11 Species Effects on Ecosystem Processes

The nature and diversity of species traits and the interactions among organisms strongly affect ecosystems. This chapter describes the patterns of species effects on ecosystem processes.

Introduction

People have massively altered the species composition of the biosphere. Human activities have modified about 75% of the ice-free surface of Earth (see Fig. 1.8; Ellis and Ramankutty 2008) through changes in land use, disturbance regime, and ecosystem management (Foley et al. 2005; MEA 2005). Human ignitions and fire suppression, for example, have altered fire frequency; many shrublands and grasslands are intensively grazed; and pollution has altered nutrient availability throughout the planet. These changes have altered plant, animal, and microbial species composition and have directly affected ecosystem processes such as primary production and nutrient cycling.

People have also deliberately or unintentionally moved thousands of species around the globe, leading toward a homogenization of the global biota (D'Antonio and Vitousek 1992). Where these species establish sustained, expanding populations in their new habitat, they represent human-caused biological invasions. As this chapter will illustrate, invasions that alter biological properties or processes can change many aspects of ecosystem structure and functioning, underscoring the importance of the organism state factor (see Chap. 1). Biological invasions are not unique in their influence on ecosystems; native species can have equivalent effects, but the rapid changes that often occur after biological invasion can be documented more clearly than can the effects of long-standing components of native communities.

A Focal Issue

Exotic species sometimes change the physical and biotic environment enough to alter the abundance of or even eliminate native species from an ecosystem. People, for example, introduced to New Zealand all of its terrestrial mammals and half of its plant species in the last 200 years (Kelly and Sullivan 2010). Mammalian introductions caused extinction of 25% of New Zealand's original bird fauna, which was rich in ground-nesting species (Tennyson 2010). Similarly, recent expansion of exotic grasses into the Sonoran Desert of the southwestern U.S. outcompetes native species and increases fuel loads. Together these changes threaten to eliminate long-lived fire-sensitive species such as the Saguaro cactus (Fig. 11.1).

Aquatic ecosystems have been even more extensively modified by species introductions. Accidental introductions of species in ballast water and fishing gear or deliberate introduction of fish and other organisms have altered the species composition of most estuaries, rivers, and

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Fig. 11.1 Buffel grass is a European grass that has transformed Sonoran desert of the Southwestern U.S. by outcompeting native species, including seedlings of Saguaro cactus (Olsson et al. in press). Over the longer term, the grass also represents a fire hazard that could eliminate adults of the fire-sensitive Saguaro cactus from its current range. Photograph courtesy of Aaryn Olsson

lakes. Fishless lakes, for example, tend to have a high diversity of birds, plants, amphibians, and invertebrates. All these groups decline in abundance and diversity when fish are introduced (Scheffer et al. 2006).

Although extinction and immigration of species are natural ecological processes, the dramatic increase in the frequency of these events (often greater than 100-fold) in recent decades is rapidly changing the patterns of biodiversity of the planet. It is therefore critical to understand which species changes are most likely to have large ecosystem consequences and to develop strategies to minimize the likelihood of introducing these species to new places.

Overview of Species Effects on Ecosystem Processes

No single species can perform all of the functional roles of organisms within a trophic level of an ecosystem. Up to this point, we have emphasized only the most general properties of organisms. We discussed primary producers, for example, as if they were a homogeneous group of organisms whose traits, such as photosynthetic rate, could be broadly predicted from climate and parent material. Under what circumstances is the diversity of organisms *within* a trophic level important to understanding ecosystem processes?

Biodiversity is the biological diversity present in a system, including genetic diversity within populations, **species diversity** within functionally similar groups of species, and the diversity of ecosystems on a landscape. From an ecosystem perspective, biodiversity can be characterized as the sum of the biological traits of all the species in the ecosystem, weighted by the abundance of each species (Grime 1998). When species are lost, the range of traits represented within the ecosystem declines, which reduces the range of conditions under which ecosystem properties can be sustained. In addition, since each species packages traits in somewhat different combinations, loss or gain of a species changes the ways in which traits interact to influence ecosystem processes.

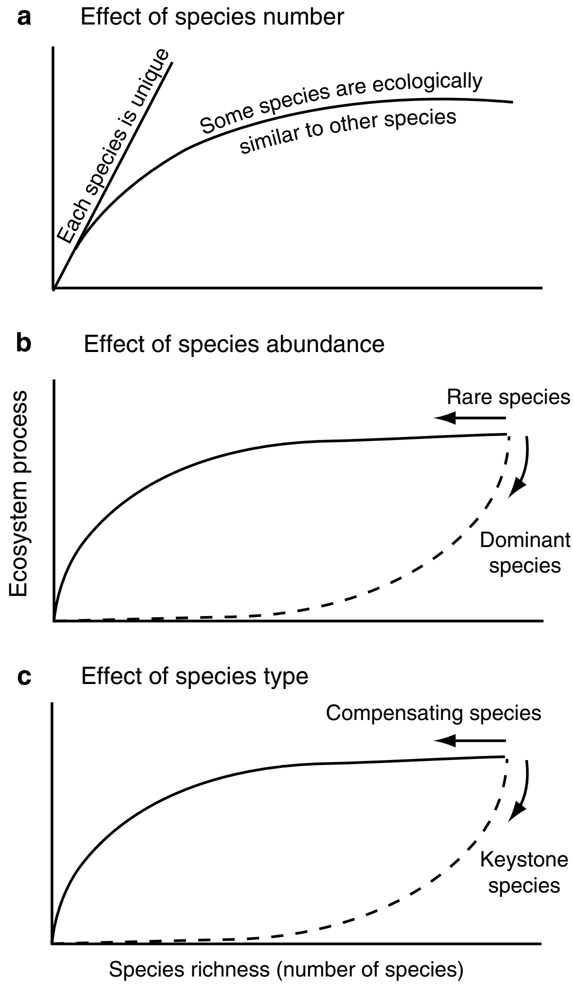

Fig. 11.2 Expected relationship between ecosystem processes and the number of species, their relative abundance, and the type of species in an ecosystem. (**a**) Some processes (or stocks) may increase (as shown) with increasing species number; others may show an exponential decrease (Vitousek and Hooper 1993). (**b**) Removal of dominant species from an ecosystem has greater impact on ecosystem processes than does removal of rare species. (**c**) Similarly, the removal of keystone species has large ecosystem effects, whereas removal of one species of a functional type allows other species in that functional type to increase in abundance; this compensation would cause only moderate impact on ecosystem processes, until most species from that functional type have been removed. The arrows show the expected change in ecosystem processes in response to species loss. Based on Sala et al. (1996)

Functional traits are the characteristics of individual organisms that impact their fitness through effects on growth, reproduction, or survival (Díaz and Cabido 2001; Violle et al. 2007).

As a first approximation, the impact of a species depends on its abundance, the geographical range that it occupies, and its per capita impact (Parker et al. 1999; Suding et al. 2008). A change in the abundance of a dominant or widespread species is more likely to affect ecosystems than is a change in abundance of a rare species (Fig. 11.2b; Sala et al. 1996) because dominant species account for most of the carbon and nutrient flow through an ecosystem and have the greatest impact on the environment (Grime 1998). Loss of dominant conifers due to pathogen or insect outbreak, for example, alters microclimate and plant biomass strongly enough to affect most ecosystem processes (Matson and Waring 1984; Kurz et al. 2008; Raffa et al. 2008). However, rare species can also play important functional roles. In a New Zealand floodplain, for example, nonnative plant species that accounted for only 3% of biomass significantly increased soil carbon, microbial biomass, and abundance of microbial-feeding and predatory nematodes (Peltzer et al. 2009). Rare species become particularly important when extreme events (e.g., insect outbreaks, wildfire, or overgrazing) or environmental changes reduce the biomass of ecologically similar dominant species (Grime 1998; Walker et al. 1999).

If all species were equally abundant and functionally different (i.e., contributed in unique ways to a given process), rates of ecosystem processes might change linearly as the number of species increased (Fig. 11.2a; Vitousek and Hooper 1993; Sala et al. 1996). Nitrogen retention, for example, might increase as species with different rooting depths or preferred forms of nitrogen absorption are added to the ecosystem. In practice, however, the relationship between species number and rate of any given ecosystem process tends to saturate with increasing number of species because some species that are added are ecologically similar to species already present in the community (Fig. 11.2a).

The degree of functional similarity among species is ecologically important (Hooper et al. 2005). A **keystone species** is ecologically distinct from all other species in the ecosystem and has a much greater impact on ecosystem or community processes than would be expected from its biomass (Fig. 11.2c; Power et al. 1996). The tsetse fly in Africa, for example, has a large effect on ecosystem processes per unit of tsetse fly biomass because it limits the density of people and their impacts (Sinclair and Norton-Griffiths 1979). Loss of a keystone species has a greater ecological impact than does the loss of a species that is functionally similar to other species because, in the latter case, the remaining species can sustain the relevant ecological functions.

Functional types are groups of species that are "ecologically similar" with respect to either their *effects* on ecosystems (**effect functional types**) or their *response* to environmental change (**response functional types**) (Díaz and Cabido 2001; Elmqvist et al. 2003; Hooper et al. 2005; Suding et al. 2008). Nitrifying bacteria, evergreen shrubs, and termites are examples of functional types that have predictable *effects* on ecosystem processes. Nitrifiers increase the mobility of available nitrogen in soils; evergreen shrubs produce well-defended leaves that have low palatability to herbivores and decompose relatively slowly; termites mix the soil vertically and redistribute surface litter to depth.

C_4 grasses and fire-adapted species are examples of functional types that may *respond* predictably to specific environmental changes. C_4 grasses outperform C_3 grasses at warm temperatures; fire-adapted species survive and resprout rapidly after fire. Ultimately, we want to know how response and effect functional properties relate to one another because this provides a mechanistic basis for understanding how changes in species composition influence ecosystem responses to environmental change. Most evergreen shrubs, for example, not only have predictable effects on the ecosystem but also show predictable responses to the environment, such as growing well at low soil nutrient availability. In contrast, C_4 grass species exhibit a wide range of growth rates and nutrient responses, making it more difficult to assess the functional consequences of climate-driven changes in their distribution.

The more species of a functional type that are present, the less likely it is that gain or loss of a single species from that functional type will have large ecosystem impacts. Our challenge, as ecologists, is to identify the traits of organisms that have strong effects on ecosystems (Paine 2000) and to predict what environmental changes might alter the abundance of these species.

Effect Functional Types

Species are most likely to have strong ecosystem effects when they alter the interactive controls (e.g., resource supply or occurrence of disturbance) that directly regulate ecosystem processes (see Chap. 1). These controls influence biogeochemical processes, biophysical processes, trophic interactions, and disturbance regime (Vitousek 1990; Chapin 2003; S.E. Hobbie, personal communication). Species that influence interactive controls indirectly affect all aspects of ecosystem functioning.

Species Effects on Biogeochemistry

Nutrient Supply

Species traits that influence nutrient inputs or losses have important ecosystem effects. The introduction of an active nitrogen fixer into a community that lacks such species augments nitrogen availability and cycling. The introduction of the exotic nitrogen-fixing tree, *Morella faya*

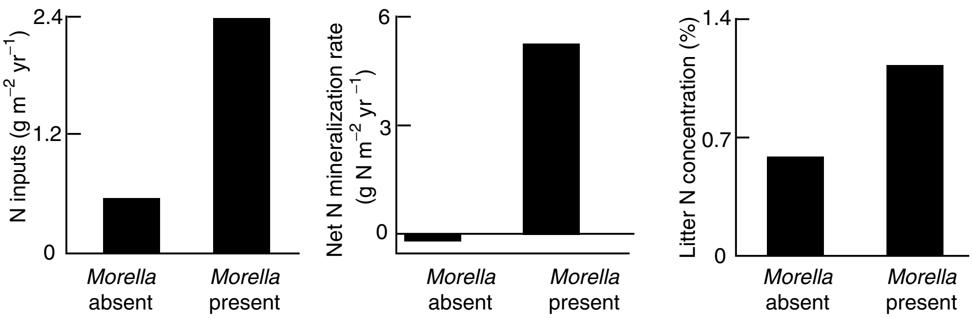

Fig. 11.3 Impact of the nitrogen-fixing tree *Morella faya* on nitrogen inputs, litter nitrogen concentration, and nitrogen mineralization rate in a Hawaiian montane forest. Data are averages ± SE (Vitousek et al. 1987)

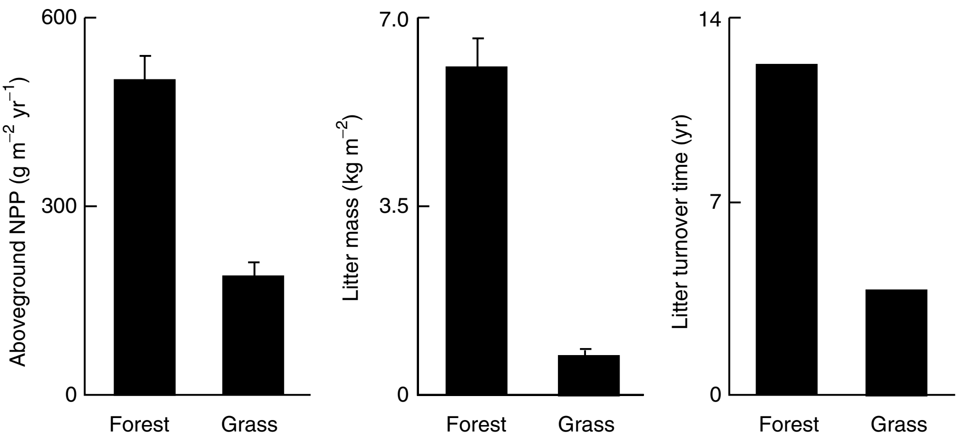

Fig. 11.4 Comparison of ecosystem processes between two exotic communities that differ in rooting depth: annual grassland and *Eucalyptus* forest in California. Data are averages ± SE (Robles and Chapin 1995)

(formerly *Myrica faya)* in Hawai'i, for example, increased nitrogen inputs, litter nitrogen concentration, nitrogen availability, and the composition of both the plant and soil faunal communities (Fig. 11.3; Vitousek et al. 1987; Vitousek 2004). A nitrogen-fixing invader is most likely to be successful in ecosystems that are nitrogen-limited, have no symbiotic nitrogen fixers, and have adequate phosphorus, micronutrients, and light (see Chap. 9; Vitousek and Howarth 1991). Thus, we expect large ecosystem impacts from invasion of nitrogen-fixing species in combinations of the following circumstances: (1) low nitrogen supply (early succession on degraded lands and in other low-nitrogen environments), (2) low competition for light or phosphorus (e.g., early in succession, canopy reduction by grazing of pastures, or phosphorus enrichment of lakes or soils), (3) preferential grazing on nitrogen-fixing species, or (4) lack of resident nitrogen-fixing species (e.g., islands that are distant from source populations) (Vitousek et al. 2002).

Deep-rooted species can increase the volume of soil tapped by an ecosystem and therefore the supply of water and nutrients available to support production. The perennial bunch grasses that once dominated California grasslands, for example, have been largely replaced by either introduced European annual grasses or planted forests; among those forests are stands of Australian *Eucalyptus*. The deep-rooted *Eucalyptus* trees access a deeper soil profile than do annual grasses, so the forest absorbs more water and nutrients. In dry, nutrient-limited ecosystems, this substantially enhances ecosystem productivity and nutrient cycling (Fig. 11.4) but reduces species diversity.

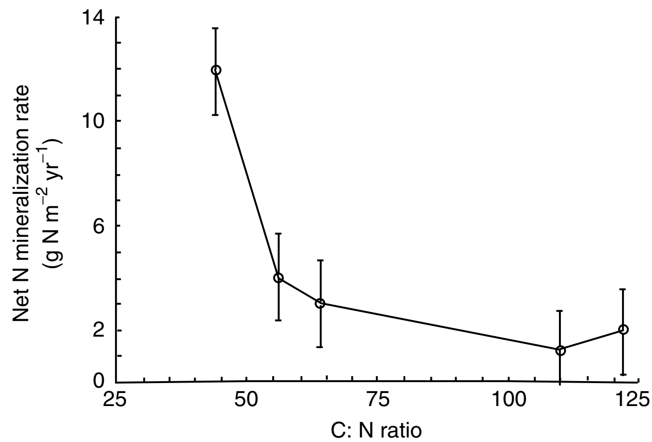

Fig. 11.5 Effects of prairie grass species that differ in C:N ratio on N mineralization, when grown on soils containing 100 g N m^{-2}. Data are averages ± 95% confidence interval (Wedin and Tilman 1990)

At a more subtle level, species coexistence in arid grasslands depends on species differences in rooting depth and the water sources that they tap (Fargione and Tilman 2005; Nippert and Knapp 2007a, b). Species may also tap resources that might otherwise be unused. The alpine snowbed species *Corydalis conorhiza*, for example, produces “snow roots” that grow upward into the snowpack, where they absorb nitrogen that would otherwise flow downslope at snowmelt and be lost from the system (Onipchenko et al. 2009).

Mycorrhizal fungi also influence the quantity of nutrients that are available to vegetation (see Chap. 8). Absence of appropriate mycorrhizae can restrict the establishment of plantations of exotic forest species.

Animals can influence the resource base of the ecosystem by foraging in one area and depositing nutrients elsewhere in feces and urine (see Chap. 10). Sheep, for example, enrich soils on hilltops where they bed down at night. Migrating salmon perform a similar nutrient-transport role in streams. They feed primarily in the open ocean, then return to small streams where they spawn, die, and decompose. The nutrients carried by the salmon from the ocean can sustain a substantial proportion of the algal and insect productivity of small streams. These nutrient subsidies are transported to adjoining terrestrial habitats by bears and otters that feed on salmon or by predators of insects that emerge from streams (Naiman et al. 2005).

Nutrient Turnover

Species differences in litter quality magnify site differences in soil fertility. Differences among plant species in tissue quality strongly influence litter decomposition rates (see Chap. 7). Litter from low-nutrient-adapted species decomposes slowly because of the negative effects on soil microbes of low concentrations of nitrogen and phosphorus and high concentrations of lignin, tannins, waxes, and other recalcitrant or toxic compounds. This slow decomposition of litter from species characteristic of nutrient-poor sites reinforces the low nutrient availability of these sites (see Fig. 10.9; Hobbie 1992; Wilson and Agnew 1992). Species adapted to high-resource sites, in contrast, produce rapidly decomposing litter due to its higher nitrogen and phosphorus content and lower concentration of recalcitrant compounds, enhancing rates of nutrient turnover in nutrient-rich sites.

Experimental planting of species on a common soil shows that species differences in litter quality can alter soil fertility quite quickly. Early successional prairie grasses, whose litter has a low C:N ratio, for example, enhance net nitrogen mineralization rate of soil within 3 years, compared to the same soil planted with late-successional species whose litter has a high C:N ratio (Fig. 11.5; Wedin and Tilman 1990).

The species composition of lakes strongly influences their biogeochemistry. Zebra mussels, for example, which have spread through

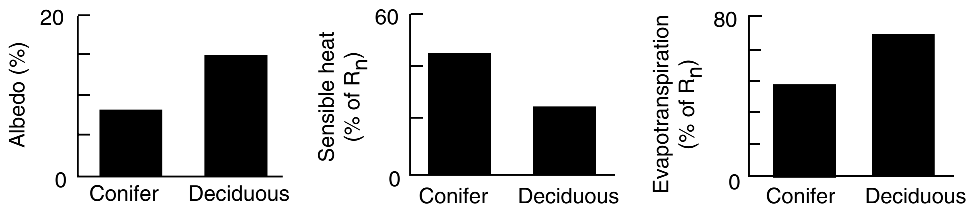

Fig. 11.6 Sensible and latent heat fluxes from deciduous and conifer boreal forests. Data are from Baldocchi et al. (2000)

freshwater systems in the Midwestern U.S., are more effective filter feeders than their native counterparts, filtering from 10% to 100% of the water column per day (Strayer et al. 1999). The resulting increase in turnover of phytoplankton and other edible particles reduces zooplankton abundance and shifts energy flow from the water column to the sediments.

Species Effects on Biophysical Processes

Species effects on microclimate influence ecosystem processes most strongly in extreme environments (Wilson and Agnew 1992; Callaway 1995; Hobbie 1995). Boreal mosses, for example, form thick mats that insulate the soil from warm summer air temperatures (Heijmans et al. 2004). The resulting low soil temperature retards decomposition, contributing to the slow rates of nutrient cycling that characterize these ecosystems (Van Cleve et al. 1991; Turetsky et al. 2010). The sequestration of nitrogen and phosphorus in undecomposed peat reduces growth of vascular plants. In hot environments, the shading of soil by plants is an important factor governing soil microclimate. Establishment of many desert cactuses, for example, often occurs in the shade of "nurse plants."

Species effects on water and energy exchange influence regional climate. The height, rooting depth, and density of the dominant species in an ecosystem govern surface roughness, which strongly influences aerodynamic conductance and therefore the efficiency of water and energy exchange between ecosystems and the atmosphere (see Chap. 4). Rough canopies generate mechanical turbulence, allowing eddies of air from the free atmosphere to penetrate deep within the plant canopy. These eddies efficiently carry water vapor from the ecosystem to the atmosphere. Individuals or species that are taller than surrounding vegetation generate canopy roughness that increases water flux from ecosystems.

Species differences in albedo and water and energy exchange can have effects that are important to the climate system. Conifers that dominate late-successional boreal forests have a low albedo and stomatal conductance and therefore transfer large amounts of sensible heat to the atmosphere. Postfire deciduous forests, in contrast, absorb less energy, due to their high albedo, and transmit more of this energy to the atmosphere as latent rather than sensible heat, resulting in less immediate warming of the atmosphere and more moisture available to support precipitation (Fig. 11.6).

Changes in vegetation caused by overgrazing can also alter regional climate. In the Middle East, for example, overgrazing reduced the cover of plant biomass. Model simulations suggest that the resulting increase in albedo reduced the total energy absorbed, the amount of sensible heat released to the atmosphere, and consequently the amount of convective uplift of the overlying air. Less moisture was therefore drawn inland from the Mediterranean Sea, resulting in less precipitation and reinforcing the vegetation changes (Charney et al. 1977). These vegetation-induced climate feedbacks could have contributed to the desertification of the Fertile Crescent.

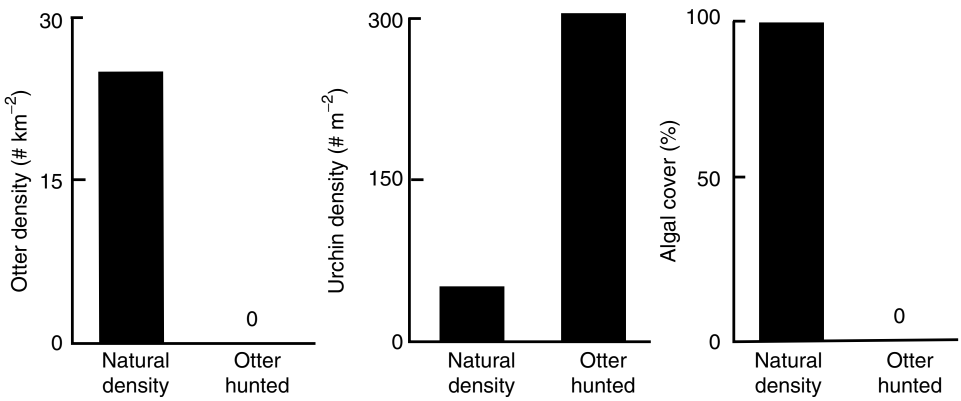

Fig. 11.7 Density of sea otters and sea urchin, and percentage cover of macroalgae in the Aleutian Islands of Alaska. Sites differed in otter density due to differential hunting pressure 300 year previously. Data are from Estes and Palmisano (1974)

Species Effects on Trophic Interactions

Species that alter trophic dynamics can have large ecosystem impacts. When top predators are removed, prey populations sometimes explode and deplete their food resources, leading to a cascade of ecological effects (see Chap. 10). These **top-down controls** are particularly well developed in aquatic systems. The removal of sea otters by Russian fur traders, for example, caused a population explosion of sea urchins that overgrazed kelp (Figs. 11.7 and 11.8; Estes and Palmisano 1974). Recent overfishing in the North Pacific may have triggered similar sea urchin outbreaks, as killer whales moved closer to shore in search of food and switched to sea otters as an alternate prey (Estes et al. 1998). In the absence of dense sea urchin populations, kelp provides the physical structure for diverse subtidal communities and attenuates waves that otherwise cause coastal erosion during storms. Similarly, on land, introduction of arctic foxes to islands reduced seabird populations and the inputs of marine-derived nutrients, causing a shift from grassland to shrubland (Croll et al. 2005).

The addition or removal of a fish species from lakes often has large keystone effects that cascade up or down the food chain (Carpenter et al. 1992; Power et al. 1996). Many nonaquatic ecosystems also exhibit strong responses to changes in predator abundance (Hairston et al. 1960; Strong 1992; Hobbs 1996). Removal of wolves, for example, releases elk populations that graze down vegetation (Beschta and Ripple 2009), and the removal of elephants or other keystone mammalian herbivores leads to encroachment of woody plants into savannas (Owen-Smith 1988). Disease organisms, such as rinderpest that attacks ungulates in Africa, can also act as a keystone species by greatly modifying competitive interactions and community structure (Bond 1993). Plant species that are introduced without their host-specific insect herbivores or pathogens often become aggressive invaders. The cactus *Opuntia*, for example, became surprisingly abundant when introduced to Australia, in part due to overgrazing, but was reduced to manageable levels by a cactus-specific herbivore *Cactoblastis* that was introduced to control it. Other species that have become aggressive in the absence of their specialist herbivores include goldenrod (*Solidago spp.*) in Europe, wild rose (*Rosa spp.*) in Argentina, and star thistle (*Centaurea spp.*) in California.

Often these top-down controls by predators or pathogens have a much greater effect on biomass and species composition of lower trophic levels than on the total flow of energy or nutrients through the ecosystem (Carpenter et al. 1985) because of greater turnover at the producer level. Intensely grazed grassland systems such as the southern and southeastern Serengeti, for example, have a low plant biomass but rapid cycling of carbon and nutrients due to rapid turnover of

Fig. 11.8 Kelp forest characteristic of otter-occupied subtidal habitat in the Aleutian Islands of Alaska compared to urchin-dominated barrens resulting from elimination of sea otters by Russian fur traders. The three dominant kelps are *Eularia* (*Alaria*), an annual species that extends toward the surface, *Laminaria*, which forms the lower canopy, and *Agarum*, which has holes in the blades. Photographs courtesy of Jim Estes and Mike Kenner

plant biomass and excretion by large mammals. Grazing prevents the accumulation of standing dead litter and hastens the return of nutrients to soil in plant-available forms (McNaughton 1985, 1988). Keystone predators or grazers thus alter the *pathway* of energy and nutrient flow, modifying the balance between plant-based or detritus-based food chains, but we know less about their effects on total energy and nutrient cycling through ecosystems.

Species Effects on Disturbance Regime

Organisms that alter disturbance regime change the relative importance of colonization and species interactions in controlling ecosystem processes. After disturbance, there are substantial changes in most ecological processes, including increased opportunities for colonization by new individuals and often an imbalance between inputs to, and outputs from, ecosystems (see Chap. 12). For this reason, animals or plants that alter disturbance frequency or severity increase the importance of processes, such as colonization, that determine community composition under nonequilibrium conditions. Plants that colonize after disturbance, in turn, affect all aspects of the subsequent functioning of ecosystems.

One of the major mechanisms by which animals affect ecosystem processes is through their action as **ecosystem engineers**, by which they create or modify habitat (Jones et al. 1994; Lawton and Jones 1995; Hobbs 1996). Gophers, pigs, and ants, for example, physically disturb the soil, creating sites for seedling establishment and favoring early successional species (Hobbs and Mooney 1991). African elephants have a similar effect, trampling vegetation and removing portions of trees (Owen-Smith 1988). By analogy, the Pleistocene megafauna may have promoted steppe grassland vegetation by trampling mosses and stimulating nutrient cycling (Zimov et al. 1995).

The shift toward early successional or less woody vegetation generally leads to a lower biomass, a higher ratio of production to biomass, and a litter quality and microenvironment that favor decomposition (see Chap. 12). The associated enhancement of mineralization can either stimulate production (Zimov et al. 1995) or promote ecosystem nitrogen loss (Singer et al. 1984), depending on the magnitude of disturbance.

Beavers in North America are ecosystem engineers that modify the physical environment at a landscape scale (Jones et al. 1994). The associated flooding of organic-rich riparian soils produces anaerobic conditions that promote methanogenesis, so beaver ponds become hot spots of methane emissions (see Chap. 13; Roulet et al. 1997). The recent recovery of beaver populations in North America after intensive trapping during the 19th and early 20th centuries has substantially altered boreal landscapes, leading to a fourfold increase in methane emissions in regions where beaver are abundant (Bridgham et al. 1995).

The major ecosystem engineers in soils are earthworms in the temperate zone and termites in the tropics (Lavelle et al. 1997). Soil mixing by these animals alters soil development and most soil processes by disrupting the formation of distinct soil horizons, reducing soil compaction, and transporting organic matter to depth (see Chap. 7). The associated soil disturbance can greatly reduce soil carbon storage and understory plant diversity (Bohlen et al. 2004).

Plants also alter disturbance regime through effects on flammability. The introduction of grasses into a forest or shrubland, for example, can increase fire frequency and cause the replacement of forest or shrubland by grassland (D'Antonio and Vitousek 1992; Mack et al. 2001; Grigulis et al. 2005). Similarly, boreal conifers are more flammable than deciduous trees because of their large leaf and twig surface area, canopies that extend to the ground surface (acting as ladders for fire to move into the canopy), low moisture content, and high resin content (Johnson 1992). The resins in boreal conifers that promote fire also retard decomposition (Flanagan and Van Cleve 1983) and contribute to fuel accumulation.

In other situations, plants are critical in reducing disturbance by stabilizing soils and reducing wind and soil erosion in early succession. This allows successional development to proceed and retains the soil resources that determine the structure and productivity of late-successional stages. Introduced dune grasses, for example, have altered soil accumulation patterns and dune morphology in the western U.S. (D'Antonio and Vitousek 1992), while introduced acacia to South Africa stabilized sand dunes and aided in the settlement of the area by Europeans. Early successional alpine vegetation stabilizes soils and reduces probability of landslides.

Response Functional Types

Species differences in environmental response broaden the range of environmental conditions under which characteristic ecosystem process rates can be sustained. The species that occupy any given ecosystem typically differ in their geographic ranges and historical responses to past climate variability (Webb and Bartlein 1992). They are therefore likely to also differ in their responses to current seasonal and interannual variation in environment and to directional changes in environment. Species in an ecosystem occur together not because they are adapted to the identical range of environmental conditions but because they can survive, compete, and reproduce in the environments where they co-occur. Therefore different species may improve their performance and be stronger competitors under cool vs. warm conditions, wet vs. dry conditions, fertile vs. unfertile conditions, or in response to changes in frequency of various disturbances or pest outbreaks. The greater the breadth of environmental tolerance represented by the suite of species in an ecosystem, the broader will be the range of conditions under which ecosystem processes such as primary and secondary production and decomposition are sustained at their characteristic rates. In this way, a diversity of environmental responses fosters resilience of ecosystem functioning to environmental variation and change (Elmqvist et al. 2003).

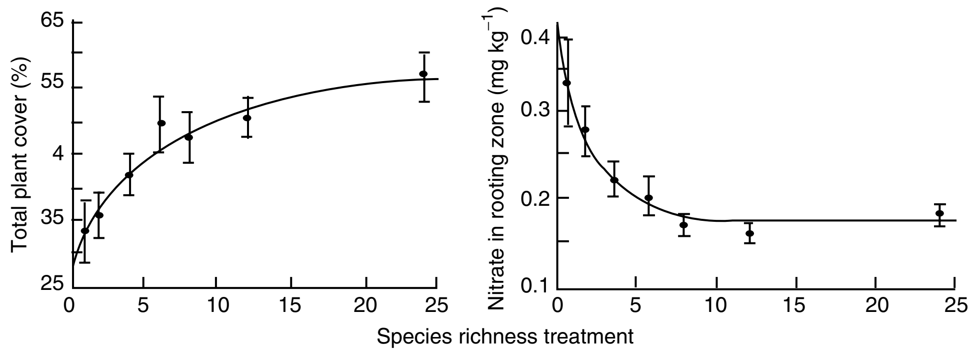

Fig. 11.9 Effect of the number of plant species sown on a plot on total plant cover and nitrate concentration in the rooting zone. Measurements were made 3 years after plots were sown. Data are averages ± SE. Redrawn from Tilman et al. (1996)

Response diversity may also enhance the efficiency of resource use and retention in ecosystems. In experimental grassland communities, for example, plots that were planted with many species had greater plant cover and lower concentrations of potentially leachable soil nitrate than did low-diversity plots (Fig. 11.9; Tilman et al. 1996). This could reflect the greater probability of encountering a productive species in more diverse communities (Hooper et al. 2005). Alternatively, the more diverse plots might use more resources if species have **complementary patterns of resource use** (e.g., each species using different types of resources, rooting depths, or seasons of absorption; Tilman 1988; Dimitrakopoulos and Schmid 2004). In the Netherlands, for example, more species-rich heathlands are productive, not because of a single productive species, but because several low-productivity species together account for substantial production (van Ruijven and Berendse 2003). Complementarity tends to develop through natural selection or sorting of species to use resources that are not fully exploited by other species.

Temperate grasslands provide field evidence for complementary patterns of resource use. C_4 grasses are generally active at warmer temperatures than are C_3 grasses. Consequently, C_3 grasses account for most early-season grass production, and C_4 species for more mid-season production. Similarly, in the Sonoran desert, a different suite of annual plants becomes active after winter vs. summer rains. In both cases, species differences in environmental response enhance annual production. In mixed-cropping agricultural ecosystems, phenological specialization to use different times of year enhances production than do species differences in rooting depth (Steiner 1982).

Diverse ecosystems are not always more productive or more efficient in using resources. Crop or forest monocultures, for example, are often just as productive as mixed cropping systems (Ewel 1986; Vandermeer 1995) or mixed-species forests (Rodin and Bazilevich 1967). The effect of **species richness** on some ecosystem process in experiments often saturates at a much lower number of species (5–10) than characterize most natural communities (Fig. 11.9). Determining the circumstances and mechanisms in which species number influences ecosystem processes is an active area of ecosystem research (Hooper et al. 2005; Naeem et al. 2009).

Response diversity is also important among animals. In Western Polynesia, a large proportion of forest trees produce fleshy fruits that are dispersed by large bats (flying foxes). There is a 60–80% overlap in diet among the bats, so, when populations of several dominant bat species were decimated by a cyclone, other bat species increased in abundance and continued dispersing fruits (Elmqvist et al. 2003). Response diversity among seed dispersers becomes increasingly important as land-use change fragments forest habitats and makes plant establishment more important to species persistence.

Integrating the Effects of Traits on Ecosystems

Functional Matrix of Multiple Traits

Organisms affect ecosystems in multiple ways through the actions of multiple traits. Functional types are a convenient simplification that enables ecologists to consider the effects of a single trait or highly correlated suite of traits on ecosystem processes. For example, we can describe functional types with respect to *either* fire tolerance, growth-related traits, temperature tolerance, rooting depth, or dispersal ability. However, many of these traits vary independently from one another, making it impossible to define a single functional type that captures all of the ways in which species affect ecosystems. For example, species effects on decomposition are mediated by several traits that vary independently of one another, including litter chemistry, labile carbon exudation, and effects on soil moisture. A **functional matrix** of traits extends the functional-types approach to consider all the traits present in an ecosystem (Eviner and Chapin 2003). Each trait (e.g., leaf lignin concentration or growth rate or rooting depth) can be treated as a continuous variable with each species in the ecosystem having a particular value for that trait. Although more complex than a one-dimensional functional-type classification, a functional matrix provides a more accurate description of species effects on ecosystems, particularly for processes that are affected by multiple species traits. In general, functional types are most useful in describing large-scale patterns of species effects, whereas a more inclusive consideration of species traits improves understanding of interactions within a specific ecosystem.

A functional matrix provides useful guidance in ecosystem restoration. Response traits identify the species that tolerate and grow well in a particular environment (Grime 2001). The suite of species that thrive in a particular environment will likely differ in their effects on the environment. By selecting appropriate species, ecologists can shape the trajectory of ecosystem development (Whisenant 1999). For example, cover crops are often selected based on their capacity to add nitrogen (Eviner and Chapin 2001). Similarly, stream restoration may require a riparian species assemblage that resists erosion (response trait) and accumulates nitrate from groundwater (response/effect trait). Once the matrix of traits is known that enable species to thrive in an environment and to have desired effects, it may be possible to identify a set of locally adapted species with the appropriate combination of traits (Eviner and Hawkes 2008). Species interactions and other (often unknown) factors create a local context that governs the relative success of species with a high restoration potential. In addition, inevitable tradeoffs (e.g., between rapid growth and resistance to drought and low soil fertility) limit the combinations of traits that can be assembled.

Linkages Between Response and Effect Traits

The effects of environmental variability and change on ecosystem processes depend on the linkages between the environmental response and the ecosystem effects of species (Suding et al. 2008). The traits that are present in an ecosystem are packaged into distinct species, each of which has a particular set of response and effect traits. If response and effect traits are tightly linked, the ecosystem will respond sensitively to environmental changes that influence these traits. Species with a high capacity for nitrogen absorption, photosynthesis, and growth, for example, respond sensitively to nitrogen supply, produce rapidly decomposing litter, and occupy nitrogen-rich sites, whereas species with low rates of these processes occupy nitrogen-poor sites. In part because of the strong linkages between response and effect traits, ecosystems respond sensitively to variation in nitrogen supply.

In other cases, however, there is little or no correlation between species response and species effect, as in the C_3–C_4 and fruit bat examples given earlier. In these cases, the coexistence of many similar species minimizes ecosystem sensitivity to environmental variation and change because the *effect* functional type (e.g., grasses) includes some species that are productive under warm, dry conditions and others that are productive under cool, wet conditions (Suding et al. 2008). Similarly, the productivity of a grassland that has both palatable and unpalatable grasses will be less sensitive to periods of intense grazing than a grassland that lacks unpalatable grasses (Walker et al. 1999).

Diversity as Insurance

Earth is currently in the midst of the sixth major extinction event in the history of life (Pimm et al. 1995). Although the causes of some of the earlier extinction events are uncertain, they probably resulted from sudden changes in physical environment caused by factors such as asteroid impacts or pulses of volcanism. Current extinction rates are at least 100-fold higher than prehuman extinction rates (Fig. 11.10; Mace et al. 2005). The current extinction event is unique in the history of life because it is biologically driven, specifically by the impact of the human species on land use, species invasions, and environmental change. Although human activities affect many processes at global scales (see Chap. 14; Vitousek 1994), the loss of species diversity is of particular concern because it is irreversible. Once a species is gone, it cannot be recovered. For this reason, it is critical to understand the functional consequences of the current large losses in species diversity (Chapin et al. 2000b).

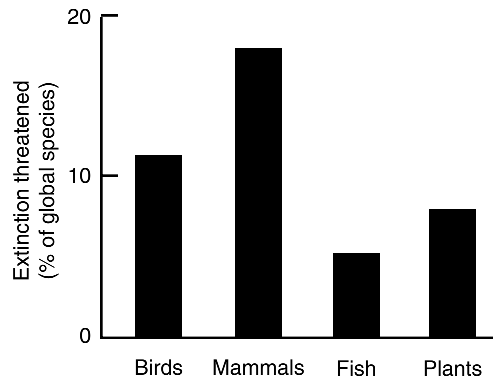

Fig. 11.10 Percentage of major vertebrate and vascular plant species that are currently threatened with extinction. Redrawn from Chapin et al. (2000b)

Diversity provides insurance against functional changes under extreme or novel conditions. Conditions that favor some species will likely reduce the competitive advantage of other functionally similar species, thus stabilizing the total biomass or activity of the entire community (McNaughton 1977; Chapin and Shaver 1985; Tilman et al. 2006). In other words, when some species increase resource capture under conditions that are favorable to them, this leaves fewer resources for other species, which therefore respond by growing less. Annual variation in weather, for example, caused at least a twofold variation production by every major vascular plant species in arctic tussock tundra. Years that were favorable for some species, however, reduced the productivity of others, so there was no significant variation in productivity at the ecosystem scale among the 5 years of study (Chapin and Shaver 1985). This stabilization of biomass and production by diversity has been observed in many (but not all) studies (Cottingham et al. 2001), including grasslands in response to water and nutrient addition (Lauenroth et al. 1978; Tilman et al. 2006) or grazing (McNaughton 1977), tundra in response to changes in temperature, light, and nutrients (Chapin and Shaver 1985), and lakes in response to acidification (Frost et al. 1995). This stability of processes provided by diversity has societal relevance. Many traditional farmers plant diverse crops, not to maximize productivity in a given year, but to decrease the risk of crop failure in a bad year (Altieri 1990).

Species diversity not only stabilizes ecosystem processes in the face of annual variation in environment but also provides insurance against drastic change in ecosystem structure or processes in response to extreme events (Walker 1992; Chapin et al. 1997). Any change in climate or climatic extremes that is severe enough to cause extinction of one species is unlikely to eliminate all members from a functional type (Walker 1995) because response and effect traits are distributed in various combinations across species (Eviner and Hawkes 2008). The more species there are in a functional-effect type, the less likely it is that any extinction event or series of such events will have serious ecosystem consequences (Holling 1986). In a laboratory experiment that manipulated species diversity of mosses, communities with high species diversity maintained a higher biomass when exposed to drought than did less diverse communities by facilitating the survival of tall dominant mosses (Mulder et al. 2001). Similarly, in field experiments, diversity contributes to sustained community composition and structure of grasslands exposed to manipulated or natural fluctuations in climate and disturbance (Grime et al. 2000; Hobbs et al. 2007; Grime et al. 2008).

Species Interactions and Ecosystem Processes

Species interactions modify the impacts of individual species on ecosystem processes. Most ecosystem processes respond in complex ways to changes in the abundance of species because *interactions* among species generally govern the extent to which species traits are expressed at the ecosystem scale. Species interactions, including mutualism, trophic interactions (predation, parasitism, and herbivory), facilitation, and competition, may affect ecosystem processes directly by modifying pathways of energy and material flow or indirectly by modifying the abundances or traits of species with strong ecosystem effects (Wilson and Agnew 1992; Callaway 1995).

Many species effects on ecosystems are indirect and not easily predicted. Species which themselves have small effects on ecosystem processes can have large indirect effects if they influence the abundance of species with large direct ecosystem effects, as described earlier for trophic interactions. Thus, a seed disperser or pollinator that has little direct effect on ecosystem processes may be essential for the persistence of a canopy species with greater direct ecosystem impact. Stream predatory invertebrates alter the behavior of their prey, making them more vulnerable to fish predation, which leads to an increase in the weight gain of fish (Soluck and Richardson 1997). In grasslands, a combination of legumes and C_4 grasses augments soil carbon sequestration because legumes promote large nitrogen inputs, and C_4 grasses use this nitrogen efficiently to produce root biomass, which enhances soil carbon storage (Fornara and Tilman 2008). Mixtures of litter from multiple species decompose and mineralize nitrogen at different rates (often more rapid) than would be predicted from each litter type by itself (Gartner and Cardon 2004). The nature of these litter interactions is sensitive to environment (Jonsson and Wardle 2008) and often reflects interactions of nutrients from one litter type with carbon chemistry of other litter types (Dijkstra et al. 2009). Animal–plant–microbe interactions modulate species effects in California grasslands (Eviner and Chapin 2005). Here, experimental plots seeded with goatgrass, which has a low litter quality (high C:N ratio), is associated with a low nitrogen mineralization rate in the absence of disturbance. However, the high root biomass of this species enhances soil cohesion, which reduces the energetic requirement for burrowing by gophers. Gophers are attracted to the goatgrass plots, and the associated disturbance enhances nitrogen mineralization above levels associated with any species in the absence of disturbance. Thus, all types of organism interactions – plant, animal, and microbial – must be considered in understanding the effects of biodiversity on ecosystem functioning. Although each of these examples is unique to a particular ecosystem, the ubiquitous occurrence of species interactions with strong ecosystem effects makes these interactions a general feature of ecosystem functioning (Chapin et al. 2000b). In many cases, changes in these interactions alter the traits that are expressed by species and therefore the effects of species on ecosystem processes. Consequently, simply knowing that a species is present or absent is insufficient to predict its impact on ecosystems. Theoretical frameworks for predicting the types and nature of these interactions are only beginning to emerge (Parker et al. 1999; Polis 1999; Eviner and Hawkes 2008; Cardinale et al. 2009).

Summary

The species diversity of Earth is changing rapidly due to frequent species extinctions (both locally and globally), introductions, and changes in abundance. We are, however, only beginning to understand the ecosystem consequences of these changes. Many species have traits that strongly affect ecosystem processes through their effects on the supply or turnover of limiting resources, microclimate, trophic interactions, and disturbance regime. The impact of these species traits on ecosystem processes depends on the abundance of a species, its functional similarity to other species in the community, and species interactions that influence the expression of important traits at the ecosystem scale.

The effects of species traits on ecosystem processes are generally so strong that changes in the species composition or diversity of ecosystems are likely to alter their functioning, although the exact nature of these changes is often difficult to predict. Functional diversity per se may be ecologically important if it leads to complementary use of resources by different species or increases the probability of including species with particular ecological effects. Because species belonging to the same functional-effect type generally differ in their response to environment, diversity in response within a functional-effect type may stabilize ecosystem processes in the face of temporal variation or directional changes in environment. Introduction of species with different functional effects to an ecosystem, in contrast, may accelerate the rate of ecosystem change.

Review Questions

1. What are functional types? What is the usefulness of the functional-type concept if all species are ecologically distinct?
2. How is the expected ecosystem impact of the loss of a species affected by (a) the number of species in the ecosystem, (b) the abundance or dominance of the species that is eliminated, or (c) the type of species that is eliminated? Explain.
3. If a new species invades or is lost from an ecosystem, which species traits are most likely to cause large changes in productivity and nutrient cycling? Give examples that illustrate the mechanism by which these species effects occur.
4. Which species traits have greatest effects on regional processes such as climate and hydrology?
5. How do species interactions influence the effect of a species on ecosystem processes?
6. How does the diversity of species *within a functional type* affect ecosystem processes? What is the mechanism by which this occurs? Why is it important to distinguish between the effects of changes in species composition within vs. between functional types?
7. What are the mechanisms by which species diversity might affect nutrient absorption or loss in an ecosystem? Suggest an experiment to distinguish between these possible mechanisms. Design an agricultural ecosystem that maintains crop productivity but has tight nutrient cycles.

Additional Reading

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