CHAPTER 3

Ecosystem functions and services

Cagan H. Sekercioglu

In our increasingly technological society, people give little thought to how dependent they are on the proper functioning of ecosystems and the crucial services for humanity that flow from them. Ecosystem services are "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997); in other words, "the set of ecosystem functions that are useful to humans" (Kremen 2005). Although people have been long aware that natural ecosystems help support human societies, the explicit recognition of "ecosystem services" is relatively recent (Ehrlich and Ehrlich 1981a; Mooney and Ehrlich 1997).

Since the entire planet is a vast network of integrated ecosystems, ecosystem services range from global to microscopic in scale (Table 3.1; Millennium Ecosystem Assessment 2005a). Ecosystems purify the air and water, generate oxygen, and stabilize our climate. Earth would not be fit for our survival if it were not for plants that have created and maintained a suitable atmosphere. Organisms decompose and detoxify detritus, preventing our civilization from being buried under its own waste. Other species help to create the soils on which we grow our food, and recycle the nutrients essential to agriculture. Myriad creatures maintain these soils, play key roles in recycling nutrients, and by so doing help to mitigate erosion and floods. Thousands of animal species pollinate and fertilize plants, protect them from pests, and disperse their seeds. And of course, humans use and trade thousands of plant, animal and microorganism species for food, shelter, medicinal, cultural, aesthetic and many other purposes. Although most people may not know what an ecosystem is, the proper functioning of the world's ecosystems is critical to human survival, and understanding the basics of ecosystem services is essential. Entire volumes have been written on ecosystem services (National Research Council 2005; Daily 1997), culminating in a formal, in-depth, and global overview by hundreds of scientists: the *Millennium Ecosystem Assessment* (2005a). It is virtually impossible to list all the ecosystem services let alone the natural products that people directly consume, so this discussion presents a brief introduction to ecosystem function and an overview of critical ecosystem services.

3.1 Climate and the Biogeochemical Cycles

Ecosystem services start at the most fundamental level: the creation of the air we breathe and the supply and distribution of water we drink. Through photosynthesis by bacteria, algae, plankton, and plants, atmospheric oxygen is mostly generated and maintained by ecosystems and their constituent species, allowing humans and innumerable other oxygen-dependent organisms to survive. Oxygen also enables the atmosphere to "clean" itself via the oxidation of compounds such as carbon monoxide (Sodhi *et al.* 2007) and another form of oxygen in the ozone layer, protects life from the sun's carcinogenic, ultraviolet (UV) rays.

Global biogeochemical cycles consist of "the transport and transformation of substances in the environment through life, air, sea, land, and ice" (Alexander *et al.* 1997). Through these cycles, the planet's climate, ecosystems, and creatures

Table 3.1 Ecosystem services, classified according to the Millennium Ecosystem Assessment (2003), and their ecosystem service providers. 'Functional units' refer to the unit of study for assessing functional contributions (ʃik) of ecosystem service providers; spatial scale indicates the scale(s) of operation of the service. Assessment of the potential to apply this conceptual framework to the service is purposefully conservative and is based on the degree to which the contributions of individual species or communities can currently be quantified (Kremen 2005).

Service	Ecosystem service providers/ trophic level	Functional units	Spatial scale	Potential to apply this conceptual framework for ecological study
Aesthetic, cultural	All biodiversity	Populations, species, communities, ecosystems	Local-global	Low
Ecosystem goods	Diverse species	Populations, species, communities, ecosystems	Local-global	Medium
UV protection	Biogeochemical cycles, micro-organisms, plants	Biogeochemical cycles, functional groups	Global	Low
Purification of air	Micro-organisms, plants	Biogeochemical cycles, populations, species, functional groups	Regional-global	Medium (plants)
Flood mitigation	Vegetation	Communities, habitats	Local-regional	Medium
Drought mitigation	Vegetation	Communities, habitats	Local-regional	Medium
Climate stability	Vegetation	Communities, habitats	Local-global	Medium
Pollination	Insects, birds, mammals	Populations, species, functional groups	Local	High
Pest control	Invertebrate parasitoids and predators and vertebrate predators	Populations, species, functional groups	Local	High
Purification of water	Vegetation, soil micro-organisms, aquatic micro-organisms, aquatic invertebrates	Populations, species, functional groups, communities, habitats	Local-regional	Medium to high*
Detoxification and decomposition of wastes	Leaf litter and soil invertebrates, soil micro-organisms, aquatic micro-organisms	Populations, species, functional groups, communities, habitats	Local-regional	Medium
Soil generation and soil fertility	Leaf litter and soil invertebrates, soil micro-organisms, nitrogen-fixing plants, plant and animal production of waste products	Populations, species, functional groups	Local	Medium
Seed dispersal	Ants, birds, mammals	Populations, species, functional groups	Local	High

* Waste-water engineers 'design' microbial communities; in turn, wastewater treatments provide ideal replicated experiments for ecological work (Graham and Smith 2004 in Kremen 2005).

are tightly linked. Changes in one component can have drastic effects on another, as exemplified by the effects of deforestation on climatic change (Phat *et al.* 2004). The hydrologic cycle is one that most immediately affects our lives and it is treated separately below.

As carbon-based life forms, every single organism on our planet is a part of the global carbon cycle. This cycle takes place between the four main reservoirs of carbon: carbon dioxide (CO_2) in the atmosphere; organic carbon compounds within organisms; dissolved carbon in water bodies; and carbon compounds inside the earth as part of soil, limestone (calcium carbonate), and buried organic matter like coal, natural gas, peat, and petroleum (Alexander *et al.* 1997). Plants play a major role in fixing atmospheric CO_2 through photosynthesis and most terrestrial carbon storage occurs in forest trees (Falkowski *et al.* 2000). The global carbon cycle has been disturbed by about 13% compared to the pre-industrial era, as opposed to 100% or more for nitrogen, phosphorous, and sulfur cycles (Falkowski *et al.* 2000). Given the dominance of carbon in shaping life and in regulating climate, however, this perturbation has already been enough to lead to significant climate change with worse likely to come in the future [IPCC (Intergovernmental Panel on Climate Change) 2007].

Because gases like CO_2, methane (CH_4), and nitrous oxide (N_2O) trap the sun's heat, especially the long-wave infrared radiation that's emitted by the warmed planet, the atmosphere creates a natural "greenhouse" (Houghton 2004). Without this greenhouse effect, humans and most other organisms would be unable to survive, as the global mean surface temperature would drop from the current 14° C to –19° C (IPCC 2007). Ironically, the ever-rising consumption of fossil fuels during the industrial age and the resultant increasing emission of greenhouse gases have created the opposite problem, leading to an increase in the magnitude of the greenhouse effect and a consequent rise in global temperatures (IPCC 2007). Since 1750, atmospheric CO_2 concentrations have increased by 34% (Millennium Ecosystem Assessment 2005a) and by the end of this century, average global temperature is projected to rise by 1.8°–6.4° C (IPCC 2007). Increasing deforestation and warming both exacerbate the problem as forest ecosystems switch from being major carbon sinks to being carbon sources (Phat *et al.* 2004; IPCC 2007). If fossil fuel consumption and deforestation continue unabated, global CO_2 emissions are expected to be about 2–4 times higher than at present by the year 2100 (IPCC 2007). As climate and life have coevolved for billions of years and interact with each other through various feedback mechanisms (Schneider and Londer 1984), rapid climate change would have major consequences for the planet's life-support systems. There are now plans under way for developed nations to finance the conservation of tropical forests in the developing world so that these forests can continue to provide the ecosystem service of acting as carbon sinks (Butler 2008).

Changes in ecosystems affect nitrogen, phosphorus, and sulfur cycles as well (Alexander *et al.* 1997; Millennium Ecosystem Assessment 2005b; Vitousek *et al.* 1997). Although nitrogen in its gaseous form (N_2) makes up 80% of the atmosphere, it is only made available to organisms through nitrogen fixation by cyanobacteria in aquatic systems and on land by bacteria and algae that live in the root nodules of lichens and legumes (Alexander *et al.* 1997). Eighty million tons of nitrogen every year are fixed artificially by industry to be used as fertilizer (Millennium Ecosystem Assessment 2005b). However, the excessive use of nitrogen fertilizers can lead to nutrient overload, eutrophication, and elimination of oxygen in water bodies. Nitrogen oxides, regularly produced as a result of fossil fuel combustion, are potent greenhouse gases that increase global warming and also lead to smog, breakdown of the ozone layer, and acid rain (Alexander *et al.* 1997). Similarly, although sulfur is an essential element in proteins, excessive sulfur emissions from human activities lead to sulfuric acid smog and acid rain that harms people and ecosystems alike (Alexander *et al.* 1997).

Phosphorous (P) scarcity limits biological nitrogen fixation (Smith 1992). In many terrestrial ecosystems, where P is scarce, specialized symbiotic fungi (mycorrhizae) facilitate P uptake by plants (Millennium Ecosystem Assessment 2005b). Even though P is among the least naturally available of major nutrients, use of phosphorous in artificial fertilizers and runoff from animal husbandry often also leads to eutrophication in aquatic systems (Millenium Ecosystem Assessment 2005b). The mining of phosphate deposits and their addition to terrestrial ecosystems as fertilizers represents a six fold increase over the natural rate of mobilization of P by the weathering of phosphate rock and by plant activity (Reeburgh 1997). P enters aquatic ecosystems mainly through erosion, but no-till agriculture and the use of hedgerows can substantially reduce the rate of this process (Millenium Ecosystem Assessment 2005a).

3.2 Regulation of the Hydrologic Cycle

One of the most vital and immediate services of ecosystems, particularly of forests, rivers and wetlands, is the provisioning and regulation of water resources. These services provide a vast range of benefits from spiritual to life-saving, illustrated by the classification of hydrologic services into five broad categories by Brauman *et al.* (2007): improvement of extractive water supply, improvement of in-stream water supply, water damage mitigation, provision of water-related cultural services, and water-associated supporting services (Figure 3.1). Although 71% of the planet is covered by water, most of this is seawater unfit for drinking or agriculture (Postel *et al.* 1996). Fresh water not locked away in glaciers and icecaps constitutes 0.77% of the planet's water (Shiklomanov 1993). To provide sufficient fresh water to meet human needs via industrial desalination (removing the salt from seawater) would cost US$3 000 billion per year (Postel and Carpenter 1997).

Quantity, quality, location, and timing of water provision determine the scale and impact of hydrologic services (Brauman *et al.* 2007). These attributes can make the difference between water as a blessing (e.g. drinking water) or a curse (e.g. floods). Water is constantly redistributed through the hydrologic cycle. Fresh water comes down as precipitation, collects in water bodies or is absorbed by the soil and plants. Some of the water flows unutilized into the sea or seeps into

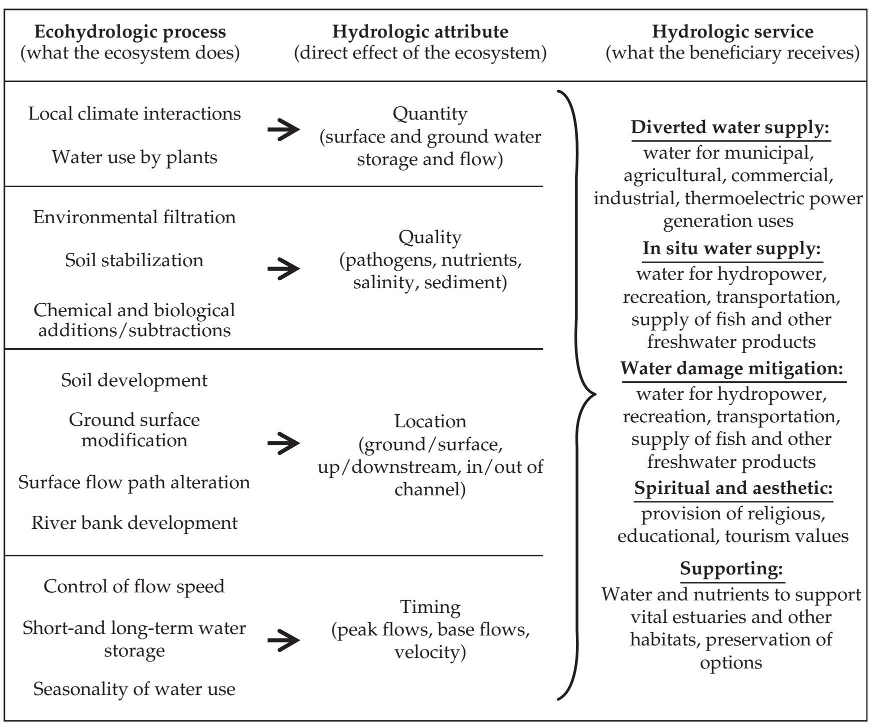

Figure 3.1 The effects of hydrological ecosystem processes on hydrological services. Reprinted from Brauman *et al.* (2007).

underground aquifers where it can remain for millennia unless extracted by people; mining this "fossil" groundwater is often unsustainable and is a serious problem in desert regions like Libya (Millennium Ecosystem Assessment 2005c). The cycle is completed when water vapor is released back into the atmosphere either through evaporation from land and water bodies or by being released from plants (transpiration) and other organisms. Rising environmental temperatures are expected to increase evaporation and consequent precipitation in some places and raise the likelihood of droughts and fires in other places, both scenarios that would have major consequences for the world's vegetation (Wright 2005). These changes in turn can lead to further climatic problems, affecting agriculture and communities worldwide. Ecosystems, particularly forests, play major roles in the regulation of the hydrologic cycle and also have the potential to moderate the effects of climate change. Tropical forests act as heat and humidity pumps, transferring heat from the tropics to the temperate zones and releasing water vapor that comes back as rain (Sodhi *et al.* 2007). Extensive tropical deforestation is expected to lead to higher temperatures, reduced precipitation, and increased frequency of droughts and fires, all of which are likely to reduce tropical forest cover in a positive feedback loop (Sodhi *et al.* 2007).

Forest ecosystems alone are thought to regulate approximately a third of the planet's watersheds on which nearly five billion people rely (Millennium Ecosystem Assessment 2005c). With increasing human population and consequent water pollution, fresh water is becoming an increasingly precious resource, especially in arid areas like the Middle East, where the scarcity of water is likely to lead to increasing local conflicts in the 21st century (Klare 2001; Selby 2005). Aquatic ecosystems, in addition to being vital sources of water, fish, waterfowl, reeds, and other resources, also moderate the local climate and can act as buffers for floods, tsunamis, and other water incursions (Figure 3.1). For example, the flooding following Hurricane Katrina would have done less damage if the coastal wetlands surrounding New Orleans had had their original extent (Day *et al.* 2007). The impact of the 24 December 2004 tsunami in Southeast Asia would have been reduced if some of the hardest-hit areas had not been stripped of their mangrove forests (Dahdouh-guebas *et al.* 2005; Danielsen *et al.* 2005). These observations support analytical models in which thirty "waru" trees (*Hibiscus tiliaceus*) planted along a 100 m by 1 meter band reduced the impact of a tsunami by 90% (Hiraishi and Harada 2003), a solution more effective and cheaper than artificial barriers.

Hydrologic regulation by ecosystems begins with the first drop of rain. Vegetation layers, especially trees, intercept raindrops, which gradually descend into the soil, rather than hitting it directly and leading to erosion and floods. By intercepting rainfall and promoting soil development, vegetation can modulate the timing of flows and potentially reduce flooding. Flood mitigation is particularly crucial in tropical areas where downpours can rapidly deposit enormous amounts of water that can lead to increased erosion, floods, and deaths if there is little natural forest to absorb the rainfall (Bradshaw *et al.* 2007). Studies of some watersheds have shown that native forests reduced flood risks only at small scales, leading some hydrologists to question directly connecting forest cover to flood reduction (Calder and Aylward 2006). However, in the first global-scale empirical demonstration that forests are correlated with flood risk and severity in developing countries, Bradshaw *et al.* (2007) estimated that a 10% decrease in natural forest area would lead to a flood frequency increase between 4% and 28%, and to a 4–8% increase in total flood duration at the country scale. Compared to natural forests, however, afforestation programs or forest plantations may not reduce floods, or may even increase flood volume due to road construction, soil compaction, and changes in drainage regimes (Calder and Aylward 2006). Non-native plantations can do more harm than good, particularly when they reduce dry season water flows (Scott *et al.* 2005).

Despite covering only 6% of the planet's surface, tropical forests receive nearly half of the world's rainfall, which can be as much as 22 500 mm during five months of monsoon season in

India (Myers 1997). In Southeast Asia, an intact old-growth dipterocarp forest intercepts at least 35% of the rainfall, while a logged forest intercepts less than 20%, and an oil palm (*Elaeis* spp.) plantation intercepts only 12% (Ba 1977). As a consequence, primary forest can moderate seasonal extremes in water flow and availability better than more intensive land uses like plantation forestry and agriculture. For example, primary forest in Ivory Coast releases three to five times as much water at the end of the dry season compared to a coffee plantation (Dosso 1981). However, it is difficult to make generalizations about hydrologic response in the tropics. For example, local soil and rainfall patterns can result in a 65-fold variation in tropical natural sedimentation rates (Bruijnzeel 2004). This underlines the importance of site-specific studies in the tropics, but most hydrologic studies of ecosystems have taken place in temperate ecosystems (Brauman *et al.* 2007).

3.3 Soils and Erosion

Without forest cover, erosion rates skyrocket, and many countries, especially in the tropics, lose astounding amounts of soil to erosion. Worldwide, 11 million km^2 of land (the area of USA and Mexico combined) are affected by high rates of erosion (Millennium Ecosystem Assessment 2005b). Every year about 75 billion tons of soil are thought to be eroded from terrestrial ecosystems, at rates 13–40 times faster than the average rate of soil formation (Pimentel and Kounang 1998). Pimentel *et al.* (1995) estimated that in the second half of the 20th century about a third of the world's arable land was lost to erosion. This means losing vital harvests and income (Myers 1997), not to mention losing lives to malnutrition and starvation. Soil is one of the most critical but also most underappreciated and abused elements of natural capital, one that can take a few years to lose and millennia to replace. A soil's character is determined by six factors: topography, the nature of the parent material, the age of the soil, soil organisms and plants, climate, and human activity (Daily *et al.* 1997). For example, in the tropics, farming can result in the loss of half the soil nutrients in less than a decade (Bolin and Cook 1983), a loss that can take centuries to restore. In arid areas, the replacement of native deep-rooted plants with shallow-rooted crop plants can lead to a rise in the water table, which can bring soil salts to the surface (salinization), cause waterlogging, and consequently result in crop losses (Lefroy *et al.* 1993).

Soil provides six major ecosystem services (Daily *et al.* 1997):

- Moderating the hydrologic cycle.
- Physical support of plants.
- Retention and delivery of nutrients to plants.
- Disposal of wastes and dead organic matter.
- Renewal of soil fertility.
- Regulation of major element cycles.

Every year enough rain falls to cover the planet with one meter of water (Shiklomanov 1993), but thanks to soil's enormous water retention capacity, most of this water is absorbed and gradually released to feed plants, underground aquifers, and rivers. However, intensive cultivation, by lowering soil's organic matter content, can reduce this capacity, leading to floods, erosion, pollution, and further loss of organic matter (Pimentel *et al.* 1995).

Soil particles usually carry a negative charge, which plays a critical role in delivering nutrient cations (positively-charged ions) like Ca2+, K+, Na+, NH4+, and Mg2+ to plants (Daily *et al.* 1997). To deliver these nutrients without soil would be exceedingly expensive as modern hydroponic (water-based) systems cost more than US$250 000 per ha (Canada's Office of Urban Agriculture 2008; Avinash 2008). Soil is also critical in filtering and purifying water by removing contaminants, bacteria, and other impurities (Fujii *et al.* 2001). Soils harbor an astounding diversity of microorganisms, including thousands of species of protozoa, antibiotic-producing bacteria (which produce streptomycin) and fungi (producing penicillin), as well as myriad invertebrates, worms and algae (Daily *et al.* 1997). These organisms play fundamental roles in decomposing dead matter, neutralizing deadly pathogens, and recycling waste into valuable nutrients. Just the nitrogen fixed by soil organisms like

Rhizobium bacteria amounts to about 100 million metric tons per year (Schlesinger 1991). It would cost at least US$320 billon/year to replace natural nitrogen fertilization with fertilizers (Daily *et al.* 1997).

As the accelerating release of CO_2, N_2O (Nitrous Oxide), methane and other greenhouse gases increasingly modifies climate (IPCC 2007), the soil's capacity to store these molecules is becoming even more vital. Per area, soil stores 1.8 times the carbon and 18 times the nitrogen that plants alone can store (Schlesinger 1991). For peatlands, soil carbon storage can be 10 times greater than that stored by the plants growing on it and peatland fires release massive amounts of CO_2 into the atmosphere (Page and Rieley 1998).

Despite soil's vital importance, 17% of the Earth's vegetated land surface (Oldeman 1998) or 23% of all land used for food production [FAO (Food and Agriculture Organization of the United Nations) 1990] has experienced soil degradation since 1945. Erosion is the best-known example of the disruption of the sedimentary cycle. Although erosion is responsible for releasing nutrients from bedrock and making them available to plants, excessive wind and water erosion results in the removal of top soil, the loss of valuable nutrients, and desertification. The direct costs of erosion total about US$250 billion per year and the indirect costs (e.g. siltation, obsolescence of dams, water quality declines) approximately $150 billion per year (Pimentel *et al.* 1995). Sufficient preventive measures would cost only 19% of this total (Pimentel *et al.* 1995).

The loss of vegetative cover increases the erosional impact of rain. In intact forests, most rain water does not hit the ground directly and tree roots hold the soil together against being washed away (Brauman *et al.* 2007), better than in logged forest or plantations (Myers 1997) where roads can increase erosion rates (Bruijnzeel 2004). The expansion of farming and deforestation have doubled the amount of sediment discharged into the oceans. Coral reefs can experience high mortality after being buried by sediment discharge (Pandolfi *et al.* 2003; Bruno and Selig 2007). Wind erosion can be particularly severe in desert ecosystems, where even small increases in vegetative cover (Hupy 2004) and reduced tillage practices (Gomes *et al.* 2003) can lessen wind erosion substantially. Montane areas are especially prone to rapid erosion (Milliman and Syvitski 1992), and revegetation programs are critical in such ecosystems (Vanacker *et al.* 2007). Interestingly, soil carbon buried in deposits resulting from erosion, can produce carbon sinks that can offset up to 10% of the global fossil fuel emissions of CO_2 (Berhe *et al.* 2007). However, erosion also lowers soil productivity and reduces the organic carbon returned to soil as plant residue (Gregorich *et al.* 1998). Increasing soil carbon capacity by 5–15% through soil-friendly tillage practices not only offsets fossil-fuel carbon emissions by a roughly equal amount but also increases crop yields and enhances food security (Lal 2004). An increase of one ton of soil carbon pool in degraded cropland soils may increase crop yield by 20 to 40 kilograms per ha (kg/ha) for wheat, 10 to 20 kg/ha for maize, and 0.5 to 1 kg/ha for cowpeas (Lal 2004).

3.4 Biodiversity and Ecosystem Function

The role of biodiversity in providing ecosystem services is actively debated in ecology. The diversity of functional groups (groups of ecologically equivalent species (Naeem and Li 1997)), is as important as species diversity, if not more so (Kremen 2005), and in most services a few dominant species seem to play the major role (Hooper *et al.* 2005). However, many other species are critical for ecosystem functioning and provide "insurance" against disturbance, environmental change, and the decline of the dominant species (Tilman 1997; Ricketts *et al.* 2004; Hobbs *et al.* 2007). As for many other ecological processes, it was Charles Darwin who first wrote of this, noting that several distinct genera of grasses grown together would produce more plants and more herbage than a single species growing alone (Darwin 1872). Many studies have confirmed that increased biodiversity improves ecosystem functioning in plant communities (Naeem and Li 1997; Tilman 1997). Different plant species capture different resources, leading to greater efficiency and higher productivity (Tilman *et al.* 1996). Due to the

Box 3.1 The costs of large-mammal extinctions
Robert M. Pringle

When humans alter ecosystems, large mammals are typically the first species to disappear. They are hunted for meat, hides, and horns; they are harassed and killed if they pose a threat; they require expansive habitat; and they are susceptible to diseases, such as anthrax, rinderpest, and distemper, that are spread by domestic animals. Ten thousand years ago, humans played at least a supporting, if not leading, role in extinguishing most of the large mammals in the Americas and Australia. Over the last 30 years, we have extinguished many large-mammal populations (and currently threaten many more) in Africa and Asia—the two continents that still support diverse assemblages of these charismatic creatures.

The ecological and economic consequences of losing large-mammal populations vary depending on the location and the ecological role of the species lost. The loss of carnivores has induced trophic cascades: in the absence of top predators, herbivores can multiply and deplete the plants, which in turn drives down the density and the diversity of other species (Ripple and Beschta 2006). Losing large herbivores and their predators can have the opposite effect, releasing plants and producing compensatory increases in the populations of smaller herbivores (e.g. rodents: Keesing 2000) and their predators (e.g. snakes: McCauley *et al.* 2006). Such increases, while not necessarily detrimental themselves, can have unpleasant consequences (see below).

Many species depend on the activities of particular large mammal species. Certain trees produce large fruits and seeds apparently adapted for dispersal by large browsers (Guimarães *et al.* 2008). Defecation by large mammals deposits these seeds and provides food for many dung beetles of varying degrees of specialization. In East Africa, the disturbance caused by browsing elephants creates habitat for tree-dwelling lizards (Pringle 2008), while the total loss of large herbivores dramatically altered the character of an ant-plant symbiosis via a complex string of species interactions (Palmer *et al.* 2008).

Box 3.1 Figure 1 White-footed mice (*Peromyscus leucopus*, shown with an engorged tick on its ear) are highly competent reservoirs for Lyme disease. When larger mammals disappear, mice often thrive, increasing disease risk. Photograph courtesy of Richard Ostfeld Laboratory.

Box 3.1 Figure 2 Ecotourists gather around a pair of lions in Tanzania's Ngorongoro Crater. Ecotourism is one of the most powerful driving forces for biodiversity conservation, especially in tropical regions where money is short. But tourists must be managed in such a way that they do not damage or deplete the very resources they have traveled to visit. Photograph by Robert M. Pringle

These examples and others suggest that the loss of large mammals may precipitate extinctions of other taxa and the relationships among them, thus decreasing the diversity of both species and interactions. Conversely, protecting the large areas needed to conserve large mammals may often serve to conserve the greater diversity of smaller organisms—the so-called umbrella effect.

The potential economic costs of losing large mammals also vary from place to place. Because

continues

Box 3.1 (Continued)

cattle do not eat many species of woody plants, the loss of wildlife from rangelands can result in bush encroachment and decreased pastoral profitability. Because some rodents and their parasites are reservoirs and vectors of various human diseases, increases in rodent densities may increase disease transmission (Ostfeld and Mills 2007; Box 3.1 Figure 1). Perhaps most importantly, because large mammals form the basis of an enormous tourism industry, the loss of these species deprives regions of an important source of future revenue and foreign exchange (Box 3.1 Figure 2).

Arguably, the most profound cost of losing large mammals is the toll that it takes on our ability to relate to nature. Being large mammals ourselves, we find it easier to identify and sympathize with similar species—they behave in familiar ways, hence the term "charismatic megafauna." While only a handful of large mammal species have gone globally extinct in the past century, we are dismantling many species population by population, pushing them towards extinction. At a time when we desperately need to mobilize popular support for conservation, the loss over the next 50 years of even a few emblematic species—great apes in central Africa, polar bears in the arctic, rhinoceroses in Asia—could deal a crippling blow to efforts to salvage the greater portion of biodiversity.

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"sampling-competition effect" the presence of more species increases the probability of having a particularly productive species in any given environment (Tilman 1997). Furthermore, different species' ecologies lead to complementary resource use, where each species grows best under a specific range of environmental conditions, and different species can improve environmental conditions for other species (facilitation effect; Hooper *et al.* 2005). Consequently, the more complex an ecosystem is, the more biodiversity will increase ecosystem function, as more species are needed to fully exploit the many combinations of environmental variables (Tilman 1997). More biodiverse ecosystems are also likely to be more stable and more efficient due to the presence of more pathways for energy flow and nutrient recycling (Macarthur 1955; Hooper *et al.* 2005; Vitousek and Hooper 1993; Worm *et al.* 2006).

Greenhouse and field experiments have confirmed that biodiversity does increase ecosystem productivity, while reducing fluctuations in productivity (Naeem *et al.* 1995; Tilman *et al.* 1996). Although increased diversity can increase the population fluctuations of individual species, diversity is thought to stabilize overall ecosystem functioning (Chapin *et al.* 2000; Tilman 1996) and make the ecosystem more resistant to perturbations (Pimm 1984). These hypotheses have been confirmed in field experiments, where species-rich plots showed less yearly variation in productivity (Tilman 1996) and their productivity during a drought year declined much less than species-poor plots (Tilman and Downing 1994). Because

Box 3.2 Carnivore conservation
Mark S. Boyce

Predation by carnivores can alter prey population abundance and distribution, and these predator effects have been shown to influence many aspects of community ecology. Examples include the effect of sea otters that kill and eat sea urchins reducing their abundance and herbivory on the kelp forests that sustain diverse near-shore marine communities of the North Pacific. Likewise, subsequent to wolf (see Box 3.2 Figure) recovery in Yellowstone National Park (USA), elk have become preferred prey of wolves resulting in shifts in the distribution and abundance of elk that has released vegetation from ungulate herbivory with associated increases in beavers, song birds, and other plants and animals.

Yet, carnivore conservation can be very challenging because the actions of carnivores often are resented by humans. Carnivores depredate livestock or reduce abundance of wildlife valued by hunters thereby coming into direct conflict with humans. Some larger species of carnivores can prey on humans. Every year, people are killed by lions in Africa, children are killed by wolves in India, and people are killed or mauled by cougars and bears in western North America (see also Box 14.3). Retaliation is invariably swift and involves killing those individuals responsible for the depredation, but furthermore such incidents of human predation usually result in fear-driven management actions that seldom consider the ecological significance of the carnivores in question.

Box 3.2 Figure Grey wolf (*Canis lupus*). Photograph from www.all-about-wolves.com.

Another consideration that often plays a major role in carnivore conservation is public opinion. Draconian methods for predator control, including aerial gunning and poisoning of wolves by government agencies, typically meets with fierce public opposition. Yet, some livestock ranchers and hunters lobby to have the carnivores eradicated. Rural people who are at risk of depredation losses from carnivores usually want the animals controlled or eliminated, whereas tourists and broader publics usually push for protection of the carnivores.

Most insightful are programs that change human management practices to reduce the probability of conflict. Bringing cattle into areas where they can be watched during calving can reduce the probability that bears or wolves will kill the calves. Ensuring that garbage is unavailable to bears and other large carnivores reduces the risk that carnivores will become habituated to humans and consequently come into conflict. Livestock ranchers can monitor their animals in back-country areas and can dispose of dead animal carcasses to reduce the risk of depredation. Killing those individuals that are known to depredate livestock can be an effective approach because individuals sometimes learn to kill livestock whereas most carnivores in the population take only wild prey. Managing recreational access to selected trails and roads can be an effective tool for reducing conflicts between large carnivores and people. Finding socially acceptable methods of predator control whilst learning to live in proximity with large carnivores is the key challenge for carnivore conservation.

more species do better at utilizing and recycling nutrients, in the long-term, species-rich plots are better at reducing nutrient losses and maintaining soil fertility (Tilman *et al.* 1996; Vitousek and Hooper 1993).

Although it makes intuitive sense that the species that dominate in number and/or biomass are more likely to be important for ecosystem function (Raffaelli 2004; Smith *et al.* 2004), in some cases, even rare species can have a role, for

Box 3.3 Ecosystem services and agroecosystems in a landscape context
Teja Tscharntke

Agroecosystems result from the transformation of natural ecosystems to promote ecosystem services, which are defined as benefits people obtain from ecosystems (MEA 2005). Major challenges in managing ecosystem services are that they are not independent of each other and attempts to optimize a single service (e.g. reforestation) lead to losses in other services (e.g. food production; Rodriguez *et al.* 2006). Agroecosystems such as arable fields and grasslands are typically extremely open ecosystems, characterized by high levels of input (e.g. labour, agrochemicals) and output (e.g. food resources), while agricultural management reduces structural complexity and associated biodiversity.

The world's agroecosystems deliver a number of key goods and services valued by society such as food, feed, fibre, water, functional biodiversity, and carbon storage. These services may directly contribute to human well-being, for example through food production, or just indirectly through ecosystem processes such as natural biological control of crop pests (Tscharntke *et al.* 2007) or pollination of crops (Klein *et al.* 2007). Farmers are mostly interested in the privately owned, marketable goods and services, while they may also produce public goods such as aesthetic landscapes or regulated water levels. Finding win-win solutions that serve both private economic gains in agroecosystems and public long-term conservation in agricultural landscapes is often difficult (but see Steffan-Dewenter *et al.* 2007). The goal of long-lasting ecosystem services providing sustainable human well-being may become compromised by the short-term interest of farmers in increasing marketable services, but incentives may encourage environment friendly agriculture. This is why governments implement payment-for-ecosystem service programs such as the agri-environment schemes in the European Community or the Chinese programs motivated by large floods on the Yangtze River (Tallis *et al.* 2008).

In addition, conservation of most services needs a landscape perspective. Agricultural land use is often focused on few species and local processes, but in dynamic, human-dominated landscapes, only a diversity of insurance species may guarantee resilience, i.e. the capacity to re-organize after disturbances (see Box 3.3 Figure). Biodiversity and associated ecosystem services can be maintained only in complex landscapes with a minimum of near-natural habitat (in central Europe roughly 20%) supporting a minimum number of species dispersing across natural and managed systems (Tscharntke *et al.* 2005). For example, pollen beetles causing economically meaningful damage in oilseed rape (canola) are naturally controlled by parasitic wasps in complex but not in simplified landscapes. Similarly, high levels of pollination and yield in coffee and pumpkin depend on a high diversity of bee species, which is only available in heterogeneous environments. The landscape context may be even more important for local biodiversity and associated ecosystem services than differences in local management, for example between organic and conventional farming or between crop fields with or without near-natural field margins, because the organisms immigrating into agroecosystems from the landscape-wide species pool may compensate for agricultural intensification at a local scale (Tscharntke *et al.* 2005).

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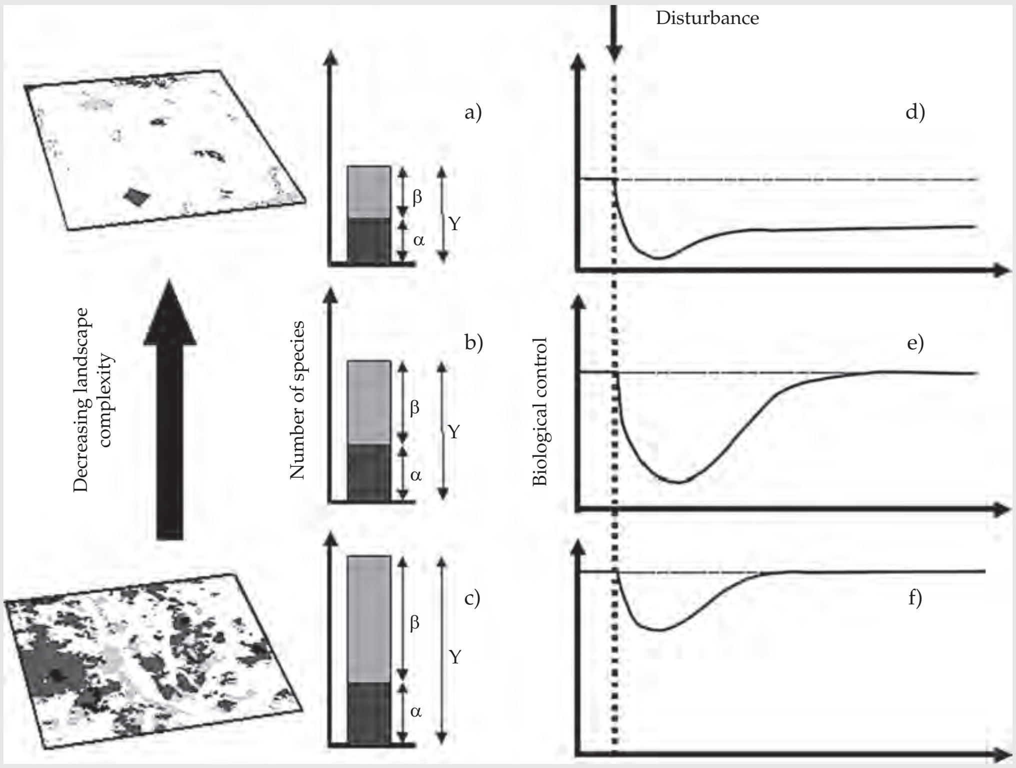
Box 3.3 (Continued)



Box 3.3 Figure Hypothesized responses to disturbance on ecosystem services such as biological control and pollination by native natural enemies and pollinators in different landscapes, showing how beta diversity (a-c) and recover of biological control and pollination after disturbance (d-f) change with landscape heterogeneity. Adapted from Tscharntke *et al.* (2007). a) and d) Intensely used monotonous landscape with a small available species pool, giving a low general level of ecosystem services, a greater dip in the service after a disturbance and an ecosystem that is unable to recover. b) and e) Intermediate landscape harboring slightly higher species richness, rendering deeper dip and slower return from a somewhat lower maximum level of biological control or pollination after a disturbance. c) and f) Heterogeneous landscape with large species richness, mainly due to the higher beta diversity, rendering high maximum level of the service, and low dip and quick return after a disturbance.

The turnover of species among patches (the dissimilarity of communities creating high beta diversity, in contrast to the local, patch-level alpha diversity) is the dominant driver of landscape-wide biodiversity. Beta diversity reflects the high spatial and temporal heterogeneity experienced by communities at a landscape scale. Pollinator or biocontrol species that do not contribute to the service in one patch may be important in other patches, providing spatial insurance through complementary resource use (see Box 3.3 Figure). Sustaining ecosystem services in landscapes depends on a high beta diversity coping with the spatial and temporal heterogeneity in a real world under Global Change.

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Box 3.3 (Continued)

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example, in increasing resistance to invasion (Lyons and Schwartz 2001). A keystone species is one that has an ecosystem impact that is disproportionately large in relation to its abundance (Hooper *et al.* 2005; Power *et al.* 1996; see Boxes 3.1, 3.2, and 5.3). Species that are not thought of as "typical" keystones can turn out to be so, sometimes in more ways than one (Daily *et al.* 1993). Even though in many communities only a few species have strong effects, the weak effects of many species can add up to a substantial stabilizing effect and seemingly "weak" effects over broad scales can be strong at the local level (Berlow 1999). Increased species richness can "insure" against sudden change, which is now a global phenomenon (Parmesan and Yohe 2003; Root *et al.* 2003). Even though a few species may make up most of the biomass of most functional groups, this does not mean that other species are unnecessary (Walker *et al.* 1999). Species may act like the rivets in an airplane wing, the loss of each unnoticed until a catastrophic threshold is passed (Ehrlich and Ehrlich 1981b).

As humanity's footprint on the planet increases and formerly stable ecosystems experience constant disruptions in the form of introduced species (Chapter 7), pollution (Box 13.1), climate change (Chapter 8), excessive nutrient loads, fires (Chapter 9), and many other perturbations, the insurance value of biodiversity has become increasingly vital over the entire range of habitats and systems, from diverse forest stands sequestering CO_2 better in the long-term (Bolker *et al.* 1995; Hooper *et al.* 2005; but see Tallis and Kareiva 2006) to forest-dwelling native bees' coffee pollination services increasing coffee production in Costa Rica (Ricketts *et al.* 2004; also see Box 3.3). With accelerating losses of unique species, humanity, far from hedging its bets, is moving ever closer to the day when we will run out of options on an increasingly unstable planet.

3.5 Mobile Links

"Mobile links" are animal species that provide critical ecosystem services and increase ecosystem resilience by connecting habitats and ecosystems as they move between them (Gilbert 1980; Lundberg and Moberg 2003; Box 3.4). Mobile links are crucial for maintaining ecosystem function, memory, and resilience (Nystrm and Folke 2001). The three main types of mobile links: genetic, process, and resource links (Lundberg and Moberg 2003), encompass many fundamental ecosystem services (Sekercioglu 2006a, 2006b). Pollinating nectarivores and seed dispersing frugivores are genetic links that carry genetic material from an individual plant to another plant or to a habitat suitable for regeneration, respectively

Box 3.4 Conservation of plant-animal mutualisms
Priya Davidar

Plant-animal mutualisms such as pollination and seed dispersal link plant productivity and ecosystem functioning, and maintain gene flow in plant populations. Insects, particularly bees, are the major pollinators of wild and crop plants worldwide, whereas vertebrates such as birds and mammals contribute disproportionately to dispersal of seeds. About 1200 vertebrate and 100 000 invertebrate species are involved in pollination (Roubik 1995; Buchmann and Nabhan 1996). Pollinators are estimated to be responsible for 35% of global crop production (Klein *et al.* 2007) and for 60–90% of the reproduction of wild plants (Kremen *et al.* 2007). It is estimated that feral and managed honey bee colonies have declined by 25% in the USA since the 1990s, and globally about 200 species of wild vertebrate pollinators might be on the verge of extinction (Allen-Wardell *et al.* 1998). The widespread decline of pollinators and consequently pollination services is a cause for concern and is expected to reduce crop productivity and contribute towards loss of biodiversity in natural ecosystems (Buchmann and Nabhan 1996; Kevan and Viana 2003). Habitat loss, modification and the indiscriminate use of pesticides are cited as major reasons for pollinator loss (Kevan and Viana 2003). This alarming trend has led to the creation of an "International Initiative for the Conservation and Sustainable use of Pollinators" as a key element under the Convention on Biodiversity, and the International Union for the Conservation of Nature has a task force on declining pollination in the Survival Service Commission.

Frugivores tend to be less specialized than pollinators since many animals include some fruit in their diet (Wheelwright and Orians 1982). Decline of frugivores from overhunting and loss of habitat, can affect forest regeneration (Wright *et al.* 2007a). Hunting pressure differentially affects recruitment of species, where seeds dispersed by game animals decrease, and small non-game animals and by abiotic means increase in the community (Wright *et al.* 2007b).

Habitat fragmentation is another process that can disrupt mutualistic interactions by reducing the diversity and abundance of pollinators and seed dispersal agents, and creating barriers to pollen and seed dispersal (Cordeiro and Howe 2001, 2003; Aguilar *et al.* 2006).

Plant-animal mutualisms form webs or networks that contribute to the maintenance of biodiversity. Specialized interactions tend to be nested within generalized interactions where generalists interact more with each other than by chance, whereas specialists interact with generalists (Bascompte and Jordano 2006). Interactions are usually asymmetric, where one partner is more dependent on the other than vice-versa. These characteristics allow for the persistence of rare specialist species. Habitat loss and fragmentation (Chapters 4 and 5), hunting (Chapter 6) and other factors can disrupt mutualistic networks and result in loss of biodiversity. Models suggest that structured networks are less resilient to habitat loss than randomly generated communities (Fortuna and Bascompte 2006).

Therefore maintenance of contiguous forests and intact functioning ecosystems is needed to sustain mutualistic interactions such as pollination and seed dispersal. For agricultural production, wild biodiversity needs to be preserved in the surrounding matrix to promote native pollinators.

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Box 3.4 (Continued)

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(Box 3.4). Trophic process links are grazers, such as antelopes, and predators, such as lions, bats, and birds of prey that influence the populations of plant, invertebrate, and vertebrate prey (Boxes 3.1 and 3.2). Scavengers, such as vultures, are crucial process links that hasten the decomposition of potentially disease-carrying carcasses (Houston 1994). Predators often provide natural pest control (Holmes *et al.* 1979). Many animals, such as fish-eating birds that nest in colonies, are resource links that transport nutrients in their droppings and often contribute significant resources to nutrient-deprived ecosystems (Anderson and Polis 1999). Some organisms like woodpeckers or beavers act as physical process linkers or "ecosystem engineers" (Jones *et al.* 1994). By building dams and flooding large areas, beavers engineer ecosystems, create new wetlands, and lead to major changes in species composition (see Chapter 6). In addition to consuming insects (trophic linkers), many woodpeckers also engineer their environment and build nest holes later used by a variety of other species (Daily *et al.* 1993). Through mobile links, distant ecosystems and habitats are linked to and influence one another (Lundberg and Moberg 2003). The long-distance migrations of many species, such as African antelopes, songbirds, waterfowl, and gray whales (*Eschrichtius robustus*) are particularly important examples of critical mobile links. However, many major migrations are disappearing (Wilcove 2008) and nearly two hundred migratory bird species are threatened or near threatened with extinction (Sekercioglu 2007).

Dispersing seeds is among the most important functions of mobile links. Vertebrates are the main seed vectors for flowering plants (Regal 1977; Tiffney and Mazer 1995), particularly woody species (Howe and Smallwood 1982; Levey *et al.* 1994; Jordano 2000). This is especially true in the tropics where bird seed dispersal may have led to the emergence of flowering plant dominance (Regal 1977; Tiffney and Mazer 1995). Seed dispersal is thought to benefit plants in three major ways (Howe and Smallwood 1982):

- Escape from density-dependent mortality caused by pathogens, seed predators, competitors, and herbivores (Janzen-Connell escape hypothesis).

- Chance colonization of favorable but unpredictable sites via wide dissemination of seeds.
- Directed dispersal to specific sites that are particularly favorable for establishment and survival.

Although most seeds are dispersed over short distances, long-distance dispersal is crucial (Cain *et al*. 2000), especially over geological time scales during which some plant species have been calculated to achieve colonization distances 20 times higher than would be possible without vertebrate seed dispersers (Cain *et al.* 2000). Seed dispersers play critical roles in the regeneration and restoration of disturbed and degraded ecosystems (Wunderle 1997; Chapter 6), including newly-formed volcanic soils (Nishi and Tsuyuzaki 2004).

Plant reproduction is particularly pollination-limited in the tropics relative to the temperate zone (Vamosi *et al.* 2006) due to the tropics greater biodiversity, and up to 98% of tropical rainforest trees are pollinated by animals (Bawa 1990). Pollination is a critical ecosystem function for the continued persistence of the most biodiverse terrestrial habitats on Earth. Nabhan and Buchmann (1997) estimated that more than 1200 vertebrate and about 289 000 invertebrate species are involved in pollinating over 90% of flowering plant species (angiosperms) and 95% of food crops. Bees, which pollinate about two thirds of the world's flowering plant species and three quarters of food crops (Nabhan and Buchmann 1997), are the most important group of pollinators (Box 3.3). In California alone, their services are estimated to be worth $4.2 billion (Brauman and Daily 2008). However, bee numbers worldwide are declining (Nabhan and Buchmann 1997) (Box 3.5). In addition to the ubiquitous European honeybee (*Apis mellifera*), native bee species that depend on natural habitats also provide valuable services to farmers, exemplified by Costa Rican forest bees whose activities increase coffee yield by 20% near forest fragments (Ricketts *et al*. 2004).

Some plant species mostly depend on a single (Parra *et al*. 1993) or a few (Rathcke 2000) pollinator species. Plants are more likely to be pollinator-limited than disperser-limited (Kelly *et al.* 2004) and a survey of pollination experiments for 186 species showed that about half were pollinator-limited (Burd 1994). Compared to seed dispersal, pollination is more demanding due to the faster ripening rates and shorter lives of flowers (Kelly *et al.* 2004). Seed disperser and pollinator limitation are often more important in island ecosystems with fewer species, tighter linkages, and higher vulnerability to disturbance and introduced species. Island plant species are more vulnerable to the extinctions of their pollinators since many island plants have lost

Box 3.5 Consequences of pollinator decline for the global food supply
Claire Kremen

Both wild and managed pollinators have suffered significant declines in recent years. Managed *Apis mellifera*, the most important source of pollination services for crops around the world, have been diminishing around the globe (NRC 2006), particularly in the US where colony numbers are now at < 50% of their 1950 levels. In addition, major and extensive colony losses have occurred over the past several years in North America and Europe, possibly due to diseases as well as other factors (Cox-Foster *et al.* 2007; Stokstad 2007), causing shortages and rapid increases in the price of pollination services (Sumner and Boriss 2006). These recent trends in honey bee health illustrate the extreme risk of relying on a single pollinator to provide services for the world's crop species. Seventy-five percent of globally important crops rely on animal pollinators, providing up to 35% of crop production (Klein *et al.* 2007).

At the same time, although records are sorely lacking for most regions, comparisons of recent with historical (pre-1980) records have indicated significant regional declines in species richness of major pollinator groups (bees and hoverflies in Britain; bees alone in the Netherlands) (Biesmeijer *et al.* 2006). Large reductions in species richness and abundance of bees have also been documented in regions of high agricultural intensity in California's

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Box 3.5 (Continued)

Central Valley (Kremen *et al.* 2002; Klein and Kremen unpublished data). Traits associated with bee, bumble bee and hoverfly declines in Europe included floral specialization, slower (univoltine) development and lower dispersal (non-migratory) species (Biesmeijer *et al.* 2006; Goulson *et al.* 2008). Specialization is also indicated as a possible correlate of local extinction in pollinator communities studied across a disturbance gradient in Canada; communities in disturbed habitat contained significantly more generalized species than those associated with pristine habitats (Taki and Kevan 2007). Large-bodied bees were more sensitive to increasing agricultural intensification in California's Central Valley, and ominously, bees with the highest per-visit pollination efficiencies were also most likely to go locally extinct with agricultural intensification (Larsen *et al.* 2005).

Thus, in highly intensive farming regions, such as California's Central Valley, that contribute comparatively large amounts to global food production (e.g. 50% of the world supply of almonds), the supply of native bee pollinators is lowest in exactly the regions where the demand for pollination services is highest. Published (Kremen *et al.* 2002) and recent studies (Klein *et al.* unpublished data) clearly show that the services provided by wild bee pollinators are not sufficient to meet the demand for pollinators in these intensive regions; such regions are instead entirely reliant on managed honey bees for pollination services. If trends towards increased agricultural intensification continue elsewhere (e.g. as in Brazil, Morton *et al.* 2006), then pollination services from wild pollinators are highly likely to decline in other regions (Ricketts *et al.* 2008). At the same time, global food production is shifting increasingly towards production of pollinator-dependent foods (Aizen *et al.* 2008), increasing our need for managed and wild pollinators yet further. Global warming, which could cause mis-matches between pollinators and the plants they feed upon, may exacerbate pollinator decline (Memmott *et al.* 2007). For these reasons, we may indeed face more serious shortages of pollinators in the future.

A recent, carefully analyzed, global assessment of the economic impact of pollinator loss (e.g. total loss of pollinators worldwide) estimates our vulnerability (loss of economic value) at Euro 153 billion or 10% of the total economic value of annual crop production (Gallai *et al.* 2009). Although total loss of pollination services is both unlikely to occur and to cause widespread famine if it were to occur, it potentially has both serious economic and human health consequences. For example, some regions of the world produce large proportions of the world's pollinator-dependent crops—such regions would experience more severe economic consequences from the loss of pollinators, although growers and industries would undoubtedly quickly respond to these changes in a variety of ways passing the principle economic burden on to consumers globally (Southwick and Southwick 1992; Gallai *et al.* 2009). Measures of the impacts on consumers (consumer surplus) are of the same order of magnitude (Euro 195–310 billion based on reasonable estimates for price elasticities, Gallai *et al.* 2009) as the impact on total economic value of crop production. Nutritional consequences may be more fixed and more serious than economic consequences, due to the likely plasticity of responses to economic change. Pollinator-dependent crop species supply not only up to 35% of crop production by weight (Klein *et al.* 2007), but also provide essential vitamins, nutrients and fiber for a healthy diet and provide diet diversity (Gallai *et al.* 2009; Kremen *et al.* 2007). The nutritional consequences of total pollinator loss for human health have yet to be quantified; however food recommendations for minimal daily portions of fruits and vegetables are well-known and already often not met in diets of both developed and underdeveloped countries.

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their ability to self-pollinate and have become completely dependent on endemic pollinators (Cox and Elmqvist 2000). Pollination limitation due to the reduced species richness of pollinators on islands like New Zealand and Madagascar (Farwig *et al.* 2004) can significantly reduce fruit sets and probably decrease the reproductive success of dioecious plant species.

Predators are important trophic process links and can control the populations of pest species. For millennia, agricultural pests have been competing with people for the food and fiber plants that feed and clothe humanity. Pests, particularly herbivorous insects, consume 25–50% of humanity's crops every year (Pimentel *et al.* 1989). In the US alone, despite the US$25 billion spent on pesticides annually (Naylor and Ehrlich 1997), pests destroy 37% of the potential crop yield (Pimentel *et al.* 1997). However, many pests have evolved resistance to the millions of tons of synthetic pesticide sprayed each year (Pimentel and Lehman 1993), largely due to insects' short generation times and their experience with millions of years of coevolution with plant toxins (Ehrlich and Raven 1964). Consequently, these chemicals poison the environment (Carson 1962), lead to thousands of wildlife fatalities every year, and by killing pests' natural enemies faster than the pests themselves, often lead to the emergence of new pest populations (Naylor and Ehrlich 1997). As a result, the value of natural pest control has been increasingly recognized worldwide, some major successes have been achieved, and natural controls now form a core component of "integrated pest management" (IPM) that aims to restore the natural pest-predator balance in agricultural ecosystems (Naylor and Ehrlich 1997).

Species that provide natural pest control range from bacteria and viruses to invertebrate and vertebrate predators feeding on insect and rodent pests (Polis *et al.* 2000; Perfecto *et al.* 2004; Sekercioglu 2006b). For example, a review by Holmes (1990) showed that reductions in moth and butterfly populations due to temperate forest birds was mostly between 40–70% at low insect densities, 20–60% at intermediate densities, and 0–10% at high densities. Although birds are not usually thought of as important control agents, avian control of insect herbivores and consequent reductions in plant damage can have important economic value (Mols and Visser 2002). Takekawa and Garton (1984) calculated avian control of western spruce budworm in northern Washington State to be worth at least US$1820/$km^2$/year. To make Beijing greener for the 2008 Olympics without using chemicals, entomologists reared four billion parasitic wasps to get rid of the defoliating moths in less than three months (Rayner 2008). Collectively, natural enemies of crop pests may save humanity at least US $54 billion per year, not to mention the critical importance of natural controls for food security and human survival (Naylor and Ehrlich 1997). Promoting natural predators and preserving their native habitat patches like hedgerows and forests may increase crop yields, improve food security, and lead to a healthier environment.

Often underappreciated are the scavenging and nutrient deposition services of mobile links. Scavengers like vultures rapidly get rid of rotting carcasses, recycle nutrients, and lead other animals to carcasses (Sekercioglu 2006a). Besides their ecological significance, vultures are particularly important in many tropical developing countries where sanitary waste and carcass disposal programs may be limited or non-existent (Prakash *et al.* 2003) and where vultures contribute to human and ecosystem health by getting rid of refuse (Pomeroy 1975), feces (Negro *et al.* 2002), and dead animals (Prakash *et al.* 2003).

Mobile links also transport nutrients from one habitat to another. Some important examples are geese transporting terrestrial nutrients to wetlands (Post *et al.* 1998) and seabirds transferring marine productivity to terrestrial ecosystems, especially in coastal areas and unproductive island systems (Sanchez-pinero and Polis 2000). Seabird droppings (guano) are enriched in important plant nutrients such as calcium, magnesium, nitrogen, phosphorous, and potassium (Gillham 1956). Murphy (1981) estimated that seabirds around the world transfer 10^4 to 10^5 tons of phosphorous from sea to land every year. Guano also provides an important source of fertilizer and income to many people living near seabird colonies.

Scavengers and seabirds provide good examples of how the population declines of ecosystem service providers lead to reductions in their services (Hughes *et al.* 1997). Scavenging and fish-eating birds comprise the most threatened avian functional groups, with about 40% and 33%, respectively, of these species being threatened or near threatened with extinction (Sekercioglu *et al.* 2004). The large declines in the populations of many scavenging and fish-eating species mean that even if none of these species go extinct, their services are declining substantially. Seabird losses can trigger trophic cascades and ecosystem shifts (Croll *et al.* 2005). Vulture declines can lead to the emergence of public health problems. In India, *Gyps* vulture populations declined as much as 99% in the 1990s (Prakash *et al.* 2003). Vultures compete with feral dogs, which often carry rabies. As the vultures declined between 1992 and 2001, the numbers of feral dogs increased 20-fold at a garbage dump in India (Prakash *et al.* 2003). Most of world's rabies deaths take place in India (World Health Organization 1998) and feral dogs replacing vultures is likely to aggravate this problem.

Mobile links, however, can be double-edged swords and can harm ecosystems and human populations, particularly in concert with human related poor land-use practices, climate change, and introduced species. Invasive plants can spread via native and introduced seed dispersers (Larosa *et al.* 1985; Cordeiro *et al.* 2004). Land use change can increase the numbers of mobile links that damage distant areas, such as when geese overload wetlands with excessive nutrients (Post *et al.* 1998). Climate change can lead to asynchronies in insect emergence and their predators timing of breeding (Both *et al.* 2006), and in flowering and their pollinators lifecycles (Harrington *et al.* 1999) (Chapter 8).

Mobile links are often critical to ecosystem functioning as sources of "external memory" that promote the resilience of ecosystems (Scheffer *et al.* 2001). More attention needs to be paid to mobile links in ecosystem management and biodiversity conservation (Lundberg and Moberg 2003). This is especially the case for migrating species that face countless challenges during their annual migrations that sometimes cover more than 20 000 kilometers (Wilcove 2008). Some of the characteristics that make mobile links important for ecosystems, such as high mobility and specialized diets, also make them more vulnerable to human impact. Protecting pollinators, seed dispersers, predators, scavengers, nutrient depositors, and other mobile links must be a top conservation priority to prevent collapses in ecosystem services provided by these vital organisms (Boxes 3.1–3.5).

3.6 Nature's Cures versus Emerging Diseases

While many people know about how plants prevent erosion, protect water supplies, and "clean the air", how bees pollinate plants or how owls reduce rodent activity, many lesser-known organisms not only have crucial ecological roles, but also produce unique chemicals and pharmaceuticals that can literally save people's lives. Thousands of plant species are used medically by traditional, indigenous communities worldwide. These peoples' ethnobotanical knowledge has led to the patenting, by pharmaceutical companies, of more than a quarter of all medicines (Posey 1999), although the indigenous communities rarely benefit from these patents (Mgbeoji 2006). Furthermore, the eroding of traditions worldwide, increasing emigration from traditional, rural communities to urban areas, and disappearing cultures and languages mean that the priceless ethnobotanical knowledge of many cultures is rapidly disappearing in parallel with the impending extinctions of many medicinal plants due to habitat loss and overharvesting (Millennium Ecosystem Assessment 2005a). Some of the rainforest areas that are being deforested fastest, like the island of Borneo, harbor plant species that produce active anti-HIV (Human Immunodeficiency Virus) agents (Chung 1996; Jassim and Naji 2003). Doubtlessly, thousands more useful and vital plant compounds await discovery in the forests of the world, particularly in the biodiverse tropics (Laurance 1999; Sodhi *et al.* 2007). However, without an effective strategy that integrates community-based habitat conservation, rewarding of local ethnobotanical knowledge, and scientific research on these compounds, many species, the local knowledge of them, and the priceless cures they offer will disappear before scientists discover them.

As with many of nature's services, there is a flip side to the medicinal benefits of biodiversity, namely, emerging diseases (Jones *et al.* 2008). The planet's organisms also include countless diseases, many of which are making the transition to humans as people increasingly invade the habitats of the hosts of these diseases and consume the hosts themselves. Three quarters of human diseases are thought to have their origins in domestic or wild animals and new diseases are emerging as humans increase their presence in formerly wilderness areas (Daily and Ehrlich 1996; Foley *et al*. 2005). Some of the deadliest diseases, such as monkeypox, malaria, HIV and Ebola, are thought to have initially crossed from central African primates to the people who hunted, butchered, and consumed them (Hahn *et al.* 2000; Wolfe *et al.* 2005; Rich *et al*. 2009). Some diseases emerge in ways that show the difficulty of predicting the consequences of disturbing ecosystems. The extensive smoke from the massive 1997–1998 forest fires in Southeast Asia is thought to have led to the fruiting failure of many forest trees, forcing frugivorous bats to switch to fruit trees in pig farms. The bats, which host the Nipah virus, likely passed it to the pigs, from which the virus made the jump to people (Chivian 2002). Another classic example from Southeast Asia is the Severe Acute Respiratory Syndrome (SARS). So far having killed 774 people, the SARS coronavirus has been recently discovered in wild animals like the masked palm civet (*Paguma larvata*) and raccoon dog (*Nyctereuteus procyonoides*) that are frequently consumed by people in the region (Guan *et al*. 2003). SARS-like coronaviruses have been discovered in bats (Li *et al*. 2005) and the virus was probably passed to civets and other animals as they ate fruits partially eaten and dropped by those bats (Jamie H. Jones, personal communication). It is probable that SARS made the final jump to people through such animals bought for food in wildlife markets.

The recent emergence of the deadly avian influenza strain H5N1 provides another good example. Even though there are known to be at least 144 strains of avian flu, only a few strains kill people. However, some of the deadliest pandemics have been among these strains, including H1N1, H2N, and H3N2 (Cox and Subbarao 2000). H5N1, the cause of the recent bird flu panic, has a 50% fatality rate and may cause another human pandemic. At low host densities, viruses that become too deadly, fail to spread. It is likely that raising domestic birds in increasingly higher densities led to the evolution of higher virulence in H5N1, as it became easier for the virus to jump to another host before it killed its original host. There is also a possibility that increased invasion of wilderness areas by people led to the jump of H5N1 from wild birds to domestic birds, but that is yet to be proven.

Malaria, recently shown to have jumped from chimpanzees to humans (Rich *et al*. 2009), is perhaps the best example of a resurging disease that increases as a result of tropical deforestation (Singer and Castro 2001; Foley *et al*. 2005; Yasuoka and Levins 2007). Pearson (2003) calculated that every 1% increase in deforestation in the Amazon leads to an 8% increase in the population of the malaria vector mosquito (*Anopheles darlingi*). In addition, some immigrants colonizing deforested areas brought new sources of malaria (Moran 1988) whereas other immigrants come from malaria-free areas and thus become ideal hosts with no immunity (Aiken and Leigh 1992). Collectively, the conditions leading to and resulting from tropical deforestation, combined with climate change, human migration, agricultural intensification, and animal trafficking create the perfect storm for the emergence of new diseases as well as the resurgence of old ones. In the face of rapid global change, ecologically intact and relatively stable communities may be our best weapon against the emergence of new diseases.

3.7 Valuing Ecosystem Services

Ecosystems and their constituent species provide an endless stream of products, functions, and services that keep our world running and make our existence possible. To many, even the thought of putting a price tag on services like photosynthesis, purification of water, and pollination of food crops may seem like hubris, as these are truly priceless services without which not only humans, but most of life would perish. A distinguished economist put it best in response to a seminar at the USA Federal Trade Commission, where the speaker downplayed the impact of global warming by saying agriculture and forestry "accounted for only three percent of the US gross national product". The economist's response was: "What does this genius think we're going to eat?" (Naylor and Ehrlich 1997).

Nevertheless, in our financially-driven world, we need to quantify the trade-offs involved in land use scenarios that maximize biodiversity conservation and ecosystem services versus scenarios that maximize profit from a single commodity. Without such assessments, special interests representing single objectives dominate the debate and sideline the integration of ecosystem services into the decision-making process (Nelson *et al*. 2009). Valuing ecosystem services is not an end in itself, but is the first step towards integrating these services into public decision-making and ensuring the continuity of ecosystems that provide the services (Goulder and Kennedy 1997; National Research Council 2005; Daily *et al.* 2009). Historically, ecosystem services have been mostly thought of as free public goods, an approach which has too frequently led to the "tragedy of the commons" where vital ecosystem goods like clean water have been degraded and consumed to extinction (Daily 1997). Too often, ecosystem services have been valued, if at all, based on "marginal utility" (Brauman and Daily 2008). When the service (like clean water) is abundant, the marginal utility of one additional unit can be as low as zero. However, as the service becomes more scarce, the marginal utility of each additional unit becomes increasingly valuable (Goulder and Kennedy 1997). Using the marginal value for a service when it is abundant drastically underestimates the value of the service as it becomes scarcer. As Benjamin Franklin wryly observed, "When the well's dry, we know the worth of water."

As the societal importance of ecosystem services becomes increasingly appreciated, there has been a growing realization that successful application of this concept requires a skilful combination of biological, physical, and social sciences, as well as the creation of new programs and institutions. The scientific community needs to help develop the necessary quantitative tools to calculate the value of ecosystem services and to present them to the decision makers (Daily *et al.* 2009). A promising example is the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) system (Daily *et al.* 2009; Nelson 2009) developed by the Natural Capital Project (www.naturalcapital.org; see Box 15.3). However, good tools are valuable only if they are used. A more difficult goal is convincing the private and public sectors to incorporate ecosystem services into their decision-making processes (Daily *et al.* 2009). Nevertheless, with the socio-economic impacts and human costs of environmental catastrophes, such as Hurricane Katrina, getting bigger and more visible, and with climate change and related carbon sequestration schemes having reached a prominent place in the public consciousness, the value of these services and the necessity of maintaining them has become increasingly mainstream.

Recent market-based approaches such as payments for Costa Rican ecosystem services, wetland mitigation banks, and the Chicago Climate Exchange have proven useful in the valuation of ecosystem services (Brauman and Daily 2008). Even though the planet's ecosystems, the biodiversity they harbor, and the services they collectively provide are truly priceless, market-based and other quantitative approaches for valuing ecosystem services will raise the profile of nature's services in the public consciousness, integrate these services into decision-making, and help ensure the continuity of ecosystem contributions to the healthy functioning of our planet and its residents.

Summary

- Ecosystem services are the set of ecosystem functions that are useful to humans.
- These services make the planet inhabitable by supplying and purifying the air we breathe and the water we drink.
- Water, carbon, nitrogen, phosphorus, and sulfur are the major global biogeochemical cycles. Disruptions of these cycles can lead to floods, droughts, climate change, pollution, acid rain, and many other environmental problems.
- Soils provide critical ecosystem services, especially for sustaining ecosystems and growing food crops, but soil erosion and degradation are serious problems worldwide.
- Higher biodiversity usually increases ecosystem efficiency and productivity, stabilizes overall ecosystem functioning, and makes ecosystems more resistant to perturbations.
- Mobile link animal species provide critical ecosystem functions and increase ecosystem resilience by connecting habitats and ecosystems through their movements. Their services include pollination, seed dispersal, nutrient deposition, pest control, and scavenging.
- Thousands of species that are the components of ecosystems harbor unique chemicals and pharmaceuticals that can save people's lives, but traditional knowledge of medicinal plants is disappearing and many potentially valuable species are threatened with extinction.
- Increasing habitat loss, climate change, settlement of wild areas, and wildlife consumption facilitate the transition of diseases of animals to humans, and other ecosystem alterations are increasing the prevalence of other diseases.

• Valuation of ecosystem services and tradeoffs helps integrate these services into public decision-making and can ensure the continuity of ecosystems that provide the services.

Relevant websites

- Millennium Ecosystem Assessment: http://www.millenniumassessment.org/
- Intergovernmental Panel on Climate Change: http://www.ipcc.ch/
- Ecosystem Marketplace: http://www.ecosystemmarketplace.com/
- United States Department of Agriculture, Forest Service Website on Ecosystem Services: http://www.fs.fed.us/ecosystemservices/
- Ecosystem Services Project: http://www.ecosystemservicesproject.org/index.htm
- Natural Capital Project: http://www.naturalcapitalproject.org
- Carbon Trading: http://www.carbontrading.com/

Acknowledgements

I am grateful to Karim Al-Khafaji, Berry Brosi, Paul R. Ehrlich, Jamie H. Jones, Stephen Schneider, Navjot Sodhi, Tanya Williams, and especially Kate Brauman for their valuable comments. I thank the Christensen Fund for their support of my conservation and ecology work.

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