (Richards 1993). The range of these numbers reflects the lack of common methods for valuing the services provided by nature in general (see Chapter 2) and pollinators in particular. Recent research in coffee ecosystems in Costa Rica (Ricketts et al. 2004) however have shown that for stingless bee pollinators, which nest only in the forest, the services provided by adjacent forest patches contribute to 20% greater coffee yields within one kilometer of the forest, and 7% overall to the income of the coffee farms.

Existing evidence indicates that species richness and composition of pollinators are linked with plant reproduction and establishment and thus with all the supporting, regulating, and provisioning services that stem from terrestrial vegetation. The direct impact of losing effective pollinators is primarily on plant reproductive success and fruit production. Most pollination systems are "somewhat generalized" (Waser et al. 1996), in that most flowers attract and can be pollinated by a range of pollinators that often vary under different climatic conditions. Therefore flowers usually will continue to be visited even if the most effective pollinators have been eliminated. Because some pollinators are much more effective than others, however, less pollen may be deposited, or it may be deposited at the wrong place on the plant, or the visits may occur at times when the flower is less receptive to receiving pollen. Rarely will plants completely fail to produce seed when their most effective pollinator is removed; they are more likely to produce less seeds or fruit of reduced viability or quantity.

Previously, low fruit production in plants was widely attributed to nutrient limitation, but increasingly studies have pointed to pollen limitation as a cause of fruiting failure (Burd 1994; Johnson and Bond 1994). The contribution of pollination to crop yields is beginning to garner attention on the scientific agenda and to be considered an essential agricultural input for optimal production. Pollination is now increasingly recognized as a key component of biodiversity and sustainable livelihoods, and an International Pollinators Initiative has been formed to address pollinator conservation.

Adequate richness and density of pollinators also influence plant genetic diversity and thus indirectly affect supporting ecosystem services related to it. Threats to pollination services may lead to genetic impoverishment of species. Pollination is the means by which genes are exchanged in a population. Where the number of individuals of a given species is low (as a result of habitat fragmentation, for instance, or selective harvesting) pollinators may carry fewer pollen grains to each flower visited (Kearns et al. 1998; Kunin 1992). In self-compatible species (where individuals may fertilize themselves), this "pollination deficit" leads directly to increased inbreeding, reduced genetic fitness, and increased susceptibility to environmental stress (Heschel and Paige 1995), as seen often in small fragmented plant populations.

Although most pollination systems tend to be generalized, the greatest risks of reproductive failure or genetic impoverishment occur in highly specialized pollination systems, where the suite of effective pollinators is the smallest. Specialized pollination systems occur most commonly in desert ecosystems (Ollerton and Kamner 2002; Waser et al. 1996). The greatest richness of bee species, for example, occurs in arid and semiarid environments such as Israel and the American Southwest (O'Toole 1993). Closely related *Acacia* tree species in Tanzania drylands flower at different times of the day, thereby reducing the opportunities for sharing pollinators (Stone et al. 1998).

Nevertheless, at a local level, whether in moist tropical systems or desert systems, there is a strong linkage between effective pollination systems and biodiversity. Larger individual fruit of more uniform shape and better seed production generally correlate with a greater number of visits from pollinators (Alderz 1966). Since changing weather conditions may favor some pollinators over others, having the largest suite of potential pollinators is the best

BOX 11.2
Global Status of Pollinators

Approximately 80% of Angiosperms, including many important agricultural species, are pollinated by animals (the rest are wind- or water-pollinated or are self-compatible). Worldwide, the number of flower-visiting species is estimated to be about 300,000 (Nabhan and Buchmann 1997). Bees (Hymenoptera: Apidae) account for 25,000–30,000 species (O'Toole and Raw 1991) and together with flies, butterflies and moths, wasps, beetles, and some other insect orders encompass the majority of pollinating species (Buchmann and Nabhan 1996). Vertebrate pollinators include bats, non-flying mammals (monkeys, rodents, lemurs, and so on), and birds.

The challenges of identifying declines in pollinators are considerable given the rarity of many species, the lack of baseline data, and high spatial and temporal variation in pollinator populations (Williams et al. 2001). Evidence is generally either direct, from isolated case studies showing declines of specific taxa in a particular place or time, or indirect, from studies of pollinator abundance across gradients of human disturbance. If, as seems to be the case, pollinator populations are reduced in areas with human disturbance, and the area affected by that disturbance is increasing, we can expect pollinator populations to decline over time.

Direct evidence of pollinator declines has been reported in at least one region or country on every continent except Antarctica, which has no pollinators. However, no consistent assessment is available at the continental level, though efforts are currently under way on at least two continents.

Marked declines of bumblebees (*Bombus* spp.) have been reported for the United Kingdom (Williams 1986), Belgium (Rasmont 1988), and eastern Germany (Peters 1972) and for native solitary bee species in Germany (Westrich 1989) and in the United Kingdom (Falk 1991). Changes have been attributed to habitat loss resulting from agricultural intensification. Day (1991) compiled information on the status of bees from several national *Red Data Lists,* identifying more than 400 listed species from north of the Alps but virtually none from the Mediterranean. Although several case studies from Poland, Lithuania, Turkey, Russia, and Ukraine are available, data are insufficient to draw conclusions about general trends in these countries (Banaszak 1995). Similarly, a widespread pollinator decline may be occurring in North America (Buchmann and Nabham 1996; Allen-Wardell et al. 1998), but conclusive data are not yet available (see special section in *Conservation Ecology* 5:1 (2001)).

Honeybee (*Apis mellifera*) colonies, both managed and wild, have undergone marked declines in both the United States and some European countries. The number of managed honeybee colonies in the United States has dropped from 5.9 million in the 1940s to 1.9 million in 1996 (Ingram et al. 1996; USDA National Agricultural Statistics Service 1997), and most feral colonies have also been lost (Kearns et al. 1998). In the European Union, honeybee colonies are reported to have declined by 16% between 1985 and 1991, with losses expected to increase (Williams et al. 1991). A major cause of honeybee declines is parasitic mites (*Varroa jacobsoni* and *Acarapsis woodi*). The range expansion of Africanized honeybees in the United States is also predicted to decrease managed honeybee colonies, largely because beekeepers fear liability lawsuits (Allen-Wardell et al. 1998).

The related Himalayan cliff bee (*Apis laboriosa*) has declined significantly. In a regional study, all but one censused cliff showed declines in number of colonies or total loss across a 15-year period (Ahmad et al. 2003). Bee population characteristics may show changes before population declines can be detected. For example, the most abundant orchid bee in lowland forest in Panama, *Euglossa imperialis,* frequently has high levels of sterile males resulting in low effective population sizes (Zayed et al. 2003). Recent research points to reduced genetic diversity in specialist bees compared with generalists (Packer et al. 2005).

Butterfly (Lepidoptera) populations have decreased in Europe, based on local and national studies in the United Kingdom, the Netherlands, and Germany. Comparison with historical records (1970–82) showed that half of British resident butterflies have disappeared from over 20% of their range and that a quarter have declined by more than 50% (Asher et al. 2001). Swaay and Warren (1999) report in the *Red Data Book of European Butterflies* that many European butterflies are under serious threat because of changing land use and agricultural intensification.

Mammalian and bird pollinators also show strong declines. Nabhan (1996) notes that 45 species of bats, 36 species on non-flying mammals, 26 species of hummingbirds, 7 species of sunbirds, and 70 species of passerine birds are of global conservation concern. The black and white ruffed lemur of Madagascar, an important pollinator of the island's celebrated Traveler's Palm, is highly threatened (Buchmann and Nabhan 1996). Lower visitation rates by bats and reduced fruit set occurred on a dry forest tree, *Ceiba grandiflora,* in disturbed habitats (Quesada et al. 2003).

Pollinator biodiversity is sensitive to a number of factors, many of them related to land use. Given that these drivers are widespread and often increasing, the indirect evidence indicates that declines in pollinators may also be increasing. In order to persist in agroecosystems, pollinators need local floral diversity and nesting sites. Large monocultures fail to provide these. For example, cultivated orchards surrounded by other orchards have significantly fewer bees than orchards surrounded by uncultivated land (Scott-Dupree and Winston 1987). On melon farms in the western United States, wild bee communities become less diverse and abundant as the proportion of natural habitat surrounding farms declines (Kremen et al. 2004). The most important species for crop pollination became locally extinct throughout large parts of the landscape. In addition, all species declined along this gradient, so more resistant species could not compensate for the loss of more sensitive species (Kremen 2004).

The implications for pollinator services are evident: only farms near natural habitats sustained communities of pollinators sufficiently large to provide needed levels of pollination (Kremen et al. 2002). Distance from natural habitat affected pollinator communities and services in a similar way on coffee farms in Costa Rica (Ricketts et al. 2004; Ricketts 2004). The sizes, shapes, and interdigitation patterns of natural habitat in an agricultural landscape may profoundly affect the persistence of pollinators.

Globally important threats to plant-pollinator systems, while based on land use practices, are driven by a number of forces of varying scales and points of origin. These include forces driving agricultural intensification and consequent habitat loss and fragmentation of wild ecosystems, climate change, use of environmental chemicals, diseases and parasites of pollinator populations, changing fire regimes, introduction of alien plants, and competition with introduced pollinators. Each of these forces may introduce what appear to be only marginal impacts, but effects can cascade through the ecosystem in ways that may have serious repercussions for pollinator populations.

For example, the introduction of domesticated livestock to grassland ecosystems may depress pollinators if the livestock pressure exceeds the levels of grazing to which the resident pollinator populations are adapted. Intensively managed livestock tend to trample pathways and water edges that otherwise serve as nesting sites and water access points for wasp and bee pollinators (Gess and Gess 1993). Changes in the herbaceous layer of vegetation, due to grazing and the introduction of tall, fire-tolerant grasses, may lead to hotter fires, which destroy the dead wood that several groups of bees use as nesting sites (Vinson et al. 1993).

insurance policy for reproductive success and consistent gene flow between plant individuals (Kremen et al. 2002).

Poor reproduction observed in several rare plants has been linked to the loss of specialized pollinators. Examples are populations of members of the Scrophularaceae plant family in South Africa (Steiner 1993) and bird-pollinated vines in Hawaii (Lord 1991). The high degree of mutualism seen in some pollination interactions is illustrated by plants such as figs, yuccas, and food plants that are both pollinated by and serve as brood sites for the larval stage of many lepidopteran pollinators. Highly specialized relationships occur between fig tree species (considered keystone species for the maintenance of several vertebrate populations in the forest) (Terborgh 1986) and their pollinators, fig wasps, making them particularly dependent on the pollinators (Wiebes 1979). Some geographical regions of the world may have a higher occurrence of specialized pollination systems than others. South Africa, for example, has hundreds of plant species that rely on long-tongued flies for pollination. Many of these plant species rely on a single long-tongued fly species (Johnson 2004).

Key pollinators for one plant species may also provide pollination services to other plants at other times of the year. For example, Sampson (1952) noted that grazing livestock may destroy or alter riparian vegetation that serves as a key resource to pollinators at certain times of the year, thus reducing the ability of those pollinators to carry out pollination services not only on the riparian vegetation but on other plants flowering at different seasons. There is a concern that pollinator declines could, through such interconnectedness, ultimately affect multiple trophic levels (Allen-Wardell et al. 1998), yet understanding of these complex and diffuse relationships is still very incomplete. A growing body of research, however, is investigating the interactions among members of "pollination webs," similar to the complex interactions that define food webs (Memmott 1999).

Human well-being and plant reproductive success are bound together by the need for a large and diverse suite of pollinators to assure continued and reliable delivery of effective pollination services. Pollination services generally cannot be reduced to a focus on a single "service provider." The world's agricultural community is presently largely relying on the domesticated honeybee, *Apis mellifera,* to provide a complex and variable service, and that specific provider is faced with a number of disease and parasite challenges. A matrix of healthy natural ecosystems, interspersed and adjacent to human settlements and agricultural fields, can provide significant insurance that pollination services remain intact.

11.3.2.2.3 Seed dispersal

The movement of seeds away from the parent plant is an essential process in plant population and community dynamics. This is achieved in various ways, including wind, water, or explosion of fruit capsules. Most plants, however, including those directly used and managed by humans, depend on seed dispersal by animals. The seeds of a large proportion of woody plants are dispersed by animals (about 80–95% in the tropics and about 30–60% in temperate forests) (Jordano 1992). Many herbaceous plants also rely on animals for their seed dispersal, but the literature on these links and on their ecosystem-service importance is much sparser than that for woody species.

Seeds can be dispersed by animals that eat the fruit and discard the seeds (frugivores) or by seed eaters. In the latter case, most seeds do not survive consumption, but the survival of a small proportion of them is enough to ensure the perpetuation of plant populations. Fruit-eating animals include insects and vertebrates,

ranging from ants to elephants, although in tropical forests a variety of frugivorous birds and mammals are the main vertebrate dispersal agents (e.g., Leighton and Leighton 1984). Species that are important for forest regeneration include those of birds, bats, monkeys (Julliot 1996), opossums (Medellin 1994), fish (Goulding 1980), and ants (Horvitz and Beattie 1980; van der Pijl 1982). Flying seed dispersers (bats and birds) are the main vectors that promote forest regeneration in human-disturbed forests by carrying seeds from adjacent habitats to disturbed areas (Gorchov et al. 1993; Silva et al. 2002).

The removal of a frugivore species may have severe effects on several plant species. Most seed dispersal systems can be characterized as generalized (many animals disperse several species of fruits) (Jordano 1987). However, even in generalized seed dispersal systems each animal species deposits seeds in a distinct pattern that affects plant distribution (Jordano and Schupp 2000). One single species of animal may operate as the disperser of several plant species. For instance, agoutis (medium-size rodents; *Dasyprocta* spp.), are the main seed dispersal agent of several large-seeded plants in tropical ecosystems and thus influence the floristic diversity of the understory (Asquith et al. 1999).

In a similar manner to pollination, reduced dispersal also may decrease the genetic diversity of plant populations, since seeds are one of the main vectors of gene flow between populations (Pacheco and Simonetti 2000). The reduction of frugivore populations may have disproportionately large effects. For example, when an animal population is reduced, its resource use shifts to the most preferred items, such that the least preferred resources are used little if at all. Not eating the fruits may have negative impacts on the populations of plants with animal-dispersed fruits. Thus reductions of animal populations (rather than extinction) may be sufficient to dramatically change the ecosystem services provided by frugivores (Redford and Feinsinger 2001).

The value of seed dispersal is hard to estimate, but many tree crops of high economic importance depend on the seed dispersal services of animals. Conversely, the persistence of large enough populations of wild vertebrates strongly depends on the availability of fruits of such crops. Several trees whose crops have an important role in local and export economies depend on seed dispersal by wild vertebrates. Examples include the Brazil nut (*Bertholletia excelsa*), which represents a multimillion-dollar business, and the açaí palm (*Euterpe oleracea*) (Baider 2000). Also, several cosmetics are based on nuts or seeds from tropical forests.

Several tree species, such as figs and palms, are also some of the most important keystone species in the tropics (Terborgh 1986; Galetti and Aleixo 1998), because they serve as food sources during periods of fruit scarcity. Monkeys, tapirs, peccaries, and several bird species rely on keystone fruit species in Neotropical forests, and empirical evidence suggests that the structure of vertebrate communities could collapse if these keystone plant species are removed from the forest (Terborgh 1986). The overharvesting of Brazil nuts, açaí palm, and Araucaria pine seeds (*Araucaria angustifolia*) in many areas—including inside protected areas—is threatening not only the plant populations but also the animals that depend on their seeds, such as peccaries, toucans, and other large-bodied frugivores (Galetti and Aleixo 1998; Solórzono-Filho 2001; Baider 2000; Moegenburg 2002).

11.3.2.3 Predation and Food Web Interactions

Indirect interactions among species are widespread in nature and refer to the effects of one species on a second species mediated by a third species. For example, a predator may increase abundances of some plant species by reducing the abundance of herbivores. It

is difficult to predict the effects of changes to these interactions because the indirect links are often poorly understood. Even if such interactions are known to exist, their strength, and hence their effects, typically vary with environmental conditions (Berlow et al. 1999). However, if these interactions are disrupted, disproportionately large, and often unexpected, alterations in ecosystem properties and services may occur.

Because indirect interactions are often not immediately obvious, and because the loss or addition of organisms with certain traits can trigger positive feedback (self-accelerating) processes in ecosystems, the introductions or removal of species can cause "ecological surprises." Human alterations of the species composition of natural ecosystems can be unintended—such as mortality due to pollution, accidental species introductions, and extinctions caused by habitat losses—or deliberate, as when actions are taken in pursuit of some management goals—such as sustained exploitation, increased production, improved provision of ecosystem services, conservation, restoration, or increased attraction of tourists. Both types of interventions can disrupt ecosystem functioning and alter the provision of ecosystem services. Although some accidental changes have improved the provision of some services, highly undesirable effects are by far more common, or at least more commonly reported. These often involve very important monetary, environmental, and cultural costs.

Not all ecosystems are equally likely to yield unexpected or unwanted results. Rich, complex food webs have higher functional redundancy and more indirect interactions, many of which are weak. A system with many weak interactions may be more resistant to environmental change or loss of individual species. In highly interconnected food webs, however, the effect of changes in richness of one functional group are less predictable and may affect the abundance of other species or the richness of other functional groups through a complex set of direct and indirect interactions (e.g., Buckland and Grime 2000). Trophically simple systems such as temperate freshwater communities have responded particularly strongly to the deletion of high trophic level species. For example, high-latitude lakes have simple food structures and low functional redundancy and therefore are highly vulnerable to food-chain disruption (Schindler 1990). Strong interactors can also cause destabilization (Luckinbill 1979). Modeling approaches also suggest that increasing diversity can increase food-web stability under the condition that most of the interactions within the food web are weak (McCann and Hastings 1997). Stability increases with dietary breadth and number of alternative prey (Fagan 1997; Morin 1999).

The traits of introduced or removed species strongly affect whether these changes will result in unexpected or unwanted disruptions. The structure and organization of communities are often dependent on a few interactions, changes in which have disproportionately large effects relative to their abundance. Therefore, preserving functional diversity and interactions may be more important than maintaining species richness per se. Introduction or removal of species for which there are few functional analogues are likely to produce the strongest effects. Specifically, introduction of species with traits not found in species already present can produce large-scale alterations of ecosystem processes and structure (such as the introduction of exotic N-fixing trees and C_4 grasses in Hawaii).

The removal of a top predator often induces increases in herbivores and thus reductions in plants, altering community structure and ecosystem properties. Predators, by preferentially eating a competitively dominant prey, may facilitate increases in abundance of other species (Paine 1969). Removal of such keystone predators can greatly reduce prey diversity, because the dominant competitor may seriously reduce populations of species. Such effects of predator removals have been extensively documented in numerous terrestrial and aquatic ecosystems (Pace et al. 1999). Ecosystems in which such effects, known as "trophic cascades," are particularly likely include physically homogeneous habitats with few consumers, food-limited predators and herbivores, systems in which predators strongly suppress herbivores, and nutrient-enriched systems. For example, in whole-lake experiments, nutrient enrichment strongly promotes trophic cascading (Carpenter et al. 1995). Trophic cascades may be smaller when mid-level omnivorous consumers compensate for the activities of the suppressed herbivores. For example, the exclusion of fish in Venezuelan rivers did not produce cascading effects, as these fish eat both insects and algae (Flecker 1996).

As mentioned earlier, interactions among species can vary spatially and temporally and may range from strongly positive to strongly negative. For example, in dry woodlands, shrubs may facilitate the establishment of tree seedlings during dry years, but they also provide habitat for beetles (*Tenebrionidae*) that eat the seedlings (Kitzberger et al. 2000). Therefore, the effects of shrubs on the trees vary in space and time. In wetter years, direct facilitation becomes less important, and net effects may become dominated by indirect negative effects caused by the herbivores.

11.3.2.4 Ecosystem Engineers

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources other than themselves to other species by causing physical changes in the biotic or abiotic materials of the environment. They may dramatically modify the composition and functioning of an ecological community (Jones et al. 1994). On land, woody plants dominate the physical structure of the habitat. Deforestation causes massive changes in habitat structure and leads to loss of species at several trophic levels (Holling 1992). Some species modify an ecosystem's disturbance regimes because they have traits that affect probabilities of disturbance. For instance, highly flammable grasses induce high fire frequency, which in turn alters community composition and ecosystem functioning (D'Antonio and Vitousek 1992; Levine et al. 2003). In hurricane-prone tropical forests, deeper-rooted trees may be less likely to fall during high winds, thereby altering understory communities (Lawton and Jones 1995). Examples of animal ecosystem engineers are numerous. Beavers damming streams, termites building mounds, and elephants killing trees are all examples of animals that modify the structure of their habitat. These modifications can strongly affect the hydrology, productivity, and the provisioning of ecosystem products (such as fish in beaver ponds).

11.3.3 Biodiversity Effects on Climate Regulation

Certain components of biodiversity, such the characteristics of the dominant species and the distribution of landscape units, influence the capacity of terrestrial ecosystems to sequester carbon and regulate climate at the local, regional, and global scales. (See also Chapter 13.) Indirect feedback to global climate may accrue because plants sequester carbon in biomass (decreasing carbon release to the atmosphere). Climate may also be altered by plants through changes in albedo, evapotranspiration, temperature, and fire regime. Changes in land use, over large land surface areas, will change how biodiversity affects climate. Equally important are the functional traits of dominant plant species and the spatial arrangement of landscape units. Thus biodiversity needs to be explicitly considered in climate change mitigation practices such as

afforestation, reforestation, slowed-down deforestation, and bio-fuel plantations.

11.3.3.1 Biophysical Feedbacks

The functional traits and structural complexity of plant canopies influence water and energy exchange through their effects on albedo (Chapter 13). Albedo is the proportion of incoming radiation that is reflected by the land surface back to space. Complex canopies trap more reflected radiation, thereby reducing albedo. In dense vegetation, albedo is determined by the properties of the dominant plant functional types, with albedo decreasing from grasses to deciduous shrubs and trees to conifers (Chapin et al. 2002). In open-canopied ecosystems, which account for 70% of the ice-free terrestrial surface (Graetz 1991), all individuals contribute to albedo, and more biologically diverse—and hence more structurally complex—communities have lower albedo (Thompson et al. 2004). For example, the increase in shrub density in Arctic tundra in response to regional warming (Sturm et al. 2001) has reduced regional albedo and increased regional heating (Chapin et al. 2000b). (See Chapter 25.)

Greater structural diversity of the canopy increases the efficiency of water and energy exchange, which influences water use efficiency of vegetation and runoff to streams. Complex canopies generate mechanical turbulence that mixes within-canopy air with the bulk atmosphere and therefore increases the efficiency with which water, heat, and CO_2 are exchanged between the ecosystem and the atmosphere. (See Chapter 13.) Mechanical turbulence depends on the structural diversity of the vegetation—the number, size, and arrangement of roughness elements such as trees or shrubs. Changes in structural diversity are particularly important when they add individuals that are taller or more wind-resistant than the surrounding vegetation. Even a low density of trees (less than 100 trees per hectare, for example) in a savanna or woodland substantially increases turbulent exchange with the atmosphere (Thompson et al. 2004).

The functional composition of vegetation (for instance, the structural complexity, phenology, or height) influences not only the total quantity of energy absorbed and exchanged with the atmosphere but also the partitioning of this energy flux among three pathways: latent heat flux (evapotranspiration) as a result of evaporation of water at the surface and its condensation in the atmosphere, sensible heat flux (heat associated with a temperature increase of the air), and ground heat flux (the heat conducted into the ground) (Oke 1987).

Forests transmit a larger proportion of their energy to the atmosphere as latent heat (evapotranspiration) than grasslands do because of their deeper roots and greater leaf area (Chapin et al. 2002). They therefore have a net moistening effect on the atmosphere (Shukla et al. 1990), which becomes a moisture source for downwind ecosystems. In the Amazon, for example, 60% of precipitation comes from water transpired by upwind ecosystems. Species with traits that enhance stand-level evapotranspiration, such as high stomatal conductance, therefore enhance the regional precipitation derived from a given moisture source. Since water is the resource that most strongly limits global plant production (Chapin et al. 2002; Gower 2002), these properties also contribute substantially to global productivity. In the boreal forest, post-fire deciduous stands have higher albedo and stomatal conductance than pre-fire conifer stands (Baldocchi et al. 2000) and therefore have a net cooling effect on climate. Because increasing temperatures will increase fire frequency, this may act as a one of the few potential negative feedbacks to high-latitude warming (Chapin et al. 2000c).

Large-scale changes in landscape patterns have effects on regional climate. The diversity of patches on a landscape exerts an additional impact on biophysical coupling between land and atmosphere and therefore on local-to-regional climate. Large patches (more than 10 kilometers in diameter) that have lower albedo and higher surface temperature than neighboring patches create cells of rising warm air above the patch (convection); this air is replaced by cooler moister air that flows laterally from adjacent patches (advection). Climate models suggest that these landscape effects substantially modify local-to-regional climate. In Western Australia, the replacement of native heath vegetation by wheatlands increased regional albedo. As a result, air tended to rise over the dark heathland, drawing moist air from the wheatlands to the heathlands. The net effect was a 10% increase in precipitation over heathlands and a 30% decrease in precipitation over croplands (Chambers 1998). Most vegetation changes generate a climate that favors the new vegetation, making it difficult to return the vegetation to its original state.

11.3.3.2 Carbon Sequestration

Biodiversity affects carbon sequestration primarily through its effects on species traits, particularly traits related to growth (which governs carbon inputs) and woodiness, a key determinant of carbon turnover rate within the plant. As described earlier, species diversity can enhance productivity through temporal and spatial niche diversification and through increasing the probability of including productive species in the community. Species differences in productivity result from a wide range of plant traits, including growth rate, allocation patterns, phenology, nutrient use efficiency, resource requirements, traits that influence access to resource pools (such as root depth or symbioses with mycorrhizae or N-fixing microorganisms), and traits that influence conditions that limit growth (such as temperature or moisture) (Lambers and Poorter 1992). Woodiness is particularly important in enhancing carbon sequestration because woody plants tend to contain more carbon, live longer, and decompose more slowly than smaller herbaceous plants.

Plant species also strongly influence carbon loss via decomposition and their effects on disturbance. Decomposition is influenced by traits linked to leaf litter quality (carbon quality and nutrient concentrations, for example), effects on soil environment (temperature, moisture, oxygen, and so on), carbon exudation rate from roots, and interactions with other species (Eviner and Chapin 2004). For example, wood decomposes more slowly than herbaceous material, and slow-growing plants characteristic of low-resource environments produce leaves that decompose more slowly than those of more rapidly growing plants (Cornelissen 1996; Pérez-Harguindeguy et al. 2000), enhancing carbon sequestration.

In general, the suite of traits that promotes rapid growth and high productivity also leads to rapid decomposition. Thus there is a tradeoff among traits that promote short-term carbon accumulation versus long-term carbon storage. Plant traits also influence the probability of disturbances such as fire, wind-throw, and human harvest, which temporarily change forests from accumulating carbon to releasing it (Valentini et al. 2000; Schulze et al. 2000). In addition to the effects of plant traits on carbon gain and loss from ecosystems, other forms of diversity can be important by influencing the spread of pests and pathogens, which are important agents of disturbance and carbon loss from ecosystems (see next section).

Landscape diversity and spatial pattern also influence carbon loss from ecosystems. In particular, the edges of forest fragments

are often places of high plant mortality because the radically altered environment at forest edges kills trees via wind throw and desiccation (e.g., Hobbs 1993 for Australia; Chen et al. 1992 for western North America; Laurance et al. 1998a for Amazonia). Elevated tree mortality leads to a decline of living biomass near forest edges (Laurance et al. 1997) and an increase in decomposition (Laurance et al. 2000). The net effect is a decline in carbon storage at the edges of forest fragments. As forest fragments decline in size, a larger proportion of the total landscape loses carbon. Another potential effect of habitat fragmentation is the alteration of natural fire regimes, either by reducing the frequency and extent of fires (for example, when fires are suppressed in the surrounding matrix) (Baker 1994) or by increased burning in ecosystems that are highly vulnerable to fire (as in tropical rainforests) (Gascon et al. 2000; Cochrane and Laurance 2002; see also Chapter 16).

11.3.4 Pest and Disease Control in Agricultural Systems

Both the diversity of natural enemies and the landscape diversity may influence pest and disease control in agricultural systems. Yields of desired products from agroecosystems may be reduced by attacks of herbivores above and below ground, fungal and microbial pathogens, and competition with weeds. Modern agriculture has focused on reducing biodiversity in order to generate monocultures of the most profitable species or genetic variety. Landscape diversity (such as the intermixing of crop and noncrop patches) and crop rotation can also reduce the need to breed for new pest and disease resistance and to discover new pesticides.

However, biodiversity may enhance pest resistance in agricultural systems through both ecological and evolutionary processes. Because of the high population densities and short life cycles of many weeds and pests, resistance to synthetic biocides typically evolves rapidly, necessitating continuing costly investments to develop and employ new synthetic biocides. Most improvements in crop resistance to herbivores, pathogens, and weeds are transitory. Use of biodiversity can reduce the frequency with which biocides need to be applied and, hence, the selective pressure and rate at which resistance evolves (Palumbi 2001).

Biodiversity-based techniques that reduce or eliminate the need for biocides can be based on the species richness of crop plants or natural enemies (pathogens or parasites). Techniques that use crop plant biodiversity to reduce or eliminate application of biocides include intercropping of genetically different strains of a single crop species, intercropping of crop plants of different species, and crop rotation. Techniques that encourage populations of predators, parasites, and pathogens of the species that attack crop plants include no-till or low-till soil management and planting of other plant species that either repel crop predators or attract them away from the crop.

11.3.4.1 Techniques Based on Crop Plant Biodiversity

The productivity of agricultural systems with high crop genetic diversity or species richness tends to be more stable over time than that of low-diversity systems, in part due to improved pest and disease control (Power and Flecker 1996; Power 1999) (see also the earlier section on ecosystem stability). Traditional agricultural systems often include substantial planned genetic and species diversity (Pretty 2002). In contrast, the low diversity of most commercial monoculture systems often results in large crop losses from a pest complex that is less diverse but more abundant than that in more diverse systems. Indeed, a low-diversity global strat-

egy of food production could potentially be destabilized by pests and disease (Tilman et al. 2002a).

A large proportion of global food production is accounted for by just three crops: wheat, rice and maize. The relative scarcity of outbreaks of diseases on these three crops is a testament to the success of plant breeding, cultivation practices, and the use of agrochemicals. Because of the rapid evolution of biocide-resistant organisms, however, these successes may not be sustainable in the long term. For example, within about one or two decades of the introduction of each of seven major herbicides, herbicide-resistant weeds were observed. Insects also frequently evolve resistance to insecticides within a decade. Resistant strains of bacterial pathogens appear within one to three years of the release of many antibiotics for livestock (Palumbi 2001).

By the beginning of the twenty-first century, some 2,645 cases of resistance of species to biocides had been recorded in insects and spiders, involving more than 310 pesticide compounds and 540 different insect species (www.cips.msu.edu/resistance/; www.cips.msu.edu/resistance/rmdb/background.html). During the 1990s, there was a 38% increase in compounds to which one or more arthropod species were resistant, and a 7% increase in arthropod species that are resistant to one or more pesticides.

Increased genetic diversity of crops nearly always decreases pathogen-related yield losses. Recently rice blast, a major and costly fungal pathogen of rice, was controlled in a large region of China by planting alternating rows of two rice varieties (Zhu et al. 2000). This tactic increased profitability and reduced the use of a potent pesticide. The use of mixtures of different crop varieties has been shown to effectively retard the spread or evolution of fungal pathogens of grains (Ngugi et al. 2001; Mundt 2002). There is some evidence that these approaches may also be useful for the control of plant viruses (Power 1991; Matson et al. 1997; Hariri et al. 2001).

High crop species richness enhances the ecosystem services derived from agriculture and often improves the stability of production over time by reducing the incidence of herbivores, pathogens, and weeds. In monoculture plantations of rubber trees, sugarcane, or cacao, the larger and more isolated the plantation, the greater the impact of herbivores on the plants of the agroecosystem (Harper 1977; Strong 1974). Plantations of cacao and rubber tend to have considerably lower levels of herbivory when adjacent to natural, diverse forests. In a review of reported tests of herbivore density in polycultures compared with monocultures, 52% of 287 herbivore species occurred at lower densities in polycultures compared with only 15% that occurred at higher density (Andow 1991). Sometimes even growing a mixture of two crops is enough for broad pest control; for example, in the Philippines, intercropping maize and peanuts helps to control the maize stemborer (Conway 1997). Numerous studies indicate that increasing crop species richness commonly decreases the severity of weed infestations (Liebman and Staver 2001). This is because greater crop species richness often increases the overall usage of available resources by the crops, leaving fewer leftover resources on which weeds can subsist.

Plant species richness also tends to suppress the spread of viral infection in crops: 89% of plant viruses with a known transmission mechanism are transmitted by plant-feeding insects (Brunt et al. 1996). Greater plant species richness reduces the abundance of their insect vectors, and so the majority of viruses that are transmitted by insects tend to be found at lower densities in polycultures than monocultures (Power and Flecker 1996). The richness of crop species in an agroecosystem has a much less predictable effect on the prevalence of microbial pathogens that do not rely on insect vectors, such as most fungi (Matson et al. 1997).

Fungal diseases are usually but not always less severe in poly-cultures than monocultures (Boudreau and Mundt 1997). Variations occur because the effects of intercropping on disease dynamics depend on a variety of factors, including microclimate effects and the spatial scale of pathogen dispersal (Boudreau and Mundt 1994; Boudreau and Mundt 1997). Crop diversification can alter microclimate in ways that either encourage or inhibit pathogen growth, depending on the characteristics of the pathogen, plants, and local environment (Boudreau and Mundt 1997). Long-distance aerial dispersal is an important survival strategy for fungal and fungus-like pathogens that cause crop diseases, such as rusts (*Uredinales*), powdery mildews (*Erysiphales*), and downy mildews (members of the protist family *Peronosporaceae*) (Brown and Hovmøller 2002). Therefore, deployment of increased crop species richness at larger spatial scales may be necessary to reduce their spread. This idea is supported by studies of increased crop genetic diversity (Zhu et al. 2000; Wolfe 2000), but untested with species diversity.

11.3.4.2 Techniques Based on the Biodiversity of Natural Enemies of Crop Predators, Parasites, and Pathogens

The species richness of natural enemies of pests increases with that of crops (Andow 1991). Compared with monocultures, species-rich agroecosystems are likely to have higher predation and parasitism rates and higher ratios of natural enemies of herbivores, all of which may contribute to lower pest densities. The spraying of biocides is much more likely to wipe out the organisms that control the pests than the pests themselves or to so reduce their predator populations that the resurgence of pests can cause considerable damage before control is reestablished (Naylor and Ehrlich 1997). Traditional subsistence systems that rely on diverse agroecosystems, such as the Javanese home garden or the milpa farming system in Mexico, typically support natural enemies of pests, such as spiders, ants, and assassin bugs (see the Javanese rice paddy case study in Chapter 26). However, the positive impacts of increased species richness on natural pest control are not universal (Altieri and Schmidt 1986).

Natural pest control services are likely to be detrimentally affected by loss of species richness (Schläpfer et al. 1999). However, in only a few cases has the role of natural enemy species richness in controlling pests been tested explicitly. Species richness of parasitoids increases parasitism rates in the armyworm caterpillars in some but not all locations in the United States (Menalled et al. 1999). Perhaps the most comprehensive understanding of the importance of predator species richness comes from spiders. There are indications of complementarity of function among spider species—that is, they catch prey using different methods, occupy different microhabitats, or are active at different times or seasons. Because of this, increasing spider species richness leads to higher and less variable predation rates and increased food web stability (Marc and Canard 1997; Riechert et al. 1999; Sunderland and Samu 2000; and see section 11.2.1 for general discussion of diversity and functional complementarity).

Recent theoretical evidence suggests that the species richness of predators and parasites of herbivorous insects may be important for the control of some types of insect pests, whereas composition, the presence of a particular predator or parasite species, may be more important than species richness for other types of pest (Wilby and Thomas 2002b), though this is yet to be rigorously tested in the field. Understanding whether and when natural enemy species richness will increase pest control is an important goal of contemporary agroecological science.

Mixtures of two or more plant species have also been developed to manipulate the density of pests and their natural enemies. For example, two kinds of plants are sometimes cultivated together with maize to control stem-borers: a plant that repels the insects and another that attracts them. This strategy has also been shown to be helpful in suppressing the parasitic weed *Striga* (Khan et al. 2000). Natural plant compounds that have been used in traditional farming systems can be useful in controlling pests in many agricultural settings. Examples include the neem tree (*Azadirachta indica*)—a natural insecticide source that has been used against rice pests in India for decades—and a variety of other plants such as the custard apple (*Annona* sp.), turmeric (*Curcuma domestica*), Simson weed (*Datura strononium*), and chili peppers (*Capsicum frutescens*) (Pretty 1995).

11.3.4.3 Integrated Pest Management and Low-till Cultivation Systems

Integrated pest management, an approach that combines traditional agricultural systems with modern techniques, includes the promotion of natural pest controls through enhanced biodiversity of crops and natural enemies of crop pests, parasites, and pathogens (as just described), the development of host-plant resistance, and the use of pesticides when absolutely necessary. IPM can be highly successful in mitigating pest pressure in regions where farmer training programs and information services are adequate (Conway 1997; Naylor and Ehrlich 1997). However, despite cases of notable success with IPM, such as the control of the brown planthopper in Indonesian rice systems (Kenmore 1984), relatively few crops are managed widely with IPM techniques on a global scale. Because of favorable pricing policies for pesticides in many locations and the knowledge-intensive nature of IPM, this practice has yet to significantly reduce the amount of pesticides applied in agriculture worldwide.

A central component of IPM is a low-till cultivation system, which maintains a permanent or semi-permanent organic cover on the soil, consisting of either a growing crop or dead organic matter in the form of a mulch or green manure. Low-till cultivation provides habitat for natural enemies to control insect pests and increases local genetic, species, and landscape diversity, as well as enhancing soil stability, organic matter content, and carbon sequestration (Sánchez 1994; Swift 1999; Pretty and Ball 2001; Lal 2004). However, this practice often relies on the heavy use of herbicides to control weeds that might otherwise be controlled by tillage and thus can have strong negative impacts on plant biodiversity (Pretty 2002). No-till with no or minimum use of herbicides is also a viable option, at least for small farms (Petersen et al. 2000; Ekboir 2002).

11.3.4.4 Summary on Biodiversity and Natural Pest Control

To summarize, the maintenance of natural pest control services is strongly dependent on biodiversity. This service benefits food security, rural household incomes, and national incomes of many countries. (See also Boxes 11.3 and 11.4.) In many cases, perhaps the majority of them, increased crop genetic diversity and species richness at different trophic levels lead to more efficient natural control of pests and diseases in agricultural systems. However, further research is required to elucidate the ecological mechanisms of pest and disease control in order to understand both the successes and failures of reduced-input agricultural systems.

Nonetheless, the available evidence suggests that conserving the genetic diversity of crops and crop relatives at a global scale and deploying that diversity locally will protect and enhance natu-

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BOX 11.3

Biodiversity and the Multifunctionality of Agricultural Systems

Modern agricultural methods brought spectacular increases in productivity (Conway 1997; Pretty 2002; Tilman et al. 2002a). Large-scale agriculture, however, brings simplification and a loss of biological diversity and thus reduces the potential of agriculture to provide ecosystem services other than food production. Worldwide, a third of the 6,500 breeds of domesticated mammals and birds are under immediate threat of extinction owing to their very small population size. Over the past century, it is believed that 5,000 animal breeds have already been lost. The situation is most serious in the already industrialized farming systems, with half of breeds at risk in Europe and a third at risk in North America. Asia, Africa, and Latin America have approximately 20% of their breeds at risk (FAO/UNEP 2000; Blench 2001). There is strong evidence that more genetic diversity keeps options open for both breeders and farmers in the face of a changing environment.

Unlike many other economic sectors, agriculture is inherently multifunctional. It jointly produces much more than just food, fiber, or oil, having a profound impact on many elements of local, national, and global economies and ecosystems (FAO 1999; see also Chapters 10 and 17). These impacts can be negative or positive. For example, an agricultural system that depletes organic matter or erodes soil while producing food imposes costs that others must bear; but one that sequesters carbon in soils and keeps both planned and unplanned species richness high enhances eco-system services other than food and fiber production. For centuries, traditional agricultural systems have contributed to ecosystem services such as regulation of water supply, soil fertility, and plant and animal pathogens and pests; storm protection and flood control; and carbon sequestration. In contrast, industrialized agriculture has become progressively more expensive in terms of energy (inorganic fertilizers, pumped irrigation, and mechanical power) (Pretty 1995), human and environmental health (toxic contamination, soil erosion and salinization, eutrophication of land and water) (Conway and Pretty 1991; Pretty 1995; Altieri 1995; EEA 1998), and social impact (rural uprooting, poverty, and economic inequity) (Pretty 2002; see also Chapter 6).

Sustainable agricultural systems that substitute goods and services derived from nature for externally derived fertilizers, pesticides, and fossil fuels enhance the provision of ecosystem services and human well-being in several ways. First, they increase the energy-efficiency of food production (Pretty 1995; Pretty and Ball 2001) (see also Chapters 8 and 26), thus decreasing the externals costs to society as a whole. Second, they enhance the provision of human health (see also Chapter 14). Third, by protecting genetic, species, and landscape diversity, they enhance the provision of biodiversity-linked regulating and supporting ecosystem services derived from it.

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ral pest control services that provide economic and food production benefits. Moreover, high–biodiversity agriculture has cultural and esthetic value and can reduce many of the externalized costs of irrigation, fertilizer, pesticide, and herbicide inputs associated with monoculture agriculture (Pretty et al. 2000 2001).

11.3.5 Biodiversity Effects on Human Disease Regulation

Human health, particularly risk of exposure to many infectious diseases, may depend on the maintenance of biodiversity in natural ecosystems. (See Chapter 14.) Over 60% of human pathogens are naturally transmitted from animals to humans (Taylor et al. 2001). Many of these are transmitted by arthropod vectors from wildlife species, creating the potential for ecological processes to affect human disease risk. A greater richness of wildlife species might be expected to sustain a greater number of pathogen species that can infect humans. However, evidence is accumulating that greater wildlife species richness may decrease the spread of wildlife pathogens to humans. The effect of biodiversity on disease risk is also expected to depend on the details of interactions between the wildlife host and arthropod vector species. Unfortunately, such data are lacking for most such diseases.

Spread of one disease for which there is data, Lyme disease, seems to be decreased by the maintenance of the biotic integrity of natural ecosystems. Lyme disease is the most common vector-transmitted disease of humans in North America, and thousands of cases occur annually in Europe and Asia as well (Ostfeld and Keesing 2000a). Where it has been studied in eastern North America, the ticks that transmit the disease primarily acquire the pathogen from the white-footed mouse, *Peromyscus leucopus* (Barbour and Fish 1993). Therefore, ecological processes that reduce the number of ticks feeding on mice have the potential to reduce disease transmission to humans.

A greater number of small mammal species could reduce the number of ticks feeding on mice either by reducing mouse abundance through competition or by attracting ticks that would otherwise have fed on mice. Modeling analyses of data collected in southeastern New York State suggests that the current level of mammal biodiversity decreases disease risk to humans by up to 50% relative to realistic scenarios of decreased biodiversity (Schmidt and Ostfeld 2001; LoGiudice et al. 2003; Ostfeld and LoGiudice 2003). In a complementary analysis of large-scale geographic gradients in mammal biodiversity, states in the eastern U.S. inhabited by more species of small mammals reported fewer cases of Lyme disease per capita (Ostfeld and Keesing 2000a).

In another survey, Lyme disease risk was over four times greater in forest fragments less than 2 hectares in area than in larger fragments that typically harbor a greater number of mammal species (Allan et al. 2003). In these latter two studies, Lyme disease risk also appeared to be a function of other variables correlated with mammal species richness, such as climate, geographic location, and the presence and abundance of specific mammal species. Together, these results strongly suggest that current biodiversity of small mammals supports public health by reducing peoples' risk of contracting Lyme disease, but that this ecosystem service is being eroded by habitat fragmentation.

Risks of other infectious diseases might also depend on biodiversity, although data to fully understand such links are sparse and inconsistent. Lyme disease is epidemiologically representative of emerging diseases in general. Vector-transmitted diseases are over twice as likely as other diseases to be emerging diseases, and 75% of emerging human diseases are naturally transmitted from animals to humans (Taylor et al. 2001). Therefore, biodiversity might be important in controlling many emergent diseases. Whether the same biological processes that appear to control Lyme disease risk also control risk of other vector-borne pathogens remains largely untested, however. Whether biodiversity can also decrease the risk of wildlife pathogens that do not require arthropod vectors for transmission to humans is even less well understood. Thus, the available data indicate that human health is supported as an ecosystem service by biodiversity in some cases, but the generality of this service is poorly known. (See also Chapter 14.)

BOX 11.4

Putting a Monetary Value on High-biodiversity Agricultural Landscapes

How much are traditional high-diversity agricultural landscapes worth? It is relatively easy to assess the negative costs of unsustainable agriculture in terms of abatement and treatment costs following pollution, increased sediment deposition into dams, the socioeconomic costs of rural uprooting, and so on. It is much more difficult to calculate the value of both the positive direct contributions of agricultural systems containing highly planned and unplanned biodiversity and the indirect effects on supporting and regulating ecosystem services. Environmental economists have developed methods for assessing people's stated preferences for environmental goods through hypothetical markets (see Chapter 2), which permits an assessment of their willingness to pay for nature's goods and services or to accept compensation for losses (Stewart et al. 1997; Hanley et al. 1998, Brouwer et al. 1999).

A variety of these assessment methods suggests that traditional agricultural landscapes are highly valued. Although it is impossible to precisely quantify this, several proxies can be used, including how much governments are willing to pay farmers to produce certain habitats or landscapes, how often the public visits the countryside, and how much they spend when they get there (Willis et al. 1993; Foster et al. 1997; Stewart et al. 1997; Hanley et al. 1998).

U.K. government programs have attempted to preserve and restore some of the habitat and other positive countryside attributes that were lost during intensification. The annual per household benefit of these areas, using a variety of valuation methods (including contingent valuation, choice experiments, and contingent ranking), varies from £2–30 to £380. If we take the range of annual benefits per household to be £10–30 and assume that this is representative of the average households' preferences for all landscapes produced by agriculture, then this suggests national benefits of the order of £200–600 million per year. Expressed on a per hectare basis, annual benefits are £20–60 per hectare of arable and pasture land.

Another study compared paired organic and nonorganic farms, and concluded that organic agriculture produces £75–125 per hectare of positive externalities each year, with particular benefits for soil health and wildlife (Cobb et al. 1998).

Another proxy measure of how much we value landscapes can be made based on actual visits made to the countryside. Each year in the United Kingdom, day and overnight visitors make some 433 million visit-days to the countryside and another 118 million to the seaside (Pretty et al. 2003). The average spent per day or night varies from nearly £17 for U.K. day visitors to £58 for overseas overnight visitors. This indicates that the 551 million visit-days to the countryside and seaside result in expenditure of £14 billion per year. This is three and a half times greater than the annual public subsidy of farming. While none of these estimates are definitive, in total they clearly indicate that the landscape is highly valued by society.

Should farmers receive public support for the ecosystem services they produce in addition to food? Should those that pollute or otherwise decrease the provision of ecosystem services to the public have to pay for restoring them? The external costs and benefits of agriculture raise important policy questions for both industrial and developing countries. Three categories of policy instruments are available: advisory and institutional measures, regulatory and legal measures, and economic instruments. In practice, effective pollution control and supply of desired public goods requires a mix of all three approaches, together with integration across sectors. Regulatory and legal measures can be used to internalize external costs: those who decrease the ecosystem-service potential of the environment below a set standard are subject to penalties. Economic instruments can also be used to make sure that those who damage the environment bear the costs of the damage and also as a reward for good behavior. A variety of economic instruments are available for achieving internalization, including environmental taxes and charges, tradable permits, and targeted use of public subsidies and incentives.

11.4 Biodiversity Effects on the Provision of Marine Ecosystem Services

The ocean covers approximately 70% of Earth's surface area and contains nearly 99% of its habitable volume, so ecosystem services disrupted in the ocean will have large global consequences. The services provided by ocean ecosystems include global materials cycling, transformation and detoxification of pollutants and wastes, support of coastal recreation and tourism, and support of world fisheries and aquatic ecosystems. (See Chapter 18.) All these services are affected by the diversity of life in the ocean, although quantification of many of the links between biodiversity and marine ecosystem services has only occurred recently (Peterson and Lubchenco 1997). Marine biodiversity provides many of the same types of services as those of terrestrial biodiversity just described, with the exceptions of pollination and seed dispersal.

11.4.1 Invasion Resistance

In several marine ecosystems, decreases in the richness of native taxa were correlated with increased survival and percentage cover of invading species. This suggests that, as in terrestrial plant ecosystems, invasion resistance is enhanced by the integrity of the native species pool. For example, diverse systems use resources such as available space more completely. In experimentally assembled benthic (sea floor) communities, decreasing the richness of

native taxa was correlated with increased survival and percent cover of invading species. Open space was the limiting resource for invaders, and a higher species richness buffered communities against invasion through increasing temporal stability (such as reducing fluctuations of open space) (Stachowicz et al. 1999). High biodiversity is also expected to contribute to community resilience by creating insurance through functional redundancy (Stachowicz et al. 2002). Although there are few studies of the effects of biodiversity in marine ecosystems, the available evidence suggests that marine systems may possess similar mechanisms of invasion resistance as found in terrestrial systems.

11.4.2 Direct and Indirect Interactions between Marine Species

11.4.2.1 Interactions between Plants and Symbiotic Microorganisms

Coral reefs and the ecosystem services they provide are seriously threatened by a hierarchy of anthropogenic threats. (See Chapter 19.) As one of the most species-rich communities on Earth, coral reefs are responsible for maintaining a vast storehouse of genetic and biological diversity. Substantial ecosystem services are provided by coral reefs, such as habitat construction, nurseries and spawning grounds for fish, nutrient cycling and carbon and nitrogen fixing in nutrient-poor environments, wave buffering, sedi-

ment stabilization, and tourism. Reef-related fisheries constitute approximately 9–12% of the world's fisheries. Coral reefs support the pelagic food web by exporting nutritional material such as mucous, wax esters, and dissolved organic matter. The total economic value of reefs and associated services is estimated as $503 million in Australia and as $900 million in the Caribbean (Moberg and Folke 1999).

Corals require a symbiosis with zooxanthellan algae, which provide carbon, and ecosystem services can be maintained only if the interaction between corals and their obligate symbiotic algae is preserved. The interaction with zooxanthellae is strain-specific and changes with temperature and biogeographic region, light environment, and depth (Baker et al. 2004). High temperatures, such as experienced globally as a result of the 1998 El Niño events, disrupt the symbiosis, make corals less resilient to other stresses, and can lead to massive coral mortality (Hughes et al. 2003). Thus there is a direct causal link between climate warming and disruption of a critical biological interaction that can trigger collapse of an entire reef system, with consequent loss of ecosystem services that are provided. (See Chapter 19.)

11.4.2.2 Ecosystem Engineers and Herbivory

Macroalgae and corals modify wave action regimes and allow sediment stabilization, greatly affecting intertidal community diversity (Lawton and Jones 1995). Corals are threatened by a variety of human impacts, and many kelp macroalgae communities are threatened by overgrazing. The effects of overgrazing may be reversible. For example, recovery of sea otter (*Enhydra lutris*) populations after decades of overhunting on the coast of western North America has promoted the reestablishment of structure-forming kelp forests and its associated community as a result of the reestablishment of the predation of herbivorous sea urchins by otters (Dayton et al. 1998; Springer et al. 2003).

11.4.2.3 Predators and Food Webs

Overfishing reduces the capacity of the marine system to continue to provide ecosystem services by impoverishing and threatening marine biodiversity, particularly top predators (Myers and Worm 2003). The loss of a top predator is likely to have effects on their prey and other species throughout the food web. Removal of fish with key characteristics from the ecosystem may result in loss of resilience and a change in the ecosystem from one equilibrium state to another (e.g., Sutherland 1974; Hughes 1994). For example, recent declines in great whales, a preferred food of killer whales, caused the killer whales to shift to sea otters. Rapid decimation of otters by killer whales took predation pressure off a keystone herbivore, urchins, which then overgrazed kelp beds and transformed them into crustose algal–dominated communities called "urchin barrens" (Springer et al. 2003).

As in terrestrial and aquatic communities, there are many examples of how biodiversity, particularly the loss of populations of individual species, influences ecosystem processes and the provisioning of ecological services. In the rocky intertidal zone, for example, most primary productivity is contributed by a few strong interacting species (Paine 2002). A loss of biodiversity that includes those species has a large effect on primary productivity. Similarly, Duarte (2000) found a strong link between ecosystem functioning and biodiversity in seagrass beds worldwide, with the caveat that ecosystem processes depend on particular members of a community rather than on species numbers.

Some species may have a disproportionately large effect relative to their abundance (Power et al. 1996). For example, the main predators of large commercial fish species are not larger fish,

but rather small jellyfish that feed on fish larvae (Purcell 1989). In addition, species loss in species-rich communities is more likely to be compensated for by increases of functionally similar species, as described early in the chapter in the section on ecosystem stability.

Many species interactions vary spatially and temporally from strongly positive to strongly negative. For example, predatory whelks (*Nucella emarginata* and *N. canaliculata*) in intertidal communities consume mussels (*Mytilus trossulus*), but also influence them indirectly through their effects on barnacles (*Balanus glandula*), habitat facilitators of mussels. These spatially and temporally fluctuating interactions have important consequences on community structure and ecosystem organization (Berlow 1999).

11.4.3 Biodiversity Effects on Climate Regulation

The major importance of marine biodiversity in climate regulation appears to be via its effect on biogeochemical cycling and carbon sequestration. The ocean, through its sheer volume and links to the terrestrial biosphere, plays a huge role in cycling of almost every material involved in biotic processes. (See Chapter 12.) Of these, the anthropogenic effects on carbon and nitrogen cycling are especially prominent.

Biodiversity influences the effectiveness of the biological pump that moves carbon from the surface ocean and sequesters it in deep waters and sediments (Berner et al.1983). Some of the carbon that is absorbed by marine photosynthesis and transferred through food webs to grazers sinks to the deep ocean as fecal pellets and dead cells. The efficiency of this trophic transfer and therefore the extent of carbon sequestration is sensitive to the species richness and composition of the plankton community (Ducklow et al. 2001). Some phytoplankton in the southern ocean, for example, are more palatable than others, so an increase in their abundance increases grazing, the formation of fecal pellets, and the export of carbon to depth. (See Chapter 25.)

The biodiversity of marine sediments can play a key role in ecosystem processes. Sedimentary habitats cover most of the ocean bottom and therefore constitute the largest single ecosystem on Earth in terms of spatial coverage. Although only a small fraction of benthic organisms that reside in and on sediments have been described and few estimates of total species numbers and biogeographic pattern have been attempted, there is sufficient information on a few species to suggest that sedimentary organisms have a significant impact on major ecological processes (Snelgrove et al. 1997). Benthic organisms contribute to the regulation of carbon, nitrogen, and sulfur cycling, to water column processes, to pollutant distribution and fate, to secondary production and transport, and to the stability of sediments. Linkages between groups of organisms and the level of functional redundancy of marine sediment biodiversity is poorly known, and there are very few empirical studies (e.g., Bellwood et al. 2004).

11.4.4 Biodiversity Effects on Pollution and Human Disease Regulation

The marine microbial community provides critical detoxification services—filtering water, reducing effects of eutrophication, and degrading toxic hydrocarbons. Very little is known about how many species are necessary to provide detoxification services, but these services may critically depend on one or a few species. For example, American oysters in Chesapeake Bay on the U.S. East Coast were once abundant but have sharply declined, and with them their filtering ecosystem services (Lenihan and Peterson 1996). Reintroduction of large populations of filtering oysters may significantly improve water clarity in the bay (Jackson et al.

2001). The process of degrading toxic hydrocarbons, such as those in an oil spill, into carbon and water requires oxygen. Nutrient pollution can generate oxygen deprivation and thereby significantly reduce the ability of marine microbes to detoxify hydrocarbons (Peterson and Lubchenco 1997).

11.5 Biodiversity, Ecosystem Services, and Human Well-being: Challenges and Opportunities

The message emerging from the evidence assessed in this chapter is clear: the loss of biodiversity can reduce the provision of ecosystem services essential for human well-being. Knowledge of the links between biodiversity and ecosystem processes is still incomplete, but existing evidence suggests that a precautionary approach may be prudent and that research should be targeted to assist with the development of appropriate management interventions.

The biggest challenges are posed by the limited understanding of the ways in which biodiversity regulates ecosystem functioning at local and regional scales and the intrinsic difficulty of predicting unexpected, accelerated, and some times irreversible changes triggered by alterations of local and regional biodiversity by human intervention. Global extinctions are serious and irreversible, but alteration of the functional composition of local communities, the extinction of local populations, or their reduction to levels that do not allow them to play strong ecosystem roles (functional extinctions) are of major concern.

The vast majority of supporting and regulating ecosystem services provided by biodiversity are delivered at the local to regional scale. Often, when the functioning of a local ecosystem has been pushed beyond a certain limit by direct or indirect biodiversity alterations, the ecosystem service losses may persist for a very long time. In this sense, modern industrial agricultural practices based on the reduction of local biodiversity to one or a very small group of desired species is a major threat to the maintenance of supporting and regulating ecosystem services.

The evidence presented in this assessment suggests than in many instances biodiversity conservation is an economically sound way of improving human well-being. Conserving and managing biodiversity sustainably can maintain a number of ecosystem services whose importance is only now starting to be recognized without necessarily compromising the delivery of economic products from ecosystems.

The idea that there is an unavoidable trade-off between biodiversity and the economic output of ecosystems ignores the external costs of intensive ecosystem exploitation. When these considerable costs are taken into account, including those of lost supporting and regulating services—in the case of agricultural intensification, for instance, external costs are related to pollution and related health hazards, erosion, and carbon emissions resulting from the burning of fossil fuel by machinery and the production of pesticides—the net benefits of intensive exploitation are substantially reduced.

Thus by minimizing external costs and maximizing nonprovisioning ecosystem services, management practices that incorporate biodiversity may represent a cost-effective option. This is particularly important for the less-favored sectors of society, such as local indigenous communities and subsistence farmers, who normally bear the largest burden of those external costs. The recognition of both the external costs and the value of supporting and regulating ecosystem services can provide a solid basis for developing appropriate schemes of biodiversity management.

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