2 Managing Ecosystems Sustainably: The Key Role of Resilience

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Introduction

The goal of ecosystem management is to provide a sustainable flow of multiple ecosystem services to society today and in the future. As an integral component of natural resource stewardship, ecosystem management recognizes the integrated nature of social–ecological systems, their inherent complexity and dynamics at multiple temporal and spatial scales, and the importance of managing to maintain future options in the face of uncertainty (Christensen et al. 1996; Table 2.1)—i.e., many of the factors governing the resilience and vulnerability of social-ecological systems. As a society, we have a poor track record of managing ecosystems sustainably in part because the short-term use of natural resources often receives higher priority than their long-term sustainability. Environmental degradation contributed to the collapse of many advanced human societies, including Babylon, the Roman Empire, and the Mayan Civilization (Turner et al. 1990, Diamond 2005). More than half of the services provided by ecosystems have declined globally in the last half-century (MEA 2005a, d), raising questions about the capacity of human societies to manage ecosystems sustainably. Rapid rates of social and environmental change have magnified the challenges of sustainable management. We advocate broadening the concept of ecosystem management to **resilience-based ecosystem stewardship**. Its goals are to respond to and shape change in social–ecological systems in order to sustain the supply and opportunities for use of ecosystem services by society. Resilience-based ecosystem stewardship builds on ecosystem management by emphasizing (1) the key role of resilience in fostering adaptation and renewal in a rapidly changing world; (2) the dynamics of social change in altering human interactions with ecosystems; and (3) the social–ecological role of resource managers as stewards who respond to and shape social–ecological change. In this chapter we address key components of ecosystem stewardship, emphasizing the ecological consequences of those human actions that can tip the balance between sustainable and nonsustainable flow of ecosystem services to society. In Chapter 3, we broaden this perspective to integrate social processes that motivate human actions.

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Table 2.1. Attributes of ecosystem management. Information from Christensen et al. (1996).

Sustainability	Intergenerational sustainability is the primary objective
Goals	Measurable goals are defined that assess sustainability of outcomes
Ecological understanding	Ecological research at all levels of organization informs management
Ecological complexity	Ecological diversity and connectedness reduces risks of unforeseen change
Dynamic change	Evolution and change are inherent in ecological sustainability
Context and scale	Key ecological processes occur at many scales, linking ecosystems to their matrix
Humans as ecosystem components	People actively participate in determining sustainable management goals
Adaptability	Management approaches will change in response to changes in scientific knowledge and human values

An **ecosystem** consists of organisms (plants, microbes, and animals—including people) and the physical components (atmosphere, soil, water, etc.) with which they interact. All ecosystems are influenced, to a greater or lesser degree, by social processes (i.e., are social–ecological systems), although ecosystem studies tend to focus on biological interactions. Using the ecosystem-service framework developed by the Millennium Ecosystem Assessment

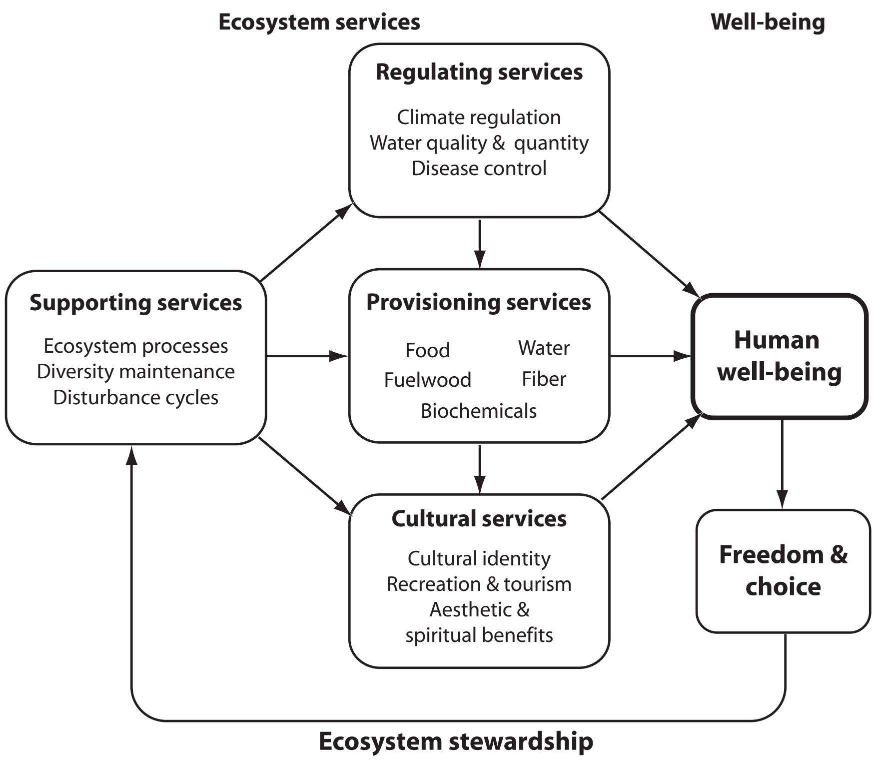

Figure 2.1. Linkages among ecosystem services, well-being of society, and ecosystem stewardship, a framework developed by the Millennium Ecosystem Assessment (MEA, 2005c). Supporting services are the foundation for the other categories of ecosystem services that are directly used by society. In addition, the goods harvested by people are influenced by landscape processes, which include regulatory services, and, in turn, influence people's connection to the land and sea (cultural services). Adapted from MEA (2005d).

TABLE 2.2. General categories of ecosystem services and examples of the societal benefits that are most directly affected.

Ecosystem services	Direct benefits to society
Supporting services	
Maintenance of soil resources	Nutrition, shelter
Water cycling	Health, waste management
Carbon and nutrient cycling	Nutrition, shelter
Maintenance of disturbance regime	Safety, nutrition, health
Maintenance of biological diversity	Nutrition, health, cultural integrity
Provisioning services	
Fresh water	Health, waste management
Food and fiber	Nutrition, shelter
Fuelwood	Warmth, health
Biochemicals	Health
Genetic resources	Nutrition, health, cultural integrity
Regulating services	
Climate regulation	Safety, nutrition, health
Erosion, water quantity/quality, pollution	Health, waste management
Disturbance propagation	Safety
Control of pests, invasions, and diseases	Health
Pollination	Nutrition
Cultural services	
Cultural identity and cultural heritage	Cultural integrity, values
Spiritual, inspirational, and aesthetic benefits	Values
Recreation and ecotourism	Health, values

(MEA 2005d), we first provide an overview of **supporting services**, which are the fundamental ecological processes that sustain ecosystem functioning (Fig. 2.1). We show how the degradation of certain key supporting services erodes resilience, leading to loss of other services that are used more directly by society. These services include (1) **provisioning services** (or **ecosystem goods**), which are products of ecosystems that are directly harvested by society; (2) **regulating services** that influence society through interactions among ecosystems in a landscape; and (3) **cultural services**, which are nonmaterial benefits that are important to society's well-being (Table 2.2). There is broad overlap among these categories of ecosystem services, and different authors have therefore classified them in different ways. Traditional foods, for example, function as both provisioning services that provide nutritional benefits and cultural services that sustain cultural relationships to the land or sea. The important point, however, is that the functioning of ecosystems benefits society in so many ways that human well-being cannot be sustained without the effective functioning of the ecosystems of which people are a part.

Supporting Services: Sustaining Ecosystem Functioning

Supporting services are the fundamental ecological processes that control the structure and functioning of ecosystems. Managers and the public often overlook these services because they are not the products directly valued by society. Moreover, they are frequently controlled by variables that change relatively slowly (i.e., **slow variables**) and are therefore taken for granted by agencies tasked with a managing a particular ecosystem good such as trees or fish. However, because of the fundamental dependence of all ecosystem services on supporting services, integrity of these services generally sustains many services that are valued more directly by society. In this section we focus on the slow variables that most frequently control ecosystem processes and therefore a broad suite of ecosystem services.

Maintenance of Soil Resources

Soils and sediments are key slow variables that regulate ecosystem processes by providing resources required by organisms. The controls over the formation, degradation, and resource-supplying potential of soils and sediments are therefore central to sound ecosystem management and to sustaining the natural capital on which society depends (Birkeland 1999, Chapin et al. 2002). The quantity of soil in an ecosystem depends largely on the balance between inputs from **weathering** (the breakdown of rocks to form soil) or deposition and losses from erosion. In addition, organisms, especially plants, add organic matter to soils through death of tissues and individuals, which is offset by losses through decomposition. If an ecosystem were at **steady state**, i.e., when inputs approximately equal outputs, the quantity of soil would remain relatively constant, providing a stable capacity to supply vegetation with water and nutrients. Natural imbalances between inputs and outputs lead to deeper soils in floodplains and at the base of hills than on hilltops. When averaged over large regions, however, changes in soil capital due to imbalances between inputs and outputs usually occur slowly—about 0.1–10 mm per century (Selby 1993). In general, the presence of a plant canopy and **litter** layer (the layer of dead leaves on the soil surface) reduces erosion. Human activities that reduce vegetation cover can increase erosion rates by several orders of magnitude, just as occurs naturally when glaciers, volcanoes, or landslides reduce vegetation cover. Under these circumstances, ecosystems can lose soils in years to decades that may have required thousands of years to accumulate, causing an essentially permanent loss of the productive capacity of ecosystems. Similarly, human modification of river channels can alter sediment inputs. In the southern USA, for example, loss of sediment inputs and subsequent soil subsidence led to the disappearance of barrier islands that had previously protected New Orleans from hurricanes. The loss of soil resources substantially reduces resilience by reducing the natural capital by which social–ecological systems can respond to change; this increases the likelihood of a regime shift to a more degraded state.

The physical and chemical properties of soils are just as important as total quantity of soil in determining the productive potential of terrestrial ecosystems. Fine particles of mineral soils (**clay**) and organic matter are particularly important in retaining water and nutrients (Brady and Weil 2001). Clay and organic matter are typically concentrated near the soil surface, where they are vulnerable to loss by erosion. Wind and **overland flow** (the movement of water across the soil surface) transport small particles more readily than large ones, tending to remove those soil components that are particularly important in water and nutrient retention. Human activities that foster wind and water erosion, such as deforestation, overgrazing, plowing, or fallowing of agricultural fields, therefore erode the water- and nutrient-retaining capacity of soils much faster than the total loss of soil volume might suggest. Preventing even modest rates of erosion is therefore critical to sustaining the productive capacity of terrestrial ecosystems.

Accelerated soil erosion is one of the most serious causes of global declines in ecosystem services and resilience. The erosional loss of fine soil particles is the direct cause of **desertification**, soil degradation that occurs in drylands (see Chapter 8). Desertification can be triggered by drought, reduced vegetation cover, overgrazing, or their interactions (Reynolds and Stafford Smith 2002, Foley et al. 2003a). When drought reduces vegetation cover, for example, goats and other livestock graze more intensively on the remaining vegetation. Extreme poverty and lack of a secure food supply often prevent people from reducing grazing pressure at times of drought, because short-term food needs take precedence over practices that might prevent erosion. Wetter regions can also experience severe erosional loss of soil, especially where vegetation loss exposes soils to overland flow. The Yellow River in China, for example, transports 1.6 billion tons of sediment annually from agricultural areas in the loess plateau at its headwaters. Similar erosional losses occurred when grasslands were plowed for agriculture in the USA during droughts of the 1930s, creating the **dustbowl**. Changes in social processes contribute substantially to regime shifts involving severe soil erosion.

Soil erosion from land represents a sediment input to lakes and estuaries. At a global scale the increased sediment input to oceans from accelerated erosion is partially offset by the increased sediment capture by reservoirs. Therefore lakes, including reservoirs, and estuaries are the aquatic ecosystems most strongly affected by terrestrial erosion. Especially in agricultural areas, these sediments represent a large influx of nutrients (**eutrophication**) to aquatic ecosystems that can be just as problematic as the loss of productive potential on land (see Chapter 9).

Water Cycling

Water is the soil resource that is used in largest quantities by plants and which most frequently limits the productivity of terrestrial ecosystems. Water enters ecosystems as precipitation. Two of the major pathways of water loss are **transpiration**, the "green water" that supports terrestrial production, and **runoff**, which replenishes groundwater and aquatic ecosystems, the "blue water" sources that are often tapped by people for domestic and industrial uses, irrigation, and hydropower (see Chapter 9). Consequently, there are inherent tradeoffs among the ecosystem services provided by water cycling, and some of the biggest challenges in water management result from these tradeoffs.

Climatic controls over water inputs in precipitation place an ultimate constraint on quantities of water cycled through ecosystems. Within this constraint the partitioning of water between transpiration and runoff depends on (1) the degree of compaction of the soil surface, which influences water infiltration into the soil, (2) soil water-holding capacity, which depends on the quantity of soil and its particle-size distribution (see Maintenance of Soil Resources), and (3) the capacity of vegetation to transpire water (Rockström et al. 1999).

Vegetation fosters infiltration and storage through several mechanisms. The plant canopy and litter reduce compaction by raindrops that otherwise tend to seal soil pores. In addition, roots and soil animals associated with vegetation create channels for water movement through the soil profile. By facilitating water infiltration (due to reduced compaction), water-holding capacity (due to production of soil organic matter), and reduced soil erosion (due to reduced overland flow), vegetation generates stabilizing feedbacks that sustain the productive potential of soils and reduce ecosystem vulnerability to drought. Human activities often disrupt these stabilizing feedbacks, thereby reducing resilience. For example, high densities of livestock or movement of heavy farm machinery at times (spring) or places (riparian corridors) where soils are wet can compact soils and reduce infiltration. Plowing reduces soil organic content substantially—often by 50% within a few years—thereby reducing soil water-holding capacity and the capacity of soils to support crop growth with natural rainfall (Matson et al. 1997). Alternative agricultural practices that conserve or rebuild soil organic content (e.g., no-till agriculture) or reduce compaction by livestock or equipment under wet conditions therefore increase the capacity of soils to supply water to crops or other vegetation.

Transpiration is tightly linked to the capacity of plants to fix carbon and therefore to their productive potential. This explains why productive agricultural systems are such prodigious consumers of water and why streamflow increases after logging. At a more subtle level, any factor that increases the productive potential of vegetation (e.g., nutrient additions from fertilizers, introduction of exotic nitrogen-fixing species; atmospheric deposition of nitrogen; replacement of shrublands by forests) will increase transpiration (green water flows) and reduce water movement to groundwater and runoff (blue water flows). The tradeoffs between transpiration and runoff have implications for the role of ecosystems in regulating water flow, as discussed later.

Carbon and Nutrient Cycling

Within a climate zone, the availabilities of belowground resources (water and nutrients) are the main factors that constrain terrestrial carbon cycling and ecosystem productivity. The carbon, nutrient, and water cycles of terrestrial ecosystems are tightly linked (Fig. 2.2; Chapin et al. 2002, 2008). The major controls are (1) climate, which governs water inputs, rates of soil development, and cycling rates of carbon, nutrients, and water; (2) the water- and nutrient-holding capacity of soils (see Maintenance of Soil Resources); and (3) the productive capacity of vegetation. In addition, carbon and nutrient cycles are physically linked because carbon forms the skeleton of organic compounds that carry nitrogen and phosphorus among plants, animals, and soils.

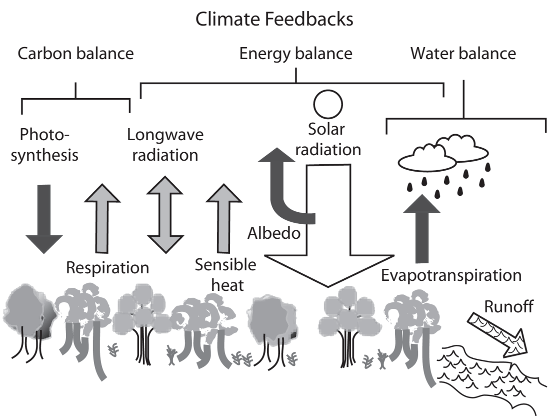

FIGURE 2.2. Three major categories of climate feedbacks (each shown by the arrows beneath the bracket) between ecosystems and the climate system. Carbon balance is the difference between CO_2 uptake by ecosystems (photosynthesis) and CO_2 loss to the atmosphere by respiration and disturbance. Energy balance is the balance between incoming solar radiation, the proportion of this incoming solar radiation that is reflected (albedo), and the transfer of the absorbed radiation to the atmosphere as sensible heat (warming the surface) or evapotranspiration (cooling the surface). Longwave radiation from the ecosystem or clouds depends on the temperature of these surfaces. Water balance between the ecosystem and atmosphere is the difference between precipitation inputs and water return in evapotranspiration; the remaining water leaves the ecosystem as runoff. Each of these ecosystem–atmosphere exchanges influences climate. Cooling effects on climate are shown by black arrows; warming effects by gray arrows. Arrows show the direction of the transfer; the magnitude of each transfer differs among ecosystems. Redrawn from Chapin et al. (2008).

Because both water and nutrient availability depend on the fine particles in soils, the factors that sustain water cycling (i.e., maintenance of vegetation and prevention of erosion) also sustain nutrient cycles. This is typical of many of the **synergies** among ecosystem services: Management practices that protect the basic integrity of ecosystem structure foster sustainability of multiple ecosystem services. This simplifies the task of ecosystem management, because most services "take care of themselves" if ecosystem structure and functioning are not seriously disrupted.

Plants are an important control point in the cycling of carbon through ecosystems, because they are the entry point for carbon and determine the chemistry of dead organic matter that eventually becomes food for decomposers. However, plant production in most intact ecosystems is limited by water and/or nutrient availability, so the productive capacity of vegetation typically adjusts to the availability of water and nutrients that a given climate and soil type provide. Consequently, across a broad range of ecosystem types, vegetation absorbs most of the nutrients that are released by the **decomposition** (chemical breakdown of dead organic matter by soil organisms). Consequently, groundwater and runoff leaving these systems have relatively low concentrations of nutrients. If, however, plant production is reduced below levels that the climate and soils can support, as for example in a fallow field or overgrazed pasture, or if nutrients are added to the system at rates that exceed the absorptive capacity of the vegetation, the excess nutrients leave the system in groundwater and runoff or as trace gases to the atmosphere (e.g., N_2O, a potent greenhouse gas that contributes to climate warming). Certain **nitrogen-fixing** plant species form mutualistic relationships with soil microorganisms that convert atmospheric nitrogen to plant-available nitrogen. The expansion of soybean and other nitrogen-fixing species has substantially increased nitrogen inputs to many agricultural regions (see Chapter 12). Industrial fixation of nitrogen, primarily to produce fertilizers, is an even larger source of nitrogen inputs to managed ecosystems. Ammonia volatilizes from fertilizers and cattle urine and enters downwind ecosystems in precipitation. In addition, fossil-fuel combustion produces nitrogen oxides (NO_x) that are a major component of acid rain. Together these anthropogenic sources of nitrogen have doubled the naturally occurring rates of nitrogen inputs to terrestrial ecosystems (Fig. 2.3; Schlesinger 1997, Vitousek et al. 1997). This massive change in global biogeochemistry weakens the internal stabilizing feedbacks that confer resilience to ecosystem processes (see Chapter 1). Reducing nitrogen inputs to levels consistent with the productive capacity of vegetation, for example, by reducing fertilizer applications, reducing air pollution, or preventing the spread of nitrogen-fixing exotic species, reduces the leakage of nitrogen from terrestrial to aquatic ecosystems.

Carbon and nutrient cycles in aquatic ecosystems run on the leftovers of terrestrial nutrient cycles. In intact landscapes with tight terrestrial nutrient cycles, the small quantity of nutrients delivered to streams spiral slowly downstream, moving through decomposers, stream invertebrates, algae, and fish (Vannote et al. 1980). Lakes are typically more nutrient-impoverished than streams, because they receive relatively

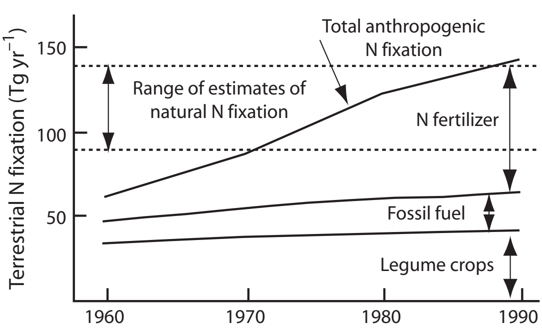

FIGURE 2.3. Anthropogenic fixation of nitrogen in terrestrial ecosystems over time compared with the range of estimates of natural biological nitrogen fixation on land. Redrawn from Vitousek et al. (1997).

little leaf litter and groundwater per unit of water surface, and sediments chemically fix much of the phosphorus that enters the lake (see Chapter 9). Aquatic organisms are well adapted to these low-nutrient conditions. Algae efficiently absorb nutrients from the water column, are eaten by invertebrate grazers that in turn are eaten by fish. When phosphorus inputs to lakes exceed the chemical fixation capacity of sediments, algae grow and reproduce more rapidly than grazers can consume them, reducing water clarity and increasing the rain of dead organic matter to depth. Here bottom-dwelling decomposers break down the dead organic matter, depleting oxygen below levels required by fish, which causes fish to die. The high phosphorus-fixation capacity of lake sediments makes most lakes quite resilient to individual eutrophication events. Once this phosphorus-sequestration mechanism is saturated, however, the sediments become a source rather than a sink of phosphorus, causing the lake to shift to a eutrophic state (Carpenter et al. 1999, Carpenter 2003; see Chapter 9).

Estuaries and the coastal zone of oceans, which are the final dumping ground of terrestrially derived nutrients, are typically quite productive. The rapid decomposition and nutrient release from sediments supports a productive bottom fishery and a rich nutrient source for the overlying water column. Chesapeake Bay, for example, was historically an extremely rich fishery that supported dense populations of Native Americans and later of European settlers. Just as in lakes, however, excessive nutrient and organic matter inputs to estuaries can be too much of a good thing, depleting oxygen and killing the organisms that would otherwise decompose and recycle the accumulating organic matter. The Mississippi River Delta, for example, has undergone a regime shift from a productive shrimp fishery to a dead zone with insufficient oxygen to support much biological activity (Rabalais et al. 2002). The biological mechanisms that limit the resilience of lakes and estuaries are well understood, but the failure of social–ecological systems to prevent regime shifts demonstrates the need to incorporate social processes into management planning (see Chapters 3 and 4).

Carbon and nutrient cycling in the water column of deep ocean basins is similar to that described for lakes, except that it is often even more nutrient-impoverished, because of the large vertical separation of ocean sediments from the surface where algal production occurs (Valiela 1995). Productive fisheries are often concentrated in zones of **upwelling** where deep nutrient-rich water moves to the surface near the edges of continental shelves or at high latitudes, where wind-driven mixing is most pronounced.

Maintenance of Biological Diversity

The known effects of biodiversity on ecosystem functioning relate most strongly to traits that govern the *effect* of species on ecosystem processes and traits that govern the *response* of species to environmental variation. These known effects of biodiversity change (both loss of key species or invasion of species with large impacts) can be fostered by maintaining species that span the spectrum of **effect diversity** and **response diversity** present in the system (Elmqvist et al. 2003, Suding et al. 2008).

Keystone species are species that have disproportionately large *effects* on ecosystems, typically because they alter critical slow variables. Ecosystems are most likely to sustain their current properties if current keystone species (or their functional equivalents) are maintained, and new ones are not introduced. Species that influence the supply of growth-limiting resources generally have large effects on the functioning of ecosystems. *Myrica faya*, for example, is a nitrogen-fixing tree introduced to nitrogen-poor ecosystems of Hawaii by the Polynesians. The resulting increases in nitrogen inputs, productivity, and canopy shading eliminated many plant species from the formerly diverse understory of this forest (Vitousek 2004). Highly mobile animals, such as salmon and sheep, act as keystone species governing nutrient supply by feeding in one place and dying or defecating somewhere else. Similarly, species that modify disturbance regime exert strong effects on ecosystem functioning through their effects on the adaptive cycle of release, renewal, and growth. The introduction of flammable grasses into a tropical forest, for example, can increase fire frequency and trigger a regime shift from forest to savanna (D'Antonio and Vitousek 1992). One of the main ways that animals affect ecosystem processes is through physical disturbance (Jones et al. 1994). Gophers, pigs, and ants, for example, disturb the soil, creating sites for seedling establishment and favoring early successional species. Elephants trample vegetation and remove portions of tree canopies, altering the competitive balance between trees and grasses in tropical savannas. Many keystone species exert their effect by modifying species interactions, for example, by eating other species (e.g., forest pests) or competing or facilitating the growth of other species (Chapin et al. 2000). Conserving key **functional types** (i.e., a group of species that have similar effects on ecosystem processes) and preventing the invasion of novel functional types reduces the likelihood of large changes in ecosystem services.

Diversity in the environmental *response* of species can stabilize ecosystem processes. Many species in a community appear functionally similar, for example, algal species in a lake or canopy trees in a tropical forest (Scheffer and van Nes 2004). What are the ecosystem consequences of changes in diversity *within* a functional type (i.e., **functional redundancy**)? Differences in environmental responses among functionally similar species provide resilience by stabilizing rates of ecosystem processes (McNaughton 1977, Chapin and Shaver 1985). In midlatitude grasslands, for example, cool-season grasses are particularly productive under cool, moist conditions, and warm-season grasses under hot, dry conditions. As environmental conditions fluctuate within and among years, different species attain a competitive advantage over other functionally similar species (i.e., other grasses), thus stabilizing rates of ecosystem processes by the entire community (Ives et al. 1999).

The functional redundancy associated with species diversity also provides insurance against more drastic changes in environment, such as those that may occur in the event of human mismanagement of ecosystems or change in climate. Radical changes in environment are unlikely to eliminate all species of a given functional type in a diverse ecosystem, allowing the surviving species to increase in abundance and maintain functions that might otherwise be seriously compromised. Overgrazing in Australian grasslands, for example, eliminated the dominant species of palatable grass, severely reducing the quantity of cattle that the ecosystem

Table 2.3. Examples of biodiversity effects on ecosystem services. We separate the diversity effects into those due to functional composition, numbers of species, genetic diversity within species, and landscape structure and diversity. Modified from Díaz et al. (2006).

Ecosystem service	Diversity component and mechanism
1. Production by societally important plants	*Functional composition*: (a) fast-growing species produce more biomass; (b) species differ in timing and spatial pattern of resource use (complementarity allows more resources to be used)
	Species number: large species pool is more likely to contain productive species
2. Stability of crop production	*Genetic diversity*: buffers production against losses to pests and environmental variability
	Species number: Cultivation of multiple species in the same plot maintains high production over a broader range of conditions
	Functional composition: species differ in their response to environment and disturbance, stabilizing production
3. Maintenance of soil resources	*Functional composition*: (a) fast-growing species enhance soil fertility; (b) dense root systems prevent soil erosion
4. Regulation of water quantity and quality	*Landscape diversity*: Intact riparian corridors reduce erosion.
	Functional composition: Fast-growing plants have high transpiration rates, reducing stream flow
5. Pollination for food production and species survival	*Functional composition*: Loss of specialized pollinators reduces fruit set and diversity of plants that reproduce successfully
	Species number: Loss of pollinator species reduces the diversity of plants that successfully reproduce (genetic impoverishment)
	Landscape diversity: Large, well-connected landscape units enable pollinators to facilitate gene flow among habitat patches
6. Resistance to invasive species with negative ecological/cultural effects	*Functional composition*: Some competitive species resist the invasion of exotic species
	Landscape structure: Roads can serve as corridors for spread of invasive species; natural habitat patches can resist spread
	Species number: Species-rich communities are likely to have less unused resources and more competitive species to resist invaders
7. Pest and disease control	*Genetic diversity or species number*: Reduces density of suitable hosts for specialized pests and diseases
	Landscape diversity: Provides habitat for natural enemies of pests
8. Biophysical climate regulation	*Functional composition*: Determines water and energy exchange, thus influencing local air temperature and circulation patterns
	Landscape structure: Influences convective movement of air masses and therefore local temperature and precipitation
9. Climate regulation by carbon sequestrations	*Landscape structure*: Fragmented landscapes have greater edge-to-area ratio; edges have greater carbon loss
	Functional composition: Small, short-lived plants store less carbon
	Species number: High species number reduces pest outbreaks that cause carbon loss
10. Protection against natural hazards (e.g., floods, hurricanes, fires)	*Landscape structure*: Influences disturbance spread and/or protection against natural hazards
	Functional composition: (a) extensive root systems prevent erosion and uprooting; (b) deciduous species are less flammable than evergreens

could support and exposing the soil to wind erosion. Fortunately, a previously rare grass species that was less palatable, survived the overgrazing and increased in abundance, when the dominant grass declined, thus maintaining grass cover and reducing potential degradation from erosion (Walker et al. 1999). These examples of diversity effects on resilience provide hints of the general importance of diversity in stabilizing ecosystem processes and associated ecosystem services (Table 2.3) and suggest that management that sustains diversity is critical to long-term sustainability.

Maintenance of Disturbance Regime

Disturbance shapes the long-term fluctuations in the structure and functioning of ecosystems and therefore their resilience and vulnerability to change. **Disturbances** are relatively discrete events that alter ecosystem structure and cause changes in resource availability or physical environment (Pickett and White 1985). Disturbance is not something that "happens" to ecosystems but is an integral part of their functioning. Species are typically adapted to the **disturbance regime** (i.e., the characteristic severity, frequency, type, size, timing, and intensity of disturbance) that shaped their evolutionary histories. Grassland and boreal species, for example, resprout rapidly after fire or have reproductive strategies that enable them to colonize recent burns (Johnson 1992). In contrast, many tropical tree species produce a pool of young seedlings that grow slowly in the understory, "waiting" until a hurricane or other event creates gaps in the canopy. The tropical tree strategy is poorly adapted to fire, which would kill the understory seedlings, and the boreal trees are poorly adapted to wind, which would leave an organic seedbed unfavorable for post-disturbance germination. Naturally occurring disturbances such as fires and hurricanes are therefore not "bad"; they are normal properties of ecosystems and indeed are essential for the long-term resilience of species and community dynamics that characterize a particular ecosystem.

The adaptive cycle that is triggered by disturbance both generates and depends upon landscape patterns of biodiversity. After disturbance (release phase) and colonization (renewal phase), ecosystems undergo **succession** (growth phase), a directional change in ecosystem properties resulting from biologically driven changes in resource supply. Succession is accompanied by changes in the sizes and types of plants, leading to a diversity of food and habitat for animals and soil microbes. These changes in species composition and diversity both cause and respond to the changing availability of light, water, and nutrients as succession proceeds, leading to characteristic changes in the cycling of carbon, water, and nutrients and the associated supply of ecosystem services. The scale of this successional dynamic ranges from individual plants (e.g., gap-phase succession in moist temperate and tropical forests) to extensive stands (e.g., flood plains or conifer forests characterized by large stand-replacing crown fires) and from years (e.g., grasslands) to centuries (e.g., many forests). Subsequent renewal of a disturbed patch draws on both on-site legacies (e.g., buried seeds and surviving individuals) and colonization from the surrounding matrix (Fig. 2.4; Nyström and Folke 2001, Folke et al. 2004). The resilience of the integrated disturbance-renewal system depends on both a diversity of functional types capable of sustaining the characteristic spectrum of ecosystem functions (effect diversity) and functional redundancy *within* functional types (response diversity). In coral reefs, for example, storms cause local extinctions that are repopulated by dispersal from the surrounding matrix. If overfishing or eutrophication eliminates some grazer species, such as parrot fish that remove invading algae to produce space for recolonizing coral larvae, the grazer-functional group is less likely to provide the conditions for successful coral recruitment. In the absence of parrot fish, algae overgrow the corals, leading to a regime shift that supports substantially less biodiversity and ecosystem services (Bellwood et al. 2004).

As climate-driven stresses become more pronounced, and local extinctions occur more frequently, the functional redundancy and

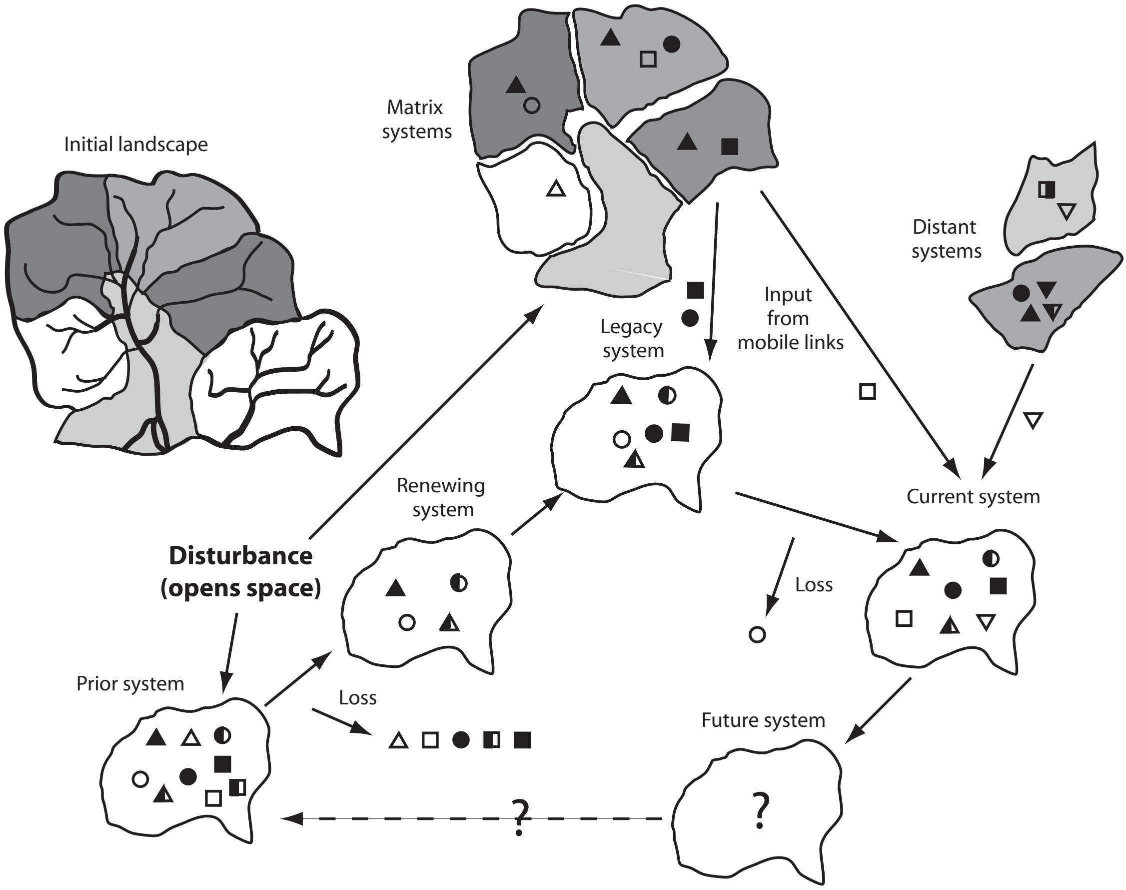

Figure 2.4. Roles of biodiversity in ecosystem renewal after disturbance (Folke et al. 2004). A disturbance such as a fire, hurricane, volcanic eruption, or war opens space in a social–ecological system. In this diagram, each shape represents a different functional group such as algal-grazing herbivores in a coral reef, and the different patterns of shading represent species within a functional group. After disturbance, some species are lost, but an on-site legacy of surviving species serves as the starting point for ecosystem renewal. For example, after boreal fire, about half of the vascular plant species are lost. The larger the *species diversity* of the pre-disturbance ecosystem, the more species and functional groups are likely to survive the disturbance. (In this figure all functional groups except "squares" survived the disturbance.) *Landscape diversity* of the matrix surrounding the patch is also important to ecosystem renewal because it provides a reservoir of diversity that can recolonize the disturbed patch through the actions of **mobile links** (biological or physical processes that link patches on a landscape). In this figure the "square" function was renewed by colonization from the matrix surrounding the ecosystem. Through time some additional species may be gained or lost. In addition, new functional groups (inverted triangles in this diagram) may invade from a distance. The greater the species diversity of the patch, the less likely is this invasion (and associated functional change). In summary, diversity in both the patch and the surrounding matrix are essential to maintaining ecosystem functioning over the long term. Although we have described the importance of diversity from an ecological perspective, the same logic holds true for economic and institutional diversity (see Chapters 3 and 4).

biodiversity of the matrix become increasingly important to landscape resilience (Elmqvist et al. 2003). Postage-stamp reserves in a matrix of agricultural monoculture, for example, are less likely to sustain their functional diversity than in a diverse landscape, especially during times of rapid environmental change (Fig. 2.4). A patchwork of hedge rows, forest patches, and riparian corridors in an agricultural landscape or of urban gardens, cemeteries, and seminatural landscaping of lawns in cities can substantially increase landscape diversity and resilience of human-dominated landscapes, even though they may occupy only a tiny fraction of the land area (Colding et al. 2006; see Chapters 12 and 13). In a rapidly changing, intensively managed world, **assisted migration** of species with low migration potential can supplement landscape biodiversity as a source of renewal (McLachlan et al. 2007). Intensively managed Fennoscandian forests, for example, have lost 70% of the insect and bird biodiversity in their wood-decomposer food webs. Climate warming now creates conditions that are conducive to migration of more southerly wood decomposers. This wood-dependent biodiversity could be regenerated if the niche becomes available (through protection of older stands and retention of green and dead trees and coarse woody debris after logging) and if the species can arrive [management of the matrix to foster migration of late successional species supplemented by assisted migration (introduction) of southerly taxa; Chapin et al. 2007].

Society typically derives benefits from most phases of a disturbance cycle. Disturbance itself reduces population densities of certain pests and diseases. Early successional stages are characterized by rapidly growing species that have tissues that are nutritious to herbivores, such as deer, and fleshy fruits that are dispersed by birds and harvested by people. Later successional stages are dominated by species that provide other types of goods, such as timber or medicines. **Swidden** (slash-and-burn) **agriculture** is a cultural system that can be an integral sustainable component of some tropical forests, as long as the traditional disturbance regime is maintained (see Chapter 7). Human activities that alter disturbance regimes, however, modify the suite of goods and services provided by the landscape. Prevention of small insect outbreaks, for example, increases the continuity of susceptible individuals and therefore the probability of larger outbreaks (Holling 1986). A **command-and-control** approach to resource management that prevents disturbances characteristic of an ecosystem often reduces resilience at regional scales by producing new conditions at all phases of the successional cycle to which local organisms are less well adapted (Holling and Meffe 1996; see Chapter 4). Decisions that alter disturbance regimes tend to address only the short-term benefits to society, such as flood control, pest control, and fire prevention, and ignore the broader context of changes that propagate through all phases of the disturbance cycle.

Ecosystem "Restoration": The Reconstruction of Degraded Ecosystems

In degraded ecosystems such as abandoned mines and degraded wetlands, active transformation to a more desirable state may be a central management goal. In this case, introduction of new functional types can foster transformation for ecosystem reconstruction or renewal (Bradshaw 1983). Introduction of nitrogen-fixing trees to abandoned mine sites in England, for example, greatly enhanced the accumulation of soil nitrogen and soil organic matter, providing the soil resources necessary to support forest succession. Planting of metal-tolerant grasses on metal-contaminated sites can play a similar role. Planting of beach grasses in coastal developments can stabilize sand dunes that might otherwise be eroded by winds and storms. Similarly, planting of salt marsh plants with different salinity tolerances along a salinity gradient can renew coastal salt marshes that were eliminated by human disturbance or by sediment deposition from upstream land-use change.

At larger scales, the introduction of a Pleistocene-like megafauna has been suggested as a strategy to convert moss-dominated unproductive Siberian tundra into a more productive steppe-like ecosystem. This regime shift could support greater animal production and partially compensate for the loss of economic subsidies to indigenous communities in the post-Soviet Russian North (Zimov et al. 1995). Parks in cities are savanna-like environments that provide important cultural services for all residents, and city gardens provide valuable nutritional and cultural benefits to people who have moved to cities from rural agricultural areas (Colding et al. 2006). In a world dominated by rapid human population growth and directional environmental change, the deliberate introduction of new functional types creates path dependence for ecosystem transformation to a new, potentially more desirable state (Choi 2007). However, deliberate species introductions have a history of creating unintended undesirable side effects. Exotic grasses used to stabilize roadsides may expand into adjacent ecosystems, or biological control agents may expand their diet to nontarget species. Consequently, the introduction of novel functional types to trigger ecosystem transformation is a tool that requires caution and can often be avoided through use of locally adapted species and genotypes.

Provisioning Services: Providing the Goods Used by Society

Provisioning services are the goods produced by ecosystems that are consumed by society. They are the most direct link between ecosystems and social systems and are therefore the ecosystem properties that receive most direct attention from managers and the public. They are fast variables that depend on supporting services in ecosystems and often exhibit rapid nonlinear responses to fluctuations in environment. Large changes may be difficult to reverse if thresholds in supporting services are exceeded. In this section we identify the major provisioning services and discuss ways to sustain their supply.

Fresh Water

Water is the ecosystem service that is most likely to directly limit well-being in the twenty-first century. Although water is the most abundant compound on Earth, only a small fraction of it (0.1%) is available to people, primarily in lakes, rivers, and shallow groundwater (see Chapter 9). People currently use 40–50% of available freshwater, with use projected to increase to 70% by 2050 (Postel et al. 1996). The shortage of clean water is particularly severe in developing nations, where future population growth and water requirements are likely to be greatest. The projected increases in human demands for fresh water will strongly impact aquatic ecosystems through eutrophication and pollution, diversion of fresh water for irrigation, and modification of flow regimes by dams and reservoirs (see Chapter 9).

Maintaining the essential role of intact ecosystems in the hydrological cycle is the single most effective way to sustain the supply and quality of fresh water for use by society. Intact ecosystems that surround reservoirs minimize sediment input, serve as a chemical and biological filter that removes pollutants and pathogenic bacteria, and buffer seasonal fluctuations in river flows, as described later. There are tradeoffs between the quantity and the quality of water provided by ecosystems. Forest clearing is sometimes suggested as a way to increase runoff and therefore the blue-water flows that can be withdrawn for human use. The clear-cutting of an experimental watershed at Hubbard Brook in the northeastern USA did indeed increase runoff fourfold (Likens et al. 1977). However, it also increased stream nitrate fluxes 16-fold because of a fourfold increase in nitrate concentration—to levels exceeding health standards for drinking water and led to loss of a spectrum of ecosystem services provided by the intact forest. Understanding the tradeoffs among water-related ecosystem services derived from green-water and blue-water flows is critical to ecosystem stewardship (Rockström et al. 1999, Gordon et al. 2008).

Expansion of human populations into arid regions is often subsidized by tapping groundwater supplies that would otherwise be unavailable to surface organisms. In dry regions 80–90% of this water is used to support irrigated agriculture, which can be highly productive once the natural constraints of water limitation are removed. The substantial cost of irrigated agriculture in turn creates incentives for intensive management with fertilizers and pesticides, leading to a cascade of associated social and economic consequences. The sustainability of irrigated agriculture depends on the rate of water use relative to resupply to the groundwater and the downstream consequences of irrigation (see Chapters 9 and 12). Many irrigated areas are supported by **fossil groundwater** that accumulated in a different climatic regime and is being removed much more rapidly than it is replenished, a practice that clearly cannot be sustained.

More than half of the water diverted for human consumption, industrial use, or agriculture is wasted. Most irrigation water, for example, evaporates rather than being absorbed by plants to support production. Management actions that increase the efficiency of water use and/or reuse water for multiple purposes can increase the effective water supply for human use without additional fresh-water diversion from ecosystems (see Chapter 9).

Food, Fiber, and Fuelwood

Management of ecosystems for the production of food, fiber, and fuelwood cause greater changes in ecosystem services and the global environment than any other human activity. Humans have transformed 40–50% of the ice-free terrestrial surface to produce food, fiber, and fuelwood (Vitousek et al. 1986, Imhoff et al. 2004). We dominate (directly or indirectly) about a third of primary productivity on land and harvest fish that use 8% of ocean production (Myers and Worm 2003). Most of the nitrogen that people add to the environment is to support agriculture, either as fertilizer or as nitrogen-fixing crops. The global human population increased fourfold during the twentieth century to 6.1 billion people, with corresponding increases in the harvest of ecosystem goods to feed, clothe, and house these people.

Two general categories of ecosystem change have enabled food and fiber production to keep pace with the growing human population. There has been **intensification** in use of existing agricultural areas through inputs of fertilizers, pesticides, irrigation, and energy-intensive technology and **extensification** through land-use conversion or modification of existing ecosystems to provide goods for human use. Meeting the needs for food and fiber of the projected 60–70% increase in human population by 2050 will further increase the demands for agricultural and forestry production. Recent increases in food production have come primarily from intensification of agriculture, with much of the expected future increase expected to come from extensification in marginal environments where largest population increases may occur. There are critical tradeoffs between intensification, which often creates pollution problems, and extensification, which eliminates many of the services associated with natural ecosystems. Appropriate management can reduce the impacts of intensive agriculture (Matson et al. 1997). For example, no-till agriculture reduces soil disturbance and therefore the decomposition of soil organic matter, enhancing the water- and nutrient-retaining capacity of soils (see Chapter 12). Careful addition of water and nutrients to match the amounts and timing of crop growth can substantially reduce losses to the environment. There are also ways in which the extensification of agriculture can minimize impacts on ecosystem services by considering the landscape framework in which it occurs. Swidden (slash-and-burn) agriculture in tropical forests, for example, can provide food in newly cleared lands and forest products in regenerating forests. With appropriate rotation length, this practice has been sustained for thousands of years (Ramakrishnan 1992). However, in areas where rotation length declined from the traditional 30-year periodicity to 10 years or less in response to recent human population growth, soils had insufficient time to regain fertility, forest species with long life cycles disappeared, and the system underwent a regime shift to intensive agriculture of cash crops with radically different social and ecological properties (Ramakrishnan 1992). Just as with water, some of the greatest opportunities to minimize tradeoffs associated with enhancing agricultural production are to explore practices that maximize the effectiveness of lands and resources to support food production in ways that are consistent with ecological sustainability and local cultural norms and values.

About 70% of marine fisheries are overexploited (see Chapter 10). Much of this fishing pressure results from the globalization of markets for fish and from perverse subsidies that enable fishermen to continue fishing even for stocks that would otherwise no longer be profitable to harvest. This illustrates the importance of social and economic factors in driving increased harvest of many provisioning services and a need for improved resource stewardship of marine ecosystems to sustain provisioning services.

Other Products

Ecosystems provide a diverse array of other products that are specific to individual ecosystems and societies. These include aesthetically and culturally valuable items such as flowers, animal skins, and shells. In addition, ecosystems constitute a vast storehouse of genetic potential to deal with current and future conditions. This includes genes from traditional cultivars or wild relatives of crops and other wild species that produce products that benefit society (see Chapter 6). For example, about 25% of currently prescribed medicines originate from plant compounds that evolved as defenses against herbivores (Dirzo and Raven 2003) and have substantial potential for bioprospecting in regions of high biodiversity (Kursar et al. 2006).

Regulating Services: Sustaining the Social–Ecological System

Regulating services influence processes beyond borders of ecosystems where they originate. They constitute some of the key cross-scale linkages that connect ecosystems on a landscape and integrate processes across temporal scales. They are, however, largely invisible to society and generally ignored by managers, so failures to sustain regulating services often have devastating consequences.

Climate Regulation

The cycling of water, carbon, and nutrients has important climatic consequences. About half of the precipitation in the Amazon basin, for example, comes from water that is recycled by evapotranspiration from terrestrial ecosystems (Costa and Foley 1999). If tropical forests were extensively cut and replaced by pastures with lower transpiration rates, this could lead to a warmer, drier climate more typical of savanna, making forest regeneration more difficult (Foley et al. 2003b, Bala et al. 2007). At high latitudes, tree-covered landscapes absorb more radiation and transfer it to the atmosphere than does adjacent snow-covered tundra. The northward movement of treeline 6,000 years ago is estimated to have contributed half of the climate warming that occurred at that time (Foley et al. 1994). Extensive human impacts on ecosystems can have similar large effects. In Western Australia the replacement of native heath vegetation by wheatlands increased regional **albedo** (reflectance). As a result, the dark heathlands absorbed more radiation than the cropland, causing air to warm and rise over the heathland and drawing moist air from the adjacent wheatlands. The net effect was a 10% increase in precipitation over heathlands and a 30% decrease in precipitation over croplands (Chambers 1998). Many vegetation changes, if they are extensive, generate a climate that favors the new vegetation, making it difficult to return vegetation to its original state (Chapin et al. 2008). This suggests that ecosystem integrity is critical to resilience of the climate system at regional scales.

Ecosystems are also important sources and sinks of greenhouse gases that determine the heat-trapping capacity of the atmosphere and therefore the temperature of our planet. Approximately half of the CO_2 released by burning fossil fuels is captured and stored by ecosystems—half on land and half in the ocean. The capacity of ecosystems to remove and store this carbon therefore exerts a strong influence on patterns and rates of climate change. Forests and peatlands are particularly effective in storing large quantities of carbon, in trees and soils, respectively. Maintaining the integrity of these ecosystem types or restoring them on degraded lands enhances the capacity of the terrestrial biosphere to store carbon. Increased recognition of the value of this climate regulatory service has led to a market in carbon credits for activities that enhance the capacity of ecosystems to store carbon (see Chapter 7).

Regulation of Erosion, Water Quantity, Water Quality, and Pollution

As discussed earlier (see Water), intact ecosystems regulate many water-related services by buffering stream flows to prevent floods and soil erosion and by filtering ground water to reduce pollutant concentrations (Rockström et al. 1999). Many of the compounds in agricultural and urban runoff are identical or similar to compounds that naturally cycle through ecosystems and are therefore used by organisms to support their growth and reproduction. Ecosystems therefore have a natural capacity to absorb these pollutants, cleansing the air or water in the process (see Chapter 9). Ecosystems also process some novel chemicals, with potentially positive and negative environmental consequences. Oil spills, for example, select for oil-degrading bacteria that use oil as an energy source, although their capacity to do so is generally limited by nutrient availability. Polychlorinated-hydrocarbon pesticides (PCBs) are a potential energy source for those organisms that evolve resistance to their toxicity. The rapid evolution that typifies microbial populations in soils and sediments sometimes selects for populations capable of degrading or converting these compounds to other products. Their activity reduces pollutant concentration. Sometimes, however, the breakdown products are even more toxic to other organisms than was the original compound, as in the conversion of insecticide DDT to DDE, or are environmentally stable and accumulate in ecosystems, as in the fat-soluble PCBs that accumulate in food chains and have caused reproductive failure in many marine birds (Carson 1962). Society therefore cannot count on ecosystems to provide a "quick fix" that solves pollution problems.

Those pollutants that are processed by ecosystems frequently alter their structure, diversity, and functioning. The processing of nitrogen derived from acid rain or agricultural pollution, for example, increases productivity, altering the competitive balance and relative abundance of species. The dominant plants often increase in size and abundance and outcompete smaller organisms, leading to a loss of species diversity. Moreover, as ecosystems cycle more nitrogen, soil nitrate concentrations increase, leading to emissions of more nitrous oxide (a potent greenhouse gas) to the atmosphere and leaching of nitrate to groundwater. As nitrate (an anion) leaches, it carries with it a cation to maintain charge balance, reducing the availability of cations such as calcium and magnesium, which can be replaced only by slow soil weathering. This is representative of many ecological responses to change, in which apparently beneficial effects of ecosystems (e.g., removal of nitrogen-based pollutants or PCBs) can initiate a cascade of unanticipated consequences. Ecological research that recognizes the complex adaptive nature of ecosystems (see Chapter 1) can increase the likelihood of anticipating some of these effects as a basis for informed policy decisions.

Natural-Hazard Reduction

Adaptations of organisms to the characteristic disturbance regime of their environment often reduce the societal impacts of disturbance. As discussed earlier, every ecosystem has a particular disturbance regime to which organisms are adapted. However, these same disturbances, such as hurricanes, wildfires, and floods, often have negative societal impacts on the built environment that people create. Incorporation of organisms adapted to a particular disturbance regime into the built environment sometimes reduces the impact of disturbances when they occur. Kelp forests in the intertidal zone, for example, dissipate energy from storm surges and protect beaches from coastal erosion, just as beach grasses protect sands from wind erosion. Floodplain trees and shrubs reduce the speed of flood waters, leading to deposition of sediments and reducing the water energy that would otherwise cause erosional changes in channel morphology. Some of the greatest challenges in managing disturbance are to identify and separate those locations where disturbances have large negative effects on human-dominated environments (e.g., towns and cities) from areas where disturbances have greater societal benefits and/or are most likely to occur. For example, concentrating suburban development in areas that are unlikely to experience fire or flooding reduces risks to the built environment. Similarly, allowing regular small disturbances (e.g., floods, prescribed fires, and insect outbreaks) to occur periodically reduces the likelihood of larger disturbances that are more difficult to control (Holling and Meffe 1996).

Regulation of Pests, Invasions, and Diseases

Biodiversity often enhances pest resistance in agricultural systems through both ecological and evolutionary processes (Díaz et al. 2006). An increasing tendency in intensive agriculture is to reduce weeds, pests, and pathogens using agrochemical pesticides. Due to their high population densities and short life cycles, however, insects and weeds typically evolve resistance to synthetic biocides within 10–20 years, necessitating continuing costly investments to develop and synthesize new biocides as current products become less effective. An alternative more resilient approach is to make greater use of natural processes that regulate pests. Increased genetic diversity of crops nearly always decreases pathogen-related yield losses (Table 2.3). Recently, a major and costly fungal pathogen of rice, rice blast, was controlled in a large region of China by planting alternating rows of two rice varieties (Zhu et al. 2000). Similarly, a high diversity of crop species reduces the incidence or severity of impact of herbivores, pathogens, and weeds (Andow 1991, Liebman and Staver 2001, Díaz et al. 2006). Sometimes these diversity effects have multiple benefits. Crop diversity treatments that reduce the abundance of insect herbivores also suppress the spread of viral infection, because plant-feeding insects transmit most plant viruses. This leads to lower viral densities in polycultures than monocultures (Power and Flecker 1996).

The species richness of **natural enemies** (pathogens, predators, and parasitoids) of pests tends to be higher in species-rich agroecosystems than in monocultures and higher in natural vegetation buffers than in fields, leading to higher ratios of natural enemies to herbivores and therefore lower pest densities. The spraying of biocides can increase vulnerability because it reduces the abundance of natural enemies more than the pests that are targeted. This allows pest populations to rebound rapidly, sometimes causing more damage than if no pesticides had been used (Naylor and Ehrlich 1997; see Chapter 12).

Invasive exotic species cost tens of millions of dollars annually in the USA, primarily in crop losses and pesticide applications (Pimentel et al. 2000). Ecosystems have mechanisms, as yet poorly understood, that reduce invasibility (Díaz et al. 2006). These include disturbance adaptations that enable certain native species to colonize and grow rapidly after disturbance, a time when invasive species might otherwise encounter little competition from other plants. In a given environment, more diverse ecosystems are less readily invaded, perhaps because local species already fill most of the potential biological roles and utilize most of the resources that might be available (Díaz et al. 2006). Invasive species most frequently colonize environments that naturally support high levels of diversity. Together these observations suggest that (1) hot spots for diversity are particularly at risk of invasion by introduced species, and (2) the loss of native species may increase invasibility.

Natural enemies also reduce ecosystem invasibility. One reason that exotic species are often so successful is that they escape their specialized natural enemies that constrain success in their region of origin. Natural enemies in the new environment often prevent these exotic species from becoming noxious pests (Mitchell and Power 2003).

Maintaining the integrity of natural ecosystems may reduce disease risk to people. Lyme disease, for example, is caused by a pathogen that is transmitted by ticks from mice and deer to people (Ostfeld and Keesing 2000). Although forest mice are the largest reservoir of the disease, deer move the disease from one forest patch to another. Exploding deer densities have increased the incidence of lyme disease in the northeastern USA in response to agricultural abandonment, expansion of suburban habitat, and elimination of the natural predators of deer. In Sweden, climate warming has increased overwinter survival of ticks, further increasing disease incidence (Lindgren et al. 2000, Lindgren and Gustafson 2001).

Currently 75% of emerging human diseases are naturally transmitted from animals to humans (Taylor et al. 2001). Clearly, efforts to control these diseases require improved understanding of social–ecological dynamics (Patz et al. 2005).

Pollination Services

Much of the world's food production depends on animal pollination, particularly for fruits and vegetables that provide a considerable portion of the vitamins and minerals in the human diet. The value of these pollination services is likely to be billions of dollars annually (Costanza et al. 1997). Pollination by animals is obviously essential for the success of plants that are not wind- or self-pollinated. These pollination services often extend well beyond a given stand and are often important in pollinating adjacent crops. Temperate orchards and tropical coffee plantations adjacent to uncultivated lands or riparian corridors often have more pollinators and are more productive than are larger orchards (Ricketts et al. 2004). Large monocultures reduce pollination services by reducing local floral diversity and nesting sites and by using insecticides that reduce pollinator abundances. Pollination webs often connect the success of a wide range of species in multiple ecosystem types (Memmott 1997).

Cultural Services: Sustaining Society's Connections to Land and Sea

Cultural Identity and Cultural Heritage

Cultural connections to the environment are powerful social forces that can foster stewardship and social–ecological sustainability (see Chapter 6). Because people have evolved as integral components of social–ecological systems, this human–nature relationship is often an important component of **cultural identity**, i.e., the current cultural connection between people and their environment (Plate 4). Cultural identity in turn links to the past through **cultural heritage**, i.e., the stories, legends, and memories of past cultural ties to the environment (de Groot et al. 2005). Cultural identity and heritage are ecosystem services that strongly influence people's sense of stewardship of social–ecological systems (Ramakrishnan 1992, Berkes 2008) and therefore offer an excellent opportunity for natural resource managers to both learn from and contribute to stakeholder efforts to sustain their livelihoods and environment (see Chapter 6). Many indigenous peoples, for example, have **traditional ecological knowledge** based on oral transmission of their cultural heritage in ways that inform current interactions with the environment (i.e., cultural identity). This cultural heritage provides information about how people coped with past environmental and social–ecological challenges and about important values that influence likely future responses to changes in both the environment and the resource management policies (Berkes 1998; see Chapter 4). Integration of traditional knowledge with the **formal knowledge** (i.e., "scientific knowledge") that often informs resource management decisions is not easy, because the "facts" (e.g., the nature of the human–environment relationship) sometimes differ between the two knowledge systems (Berkes 2008). Both knowledge systems are important if they influence the ways in which stakeholders perceive and interact with their environment. The linkage between knowledge systems (as informed by cultural heritage), perceptions, and actions is at least as important to understanding and predicting human actions as are the biophysical mechanisms that are believed to underlie scientific knowledge. Social learning that builds new frameworks to sustain social–ecological systems is most likely to occur if both traditional and formal knowledge are treated with respect rather than subjugating traditional knowledge to western science.

Local knowledge held by farmers, ranchers, fishermen, resource managers, engineers, and city dwellers is also valuable. As in the case of indigenous knowledge, local knowledge consists of "facts" based on cultural heritage and observations that determine how people respond to and affect their environment. Many local residents, whether indigenous or not, spend more time interacting with their environment than do policy makers and therefore have a different suite of observations and perceptions. **Co-management** of natural resources by resource managers and local stakeholders provides one mechanism to integrate these knowledge systems and perspectives in ways that increase the likelihood of effective policy implementation (see Chapter 4).

Traditional knowledge systems are being eroded by social and technological changes. Many indigenous traditional knowledge systems are maintained orally and are therefore tightly linked to language. There are about 5,000 indigenous languages, half of them in tropical and subtropical forests (de Groot et al. 2005). Many of these languages are threatened by national efforts to assimilate people into one or a few national languages. Language loss and cultural assimilation generally erode traditional knowledge, so efforts to sustain local languages and cultures can be critical to sustaining the knowledge and practices by which people traditionally interacted with ecosystems. Similarly, sustaining opportunities for locally adapted approaches to farming, ranching, and fishing preserves practices that may sustain local use of natural resources (Olsson et al. 2004b). Obviously, many local practices, whether indigenous or otherwise, do not contribute to sustainable management in a modern world, but they nonetheless provide information about perceptions, tradeoffs, and institutions that are a source of resilience for developing new frameworks to sustain social–ecological systems in a rapidly changing world.

Spiritual, Inspirational, and Aesthetic Services

The spiritual, inspirational, and aesthetic services provided by ecosystems are important motivations for conservation and long-term sustainability. "The most common element of all religions throughout history has been the inspiration they have drawn from nature, leading to a belief in non-physical (usually supernatural) beings" (de Groot et al. 2005). These spiritual services provided by ecosystems for both personal reflection and more organized experiences have proven to be a powerful force for conservation. Sacred groves in northeast India and Madagascar, for example, are major reservoirs of biodiversity and places where people maintain their sense of connection with the land in landscapes that are increasingly converted to agriculture to meet the food needs of local people (Ramakrishnan 1992, Elmqvist et al. 2007). Often these sacred groves are maintained and protected by local institutions (see Chapters 6 and 7). Well-meaning national and international efforts to protect these few remaining sites of high conservation value by placing them under national control sometimes undermine local institutions and lead to degradation rather than protection. This underscores the importance of understanding the social context of cultural services, when addressing conservation and sustainability goals (Elmqvist et al. 2007).

The inspirational qualities of landscapes that motivated ancient Greek philosophers, Thoreau's writings, French Impressionist paintings, and Beethoven's symphonies continue to inspire people everywhere through both direct experience and increasingly television, films, and the Internet. This provides natural resource managers with a diverse set of media that can supplement personal experience in reinforcing the human–environment connection (Swanson et al. 2008).

The aesthetic and inspirational properties of landscapes are closely linked. Research suggests that aesthetic preferences are surprisingly similar among people from very different cultural and ecological backgrounds (Ulrich 1983, Kaplan and Kaplan 1989, de Groot et al. 2005). For example, when asked which is more aesthetically pleasing, people generally prefer natural over built environments and park/savanna-like environments over arid or forest environments, regardless of their background. People do differ in aesthetic preferences, of course. Farmers and low-income groups generally prefer human-modified over natural landscapes, whereas city dwellers and high-income groups have an aesthetic preference for natural landscapes. In addition, the view of western Euro-Americans toward wilderness has changed through history from a perception of wilderness as a hostile land until the late seventeenth century toward a more romantic view of wilderness in the eighteenth and nineteenth centuries. Even today, wilderness views are changing as people move to cities and change their patterns of use of remote lands (de Groot et al. 2005). At a time of rapid global change, it seems important to explore potential changes in the spiritual, inspirational, and aesthetic benefits that people derive from ecosystems and the resulting human decisions and actions that influence their environment.

Iconic species are species that symbolize important nature-based societal values. Protection of these species can mobilize public support for protection of values that might otherwise be difficult to quantify and defend as management goals. Polar bears, wolves, Siberian tigers, eagles, and whales, for example, are top predators whose population dynamics are sensitive to habitat fragmentation and to factors that might affect their prey species. Panda bears and spotted owls require ecosystems with structural properties typical of old-growth ecosystems. Ecosystem management that protects the habitat of these species often sustains a multitude of other services.

Recreation and Ecotourism

Recreation and tourism have always been important benefits that people gain from ecosystems, sometimes as rituals and pilgrimages, sometimes just for pleasure and enjoyment. For example, about a billion people (15% of the global population) visit the Ganges River annually. Nature tourism accounts for about 20% of international travel and is increasing 20–30% annually. At a more local scale, people use parks and other ecosystems as important components of daily life. Cultural and nature-based tourism constitutes 3–10% of GDP (gross domestic product) in advanced economies and up to 40% in developing economies. It is *the* main source of foreign currency for at least 38% of countries (de Groot et al. 2005). Clearly there are both personal and economic incentives to manage the recreational opportunities provided by ecosystems in ways that do not degrade over time.

Synergies and Tradeoffs among Ecosystem Services

Ecosystems that maintain their characteristic supporting services provide a broad spectrum of ecosystem services with minimal management effort. At a finer level of resolution, **bundles of services** can be identified that have particularly tight linkages. This creates **synergies** in which management practices that sustain a few key services also sustain other synergistic services. For example, management of fire and grazing in drylands to maintain grass cover minimizes soil erosion (sustaining most supporting services), sustains the capacity to support grazers, and reduces vulnerability to invasion by exotic shrubs (see Chapter 8). Management of fisheries to sustain bottom habitat through restrictions on trawling or to maintain populations of top predators reduces the likelihood of fishery collapse. In general, management that sustains slow variables (soil resource supply, disturbance regime, and functional types of species) sustains a broad suite of ecosystem services. Managers are often tasked with managing one or a few fast variables such as the supply of corn, deer, timber, or water, each of which might be augmented in the short term by policies that reduce the flow of other ecosystem services (**tradeoffs**). However, even these fast variables that are the immediate responsibility of managers are best sustained over the long term through attention to slow variables that govern the flow of these and a broader suite of services.

Tradeoffs most frequently emerge when people seek to enhance the flow of one or a few services (Table 2.4). For example, agricultural production of food typically requires the replacement of some naturally occurring ecosystem by a crop with the corresponding loss of some regulatory and cultural services. Management of forests to produce timber as a crop (short rotations of a single species) involves similar tradeoffs between the efficient production of a single species and the cultural and regulatory services provided by more diverse forests (see Chapter 7). Many management choices involve **temporal tradeoffs** between short-term benefits and long-term capacity of ecosystems to provide services to future generations. Management of lands to provide multiple services (i.e., multiple-use management) requires identification of tradeoffs among services and decisions that reflect societal choices among the costs and benefits associated with particular options.

Given the large number of essential services provided by ecosystems (e.g., about 40 identified by the MEA), which services should receive highest management priority? One approach is to sustain supporting services that underpin most other ecosystem services, as described earlier. During times of rapid social or environmental change, however, inevitable tradeoffs arise that make objective decisions difficult. Under these circumstances, it may prove valuable to identify **critical ecosystem services**, i.e., those services that (1) society depends on or values; (2) are undergoing (or are vulnerable to) rapid change; and/or (3) have no technological or off-site substitutes (Ann Kinzig, pers.com.). Stakeholders often disagree about which ecosystem services are most critical, so identification of these services benefits from broad stakeholder participation (Fischer 1993, Shindler and Cramer 1999).

Facing the Realities of Ecosystem Management

Sustainability: Balancing Short-Term and Long-Term Needs

Sustainability requires the use of the environment and resources to meet the needs of the present without compromising the ability of future generations to meet their own needs (WCED 1987; see Chapter 1). Balancing the temporal tradeoff between short-term desires and long-term opportunities is a fundamental challenge for ecosystem stewards. The demands by current stakeholders are always more certain

Table 2.4. Examples of synergies and tradeoffs among ecosystem services.

Synergies
Supporting services: maintenance of soil resources, biodiversity, carbon, water, and nutrient cycling
Water resources: water provisioning, maintenance of soil resources, regulation of water quantity and quality by maintaining intact ecosystems, flood prevention
Food/timber production capacity: food/timber provisioning, maintenance of soil resources, genetic diversity of crops/forest
Climate regulation: maintenance of soil resources, regulation of water quantity by maintaining ecosystem structure
Cultural services: maintenance of supporting services (including biodiversity), suite of cultural services

Tradeoffs
Efficiency vs sustainability:
Short-term vs long-term supply of services
Food production vs services provided by intact natural ecosystems
Intensive vs extensive management to provide food or fiber
Recreation vs traditional cultural services

and outspoken than those of future generations, creating pressures to manage resources for short-term benefits. Ecosystem stewardship implies, however, a responsibility to sustain ecosystems so that future generations can meet their needs. How do we do this, if we do not know what future generations will want and need? The simplest approach is to sustain the **inclusive wealth** of the system, i.e., the total capital (natural, manufactured, human, and social) that constitutes the productive base available to society (see Chapter 1). Since natural and social capital are the most difficult components of capital to renew, once they are degraded, these are the most critical components of inclusive wealth to sustain. Social capital is discussed in Chapter 3; here we focus on natural capital.

Future generations depend most critically on those components of natural capital that cannot be regenerated or created over time scales of years to decades. These always include (1) soil resources that govern the productive potential of the land; (2) biodiversity that constitutes the biological reservoir of future options; (3) regulation of the climate system that governs future environment; and (4) cultural identity and inspirational services that provide a connection between people and the land or sea. Earlier we described strategies for sustaining each of these classes of ecosystem services. Other more specific needs of future generations, such as specific types of food or recreation, are less certain and therefore less critical to sustain in precisely their current form.

At intermediate time scales (e.g., years to decades), it is more plausible to assume that the needs of people in the future will be similar to those of today, leading to a more constrained (and therefore more precisely defined) set of tradeoff decisions. Depletion of fossil groundwater to meet irrigation needs today reduces the water available in the future—for example, for domestic water consumption. Forests or fish stocks that are harvested more rapidly than they can regenerate reduce the services in coming years to decades. **Maximum sustained yield** was a policy that sought to maximize the harvest of forests, fish, and wildlife to meet current needs, while sustaining the potential to continue these yields in the future. Although intended to prevent overharvest, these policies often proved unsustainable because of overly optimistic assumptions about the current status and recovery potential of managed populations (see Chapters 7 and 10).

Economists often **discount** (i.e., reduce) estimates of the future value of manufactured goods and services because of opportunity costs (i.e., the opportunities foregone to spend the money on current goods). Discounting the future is *not* appropriate, however, for temporal tradeoffs involving those ecosystem services that cannot be restored once they are lost, for example, fossil ground water, biodiversity, or sacred groves in a highly modified landscape (Heal 2000). These services will be at least as valuable, and perhaps much more valuable, in the future than they are today (Heal 2000).

Multiple Use: Negotiating Conflicting Desires of Current Stakeholders

Tradeoffs among ecosystem services valued by society generate frequent conflicts about management of ecosystem services. Clearing forests to provide new agricultural land, for example, represents a tradeoff between the benefits of harvested timber and increased potential for food production and the loss of other services previously provided by the forest such as regulation of water quality and climate. Recreational use of an area by snow machines and wilderness skiers creates tradeoffs between the services sought by each group. There are also tradeoffs in allocation of fresh water among natural desert landscapes, agriculturalists, ranchers, and urban residents. These are just a few of the many tradeoffs faced by ecosystem stewards. How does a manager balance these tradeoffs or choose among them? There is no simple answer to this question, but the following questions raise issues that warrant consideration. What are the gains and losses in *bundles* of ecosystem services associated with alternative management options? How much weight do we give to gains and losses that are uncertain but potentially large? Are there new options that might provide many of the same benefits but reduce potential losses in services? Who wins and who loses? Can conflicts be reduced by landscape approaches that separate in time or space the services that different stakeholders seek to sustain? The social dimensions of tradeoffs among ecosystem services are at least as important as the ecological ones, so we address these questions in a social–ecological context in Chapter 4. We then provide numerous examples of challenges and strategies for managing synergies and tradeoffs in Chapters 6–14 and summarize the lessons learned in Chapter 15.

Adjusting to Change

Managing ecosystems in the context of dynamic and uncertain change is an integral component of resilience-based ecosystem stewardship. Many changes, such as those associated with interannual variability in weather, cycles of disturbance and succession, and economic fluctuations are widely accepted as normal components of the internal variability of social–ecological systems. Facilitating change is sometimes an explicit management objective, for example, in sustainable development projects, where the goal is to enhance well-being, while sustaining the capacity of ecosystems to provide services (WCED 1987). In reclamation and restoration projects, the goal is to enhance ecological integrity, while sustaining the social and economic benefits accrued from development. In still other cases, regional change may be driven by exogenous changes in climate, introduction of exotic species, human migration, and/or globalization of culture and economy. Many of these latter changes are persistent trends that will inevitably cause changes in social–ecological systems (see Chapters 1 and 5). The critical implications of managing change include (1) identifying the persistent changes that are occurring or might occur and assessing their plausible trajectories; (2) understanding that attempts to prevent change or to maintain indefinitely the current flow of ecosystem goods (e.g., production of cattle or pulpwood) may be unrealistic; and (3) continuously reassessing the social–ecological long- and short-term goals of ecosystem stewardship in light of the challenges and opportunities associated with change.

Identifying persistent (directional) trends in important controls such as climate and human demography and projecting plausible trends into the future is often a more realistic basis for planning than assuming that the future will be like the past. Although the future can never be predicted with certainty, planning in the context of expected changes can be helpful. Some of these changes may be difficult for individual managers to alter (e.g., climate change), but the trajectory of other changes, for example, in sustainable development or ecological restoration projects, can be strongly influenced by management decisions because these decisions create legacies and path dependencies that influence future outcomes. That, after all, is the purpose of management. In general, those changes that sustain or enhance natural and social capital will likely benefit society [see Sustainability (this chapter), Chapters 4 and 5].

One limitation of maximum sustained yield as a management paradigm is that it usually fails to account for variability and change (particularly persistent directional changes) in those yield-influencing processes that managers cannot control (see Chapter 7). Recognition of this problem was one of the primary motivations for a move toward ecosystem management as a more comprehensive approach to natural resource management.

Ecosystems are not the only parts of social–ecological systems to undergo persistent directional changes. Changes in societal goals are essential to consider. This requires active communication and engagement with a variety of stakeholders to enable them to participate meaningfully in the management process (see Chapters 4 and 5).

Regulations and Politics: Practicing the Art of the Possible

Many of greatest challenges faced by resource stewards reflect the social and institutional environment in which they work. Differences among stakeholders in goals and norms, power relationships, regulatory and financial constraints, personalities, and other social and institutional factors often dominate the day-to-day challenges faced by resource managers. Social processes are therefore an integral component of ecosystem stewardship (see Chapters 3 and 4). At times of rapid social or environmental change, frameworks for managing natural resources may become dysfunctional, requiring communication with a broader set of stakeholders and openness to new ways of doing things (see Chapter 5).

Summary

Resilience-based ecosystem stewardship involves responding to and shaping change in social–ecological systems to sustain the supply and opportunities for use of ecosystem services by society. The capacity of ecosystems to supply these services depends on underlying supporting services, such as the supply of soil resources; cycling of water, carbon, and nutrients; and the maintenance of biological diversity at stand and landscape scales. The resilience of these supporting services depends on maintaining a disturbance regime to which local organisms are adapted. Directional changes in these supporting services inevitably alter the capacity of ecosystems to provide services to society. An understanding of these linkages provides a basis for not only sustaining the services provided by intact ecosystems but also enhancing the capacity of degraded ecosystems to provide these services by manipulating pathways for ecosystem renewal.

Both managers and the public generally recognize the value of provisioning services such as water, food, fiber, and fuelwood. It is therefore not surprising that the links between supporting and provisioning services are generally well understood by ecosystem managers and local resource users. This provides a strong local and scientific basis to manage ecosystems sustainably for these goods. In contrast, regulatory services (e.g., the regulation of climate and air quality, water quantity and quality, pollination services, and risks of disease and of natural hazards), although generally recognized as important by society, are often overlooked when discussions focus on the short-term supply of provisioning services. Some of the greatest opportunities and challenges in ecosystem management involve the stewardship of ecosystems to provide bundles of services that both meet the short-term needs of society and sustain regulatory services that are essential for their secure supply at larger temporal and spatial scales.

The long-term well-being of society depends substantially on the cultural services provided by ecosystems, including aesthetic, spiritual, and recreational values. These values often motivate support for sustainable stewardship practices, if the basic material needs of society are met. Understanding this hierarchy of societal needs, which provides the social context for ecosystem stewardship is the central topic of Chapter 3.

Review Questions

1. What slow variables are usually most important in sustaining ecosystem services? How are these likely to be altered by climate change in the ecosystem where you live? What are the likely societal consequences of these changes?
2. Describe a strategy for enhancing the supply of ecosystem services for a degraded ecosystem such as an abandoned mine or an overgrazed pasture.
3. What are the advantages and disadvantages of managing an ecosystem to maximize the production of a specific resource such as trees or fish? How would your management strategy differ if your goal were to maximize harvest over the short term (e.g., 5 years) vs the long term (several centuries). How might directional social or environmental change influence your long-term strategy?
4. If the future is uncertain and you do not know what future generations will want or need, how can you manage ecosystems sustainably to meet these needs?
5. Explain the mechanisms by which biodiversity influences supporting services, provisioning services, and cultural services.

Additional Readings

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