

ECOSYSTEM SERVICES: Benefits Supplied to Human Societies by Natural Ecosystems

by

Gretchen C. Daily, Susan Alexander, Paul R. Ehrlich, Larry Goulder, Jane Lubchenco, Pamela A. Matson, Harold A. Mooney, Sandra Postel, Stephen H. Schneider, David Tilman, George M. Woodwell

SUMMARY

Human societies derive many essential goods from natural ecosystems, including seafood, game animals, fodder, fuelwood, timber, and pharmaceutical products. These goods represent important and familiar parts of the economy. What has been less appreciated until recently is that natural ecosystems also perform fundamental life-support services without which human civilizations would cease to thrive. These include the purification of air and water, detoxification and decomposition of wastes, regulation of climate, regeneration of soil fertility, and production and maintenance of biodiversity, from which key ingredients of our agricultural, pharmaceutical, and industrial enterprises are derived. This array of services is generated by a complex interplay of natural cycles powered by solar energy and operating across a wide range of space and time scales. The process of waste disposal, for example, involves the life cycles of bacteria as well as the planet-wide cycles of major chemical elements such as carbon and nitrogen. Such processes are worth many trillions of dollars annually. Yet because most of these benefits are not traded in economic markets, they carry no price tags that could alert society to changes in their supply or deterioration of underlying ecological systems that generate them. Because threats to these systems are increasing, there is a critical need for identification and monitoring of ecosystem services both locally and globally, and for the incorporation of their value into decision-making processes.

Historically, the nature and value of Earth's life support systems have largely been ignored until their disruption or loss highlighted their importance. For example, deforestation has belatedly revealed the critical role forests serve in regulating the water cycle -- in particular, in mitigating floods, droughts, the erosive forces of wind and rain, and silting of dams and irrigation canals. Today, escalating impacts of human activities on forests, wetlands, and other natural ecosystems imperil the delivery of such services. The primary threats are land use changes that cause losses in biodiversity as well as disruption of carbon, nitrogen, and other biogeochemical cycles; human-caused invasions of exotic species; releases of toxic substances; possible rapid climate change; and depletion of stratospheric ozone.

Based on available scientific evidence, we are certain that:

- Ecosystem services are essential to civilization.
- Ecosystem services operate on such a grand scale and in such intricate and little-explored ways that most could not be replaced by technology.
- Human activities are already impairing the flow of ecosystem services on a large scale.
- If current trends continue, humanity will dramatically alter virtually all of Earth's remaining natural ecosystems within a few decades.

In addition, based on current scientific evidence, we are confident that:

- Many of the human activities that modify or destroy natural ecosystems may cause deterioration of ecological services whose value, in the long term, dwarfs the short-term economic benefits society gains from those activities.
- Considered globally, very large numbers of species and populations are required to sustain ecosystem services.
- The functioning of many ecosystems could be restored if appropriate actions were taken in time.

We believe that land use and development policies should strive to achieve a balance between sustaining vital ecosystem services and pursuing the worthy short-term goals of economic development.

INTRODUCTION

Many societies today have technological capabilities undreamed of in centuries past. Their citizens have such a global command of resources that even foods flown in fresh from all over the planet are taken for granted, and daily menus are decoupled from the limitations of regional growing seasons and soils. These developments have focused so much attention upon human-engineered and exotic sources of fulfillment that they divert attention from the local biological underpinnings that remain essential to economic prosperity and other aspects of our well-being.

These biological underpinnings are encompassed in the phrase ecosystem services, which refers to a wide range of conditions and processes through which natural ecosystems, and the species that are part of them, help sustain and fulfill human life. These services maintain biodiversity and the production of ecosystem goods, such as seafood, wild game, forage, timber, biomass fuels, natural fibers, and many pharmaceuticals, industrial products, and their precursors. The harvest and trade of these goods represent important and familiar parts of the human economy.

List of Specific Examples of Ecosystem Services

In addition to the production of goods, ecosystem services support life through (Holdren and Ehrlich 1974; Ehrlich and Ehrlich 1981) the following:

- purification of air and water
- mitigation of droughts and floods
- generation and preservation of soils and renewal of their fertility
- detoxification and decomposition of wastes
- pollination of crops and natural vegetation
- dispersal of seeds
- cycling and movement of nutrients
- control of the vast majority of potential agricultural pests
- maintenance of biodiversity
- protection of coastal shores from erosion by waves
- protection from the sun's harmful ultraviolet rays
- partial stabilization of climate
- moderation of weather extremes and their impacts
- provision of aesthetic beauty and intellectual stimulation that lift the human spirit

Although the distinction between "natural" and "human-dominated" ecosystems is becoming increasingly blurred, we emphasize the natural end of the spectrum, for three related reasons. First, the services flowing from natural ecosystems are greatly undervalued by society. For the most part, they are not traded in formal markets and so do not send price signals that warn of changes in their supply or condition. Furthermore, few people are conscious of the role natural ecosystem services play in generating those ecosystem goods that are traded in the marketplace. As a result, this lack of awareness helps drive the conversion of natural ecosystems to human-dominated systems (e.g., wheatlands or oil palm fields), whose economic value can be expressed, at least in part, in standard currency. The second reason to focus on natural ecosystems is that many human-initiated disruptions of these systems -- such as introductions of exotic species, extinctions of native species, and alteration of the gaseous composition of the atmosphere through fossil fuel burning -- are difficult or impossible to reverse on any time scale relevant to society. Third, if awareness is not increased and current trends continue, humanity will dramatically alter Earth's remaining natural ecosystems within a few decades (Daily 1997a, b).

The lack of attention to the vital role of natural ecosystem services is easy to understand. Humanity came into being after most ecosystem services had been in operation for hundreds of millions to billions of years. These services are so fundamental to life that they are easy to take for granted, and so large in scale that it is hard to imagine that human activities could irreparably disrupt them. Perhaps a thought experiment that removes these services from the familiar backdrop of the Earth is the best way to illustrate both the importance and complexity of ecosystem services, as well as how ill-equipped humans are to recreate them. Imagine, for example, human beings trying to colonize the moon.

Assume for the sake of argument that the moon had already miraculously acquired some of the basic conditions for supporting human life, such as an atmosphere, a climate, and a physical soil structure similar to those on Earth. The big question facing human colonists would then be, which of Earth's millions of species would need to be transported to the moon to make that sterile surface habitable?

One could tackle that question systematically by first choosing from among all the species exploited directly for food, drink, spices, fiber, timber, pharmaceuticals, and industrial products such as waxes, rubber, and oils. Even if one were highly selective, the list could amount to hundreds or even thousands of species. And that would only be a start, since one would then need to consider which species are crucial to supporting those used directly: the bacteria, fungi, and invertebrates that help make soil fertile and break down wastes and organic matter; the insects, bats, and birds that pollinate flowers; and the grasses, herbs, and trees that hold soil in place, regulate the water cycle, and supply food for animals. The clear message of this exercise is that no one knows which combinations of species -- or even approximately how many -- are required to sustain human life.

Rather than selecting species directly, one might try another approach: Listing the ecosystem services needed by a lunar colony and then guessing at the types and numbers of species required to perform each. Yet determining which species are critical to the functioning of a particular ecosystem service is no simple task. Let us take soil fertility as an example. Soil organisms are crucial to the chemical conversion and physical transfer of essential nutrients to higher plants. But the abundance of soil organisms is absolutely staggering. Under a square-yard of pasture in Denmark, for instance, the soil is inhabited by roughly 50,000 small earthworms and their relatives, 50,000 insects and mites, and nearly 12 million roundworms. And that tally is only the beginning. The number of soil animals is tiny compared to the number of soil microorganisms: a pinch of fertile soil may contain over 30,000 protozoa, 50,000 algae, 400,000 fungi, and billions of individual bacteria (Overgaard-Nielsen 1955; Rouatt and Katznelson 1961; Chanway 1993). Which must colonists bring to the moon to assure lush and continuing plant growth, soil renewal, waste disposal, and so on? Most of these soil-dwelling species have never been subjected to even cursory inspection: no human eye has ever blinked at them through a microscope, no human hand has ever typed out a name or description of them, and most human minds have never spent a moment reflecting on them. Yet the sobering fact is, as E. O. Wilson put it: they don't need us, but we need them (Wilson 1987).

THE CHARACTER OF ECOSYSTEM SERVICES

Moving our attention from the moon back to Earth, let us look more closely at the services nature performs on the only planet we know that is habitable. Ecosystem services and the systems that supply them are so interconnected that any classification of them is necessarily rather arbitrary. Here we briefly explore a suite of overarching services that operate in ecosystems worldwide.

Production of Ecosystem Goods

Humanity obtains from natural ecosystems an array of ecosystem goods—organisms and their parts and products that grow in the wild and that are used directly for human benefit. Many of these, such as fishes and animal products, are commonly traded in economic markets. The annual world fish catch, for example, amounts to about 100 million metric tons and is valued at between \$50 billion and \$100 billion; it is the leading source of animal protein, with over 20% of the population in Africa and Asia dependent on fish as their primary source of protein (UNFAO 1993). The commercial harvest of freshwater fish worldwide in 1990 totaled approximately 14 million tons and was valued at about \$8.2 billion (UNFAO 1994). Interestingly, the value of the freshwater sport fishery in the U.S. alone greatly exceeds that of the global commercial harvest, with direct expenditures in 1991 totaling about \$16 billion. When this is added to the value of the employment generated by sport fishing activities, it raises the total to \$46 billion (Felder and Nickum 1992, cited in Postel and Carpenter 1997). The future of these fisheries is in question, however, because fish harvests have approached or exceeded sustainable levels virtually everywhere. Nine of the world's major marine fishing areas are in decline due to overfishing, pollution, and habitat destruction. (UNFAO 1993; Kaufman and Dayton 1997).

Turning our attention to the land, grasslands are an important source of marketable goods, including animals used for labor (horses, mules, asses, camels, bullocks, etc.) and those whose parts or products are consumed (as meat, milk, wool, and leather). Grasslands were also important as the original source habitat for most domestic animals such as cattle, goats, sheep, and horses, as well as many crops, such as wheat, barley, rye, oats, and other grasses (Sala and Paruelo 1997). In a wide variety of terrestrial habitats, people hunt game animals such as waterfowl, deer, moose, elk, fox, boar and other wild pigs, rabbits, and even snakes and monkeys. In many countries, game meat forms an important part of local diets and, in many places, hunting is an economically and culturally important sport.

Natural ecosystems also produce vegetation used directly by humans as food, timber, fuelwood, fiber, pharmaceuticals and industrial products. Fruits, nuts, mushrooms, honey, other foods, and spices are extracted from many forest species. Wood and other plant materials are used in the construction of homes and other buildings, as well as for the manufacture of furniture, farming implements, paper, cloth, thatching, rope, and so on. About 15 percent of the world's energy consumption is supplied by fuelwood and other plant material; in

developing countries, such "biomass" supplies nearly 40 percent of energy consumption (Hall et al. 1993), although the portion of this derived from natural rather than human-dominated ecosystems is undocumented. In addition, natural products extracted from many hundreds of species contribute diverse inputs to industry: gums and exudates, essential oils and flavorings, resins and oleoresins, dyes, tannins, vegetable fats and waxes, insecticides, and multitudes of other compounds (Myers 1983; Leung and Foster 1996). The availability of most of these natural products is in decline due to ongoing habitat conversion.

Generation and Maintenance of Biodiversity

Biological diversity, or biodiversity for short, refers to the variety of life forms at all levels of organization, from the molecular to the landscape level. Biodiversity is generated and maintained in natural ecosystems, where organisms encounter a wide variety of living conditions and chance events that shape their evolution in unique ways. Out of convenience or necessity, biodiversity is usually quantified in terms of numbers of species, and this perspective has greatly influenced conservation goals. It is important to remember, however, that the benefits that biodiversity supplies to humanity are delivered through populations of species residing in living communities within specific physical settings— in other words, through complex ecological systems, or ecosystems (Daily and Ehrlich 1995). For human beings to realize most of the aesthetic, spiritual, and economic benefits of biodiversity, natural ecosystems must therefore be accessible. The continued existence of coniferous tree species somewhere in the world would not help the inhabitants of a town inundated by flooding because of the clearing of a pine forest upstream. Generally, the flow of ecosystem goods and services in a region is determined by the type, spatial layout, extent, and proximity of the ecosystems supplying them. Because of this, the preservation of only one minimum viable population of each non-human species on Earth in zoos, botanical gardens, and the world's legally protected areas would not sustain life as we know it. Indeed, such a strategy, taken to extreme, would lead to collapse of the biosphere, along with its life support services.

As described in the previous section, biodiversity is a direct source of ecosystem goods. It also supplies the genetic and biochemical resources that underpin our current agricultural and pharmaceutical enterprises and may allow us to adapt these vital enterprises to global change. Our ability to increase crop productivity in the face of new pests, diseases, and other stresses has depended heavily upon the transfer to our crops of genes from wild crop relatives that confer resistance to these challenges. Such extractions from biodiversity's "genetic library" account for annual increases in crop productivity of about 1 percent, currently valued at \$1 billion (NRC 1992). Biotechnology now makes possible even greater use of this natural storehouse of genetic diversity via the transfer to crops of genes from any kind of organism—not simply crop relatives—and it promises to play a major role in future yield increases. By the turn of the century, farm-level sales of the products of agricultural biotechnology, just now entering

the marketplace, are expected to reach at least \$10 billion per year (World Bank 1991, cited in Reid et al. 1996).

In addition to sustaining the production of conventional crops, the biodiversity in natural ecosystems may include many potential new foods. Human beings have utilized around 7,000 plant species for food over the course of history and another 70,000 plants are known to have edible parts (Wilson 1989). Only about 150 food plants have ever been cultivated on a large scale, however. Currently, 82 plant species contribute 90 percent of national per-capita supplies of food plants (Prescott-Allen and Prescott-Allen 1990), although a much smaller number of these supply the bulk of the calories humans consume. Many other species, however, appear more nutritious or better suited to the growing conditions that prevail in important regions than the standard crops that dominate world food supply today. Because of increasing salinization of irrigated croplands and the potential for rapid climate change, for instance, future food security may come to depend on drought- and salt-tolerant varieties that now play comparatively minor roles in agriculture.

Turning to medicinal resources, a recent survey showed that of the top 150 prescription drugs used in the United States, 118 are based on natural sources: 74% on plants, 18% on fungi, 5% on bacteria, and 3% on one vertebrate (snake) species. Nine of the top ten drugs in this list are based on natural plant products (Grifo and Rosenthal, in press, as cited in Dobson 1995). The commercial value of pharmaceuticals in the developed nations exceeds \$40 billion per year (Principe 1989). Looking at the global picture, approximately 80% of the human population relies on traditional medical systems, and about 85% of traditional medicine involves the use of plant extracts (Farnsworth et al. 1985).

Saving only a single population of each species could have another cost. Different populations of the same species may produce different types or quantities of defensive chemicals that have potential use as pharmaceuticals or pesticides (McCormick et al. 1993); and they may exhibit different tolerances to environmental stresses such as drought or soil salinity. For example, the development of penicillin as a therapeutic antibiotic took a full 15 years after Alexander Fleming's famous discovery of it in common bread mold. In part, this was because scientists had great difficulty producing, extracting, and purifying the substance in needed quantities. One key to obtaining such quantities was the discovery, after a worldwide search, of a population of Fleming's mold that produced more penicillin than the original (Dowling 1977). Similarly, plant populations vary in their ability to resist pests and disease, traits important in agriculture. Many thousands of varieties of rice from different locations were screened to find one with resistance to grassy stunt virus, a disease that posed a serious threat to the world's rice crop (Myers 1983). Despite numerous examples like these, many of the localities that harbor wild relatives of crops remain unprotected and heavily threatened.

Climate and Life

Earth's climate has fluctuated tremendously since humanity came into being. At the peak of the last ice age 20,000 years ago, for example, much of Europe and North America were covered by mile-thick ice sheets. While the global climate has been relatively stable since the invention of agriculture around 10,000 years ago, periodic shifts in climate have affected human activities and settlement patterns. Even relatively recently, from 1550-1850, Europe was significantly cooler during a period known as the Little Ice Age. Many of these changes in climate are thought to be caused by alterations in Earth's orbital rotation or in the energy output of the sun, or even by events on the Earth itself—sudden perturbations such as violent volcanic eruptions and asteroid impacts or more gradual tectonic events such as the uplift of the Himalayas. Remarkably, climate has been buffered enough through all these changes to sustain life for at least 3.5 billion years (Schneider and Londer 1984). And life itself has played a role in this buffering.

Climate, of course, plays a major role in the evolution and distribution of life over the planet. Yet most scientists would agree that life itself is a principal factor in the regulation of global climate, helping to offset the effects of episodic climate oscillations by responding in ways that alter the greenhouse gas concentrations in the atmosphere. For instance, natural ecosystems may have helped to stabilize climate and prevent overheating of the Earth by removing more of the greenhouse gas carbon dioxide from the atmosphere as the sun grew brighter over millions of years (Alexander et al. 1997). Life may also exert a destabilizing or positive feedback that reinforces climate change, particularly during transitions between interglacial periods and ice ages. One example: When climatic cooling leads to drops in sea level, continental shelves are exposed to wind and rain, causing greater nutrient runoff to the oceans. These nutrients may fertilize the growth of phytoplankton, many of which form calcium carbonate shells. Increasing their populations would remove more carbon dioxide from the oceans and the atmosphere, a mechanism that should further cool the planet. Living things may also enhance warming trends through such activities as speeding up microbial decomposition of dead organic matter, thus releasing carbon dioxide to the atmosphere (Schneider and Boston 1991; Allegre and Schneider 1994). The relative influence of life's stabilizing and destabilizing feedbacks remains uncertain; what is clear is that climate and natural ecosystems are tightly coupled, and the stability of that coupled system is an important ecosystem service.

Besides their impact on the atmosphere, ecosystems also exert direct physical influences that help to moderate regional and local weather. For instance, transpiration (release of water vapor from the leaves) of plants in the morning causes thunderstorms in the afternoon, limiting both moisture loss from the region and the rise in surface temperature. In the Amazon, for example, 50% of the mean annual rainfall is recycled by the forest itself via evapotranspiration—

that is, evaporation from wet leaves and soil combined with transpiration (Salati 1987). Amazon deforestation could so dramatically reduce total precipitation that the forest might be unable to reestablish itself following complete destruction (Shukla et al. 1990). Temperature extremes are also moderated by forests, which provide shade and surface cooling and also act as insulators, blocking searing winds and trapping warmth by acting as a local greenhouse agent.

Mitigation of Floods and Droughts

An enormous amount of water, about 119,000 cubic kilometers, is rained annually onto the Earth's land surface—enough to cover the land to an average depth of 1 meter (Shiklomanov 1993). Much of this water is soaked up by soils and gradually metered out to plant roots or into aquifers and surface streams. Thus, the soil itself slows the rush of water off the land in flash floods. Yet bare soil is vulnerable. Plants and plant litter shield the soil from the full, destructive force of raindrops and hold it in place. When landscapes are denuded, rain compacts the surface and rapidly turns soil to mud (especially if it has been loosened by tillage); mud clogs surface cavities in the soil, reduces infiltration of water, increases runoff, and further enhances clogging. Detached soil particles are splashed downslope and carried off by running water (Hillel 1991).

Erosion causes costs not only at the site where soil is lost but also in aquatic systems, natural and human-made, where the material accumulates. Local costs of erosion include losses of production potential, diminished infiltration and water availability, and losses of nutrients. Downstream costs may include disrupted or lower quality water supplies; siltation that impairs drainage and maintenance of navigable river channels, harbors, and irrigation systems; increased frequency and severity of floods; and decreased potential for hydroelectric power as reservoirs fill with silt (Pimentel et al. 1995). Worldwide, the replacement cost of reservoir capacity lost to siltation is estimated at \$6 billion per year.

In addition to protecting soil from erosion, living vegetation—with its deep roots and above-ground evaporating surface—also serves as a giant pump, returning water from the ground into the atmosphere. Clearing of plant cover disrupts this link in the water cycle and leads to potentially large increases in surface runoff, along with nutrient and soil loss. A classic example comes from the experimental clearing of a New Hampshire forest, where herbicide was applied to prevent regrowth for a 3-year period after the clearing. The result was a 40 percent increase in average stream flow. During one four-month period of the experiment, runoff was more than 5 times greater than before the clearing (Bormann 1968). On a much larger scale, extensive deforestation in the Himalayan highlands appears to have exacerbated recent flooding in Bangladesh, although the relative roles of human and natural forces remain debatable (Ives and Messerli 1989). In addition, some regions of the world, such as parts of Africa, are experiencing an increased frequency and severity of drought, possibly associated with extensive deforestation.

Wetlands are particularly well-known for their role in flood control and can often reduce the need to construct flood control structures. Floodplain forests and high salt marshes, for example, slow the flow of floodwaters and allow sediments to be deposited within the floodplain rather than washed into downstream bays or oceans. In addition, isolated wetlands such as prairie potholes in the Midwest and cypress ponds in the Southeast, serve as detention areas during times of high rainfall, delaying saturation of upland soils and overland flows into rivers and thereby damping peak flows. Retaining the integrity of these wetlands by leaving vegetation, soils, and natural water regimes intact can reduce the severity and duration of flooding along rivers (Ewel 1997). A relatively small area of retained wetland, for example, could have largely prevented the severe flooding along the Mississippi River in 1993.

Services Supplied by Soil

Soil represents an important component of a nation's assets, one that takes hundreds to hundreds of thousands of years to build up and yet very few years to be lost. Some civilizations have drawn great strength from fertile soil; conversely, the loss of productivity through mismanagement is thought to have ushered many once flourishing societies to their ruin (Adams 1981). Today, soil degradation induced by human activities afflicts nearly 20 percent of the Earth's vegetated land surface (Oldeman et al. 1990).

In addition to moderating the water cycle, as described above, soil provides five other interrelated services (Daily et al. 1997). First, soil shelters seeds and provides physical support as they sprout and mature into adult plants. The cost of packaging and storing seeds and of anchoring plant roots would be enormous without soil. Human-engineered hydroponic systems can grow plants in the absence of soil, and their cost provides a lower bound to help assess the value of this service. The costs of physical support trays and stands used in such operations total about US\$55,000 per hectare (for the Nutrient Film Technique Systems; FAO 1990).

Second, soil retains and delivers nutrients to plants. Tiny soil particles (less than 2 microns in diameter), which are primarily bits of humus and clays, carry a surface electrical charge that is generally negative. This property holds positively charged nutrients—cations such as calcium and magnesium—near the surface, in proximity to plant roots, allowing them to be taken up gradually. Otherwise, these nutrients would quickly be leached away. Soil also acts as a buffer in the application of fertilizers, holding onto the fertilizer ions until they are required by plants. Hydroponic systems supply water and nutrients to plants without need of soil, but the margin for error is much smaller—even small excesses of nutrients applied hydroponically can be lethal to plants. Indeed, it is a complex undertaking to regulate the nutrient concentrations, pH, and salinity of the nutrient solution in hydroponic systems, as well as the air and solution temperature, humidity, light, pests, and plant diseases. Worldwide, the area under hydroponic culture is only a

few thousand hectares and is unlikely to grow significantly in the foreseeable future; by contrast, global cropped area is about 1.4 billion hectares (USDA 1993).

Third, soil plays a central role in the decomposition of dead organic matter and wastes, and this decomposition process also renders harmless many potential human pathogens. People generate a tremendous amount of waste, including household garbage, industrial waste, crop and forestry residues, and sewage from their own populations and their billions of domesticated animals. A rough approximation of the amount of dead organic matter and waste (mostly agricultural residues) processed each year is 130 billion metric tons, about 30 percent of which is associated with human activities (derived from Vitousek et al. 1986). Fortunately, there is a wide array of decomposing organisms—ranging from vultures to tiny bacteria—that extract energy from the large, complex organic molecules found in many types of waste. Like assembly-line workers, diverse microbial species process the particular compounds whose chemical bonds they can cleave and pass along to other species the end products of their specialized reactions. Many industrial wastes, including soaps, detergents, pesticides, oil, acids, and paper, are detoxified and decomposed by organisms in natural ecosystems if the concentration of waste does not exceed the system's capacity to transform it. Some modern wastes, however, are virtually indestructible, such as some plastics and the breakdown products of the pesticide DDT.

The simple inorganic chemicals that result from natural decomposition are eventually returned to plants as nutrients. Thus, the decomposition of wastes and the recycling of nutrients—the fourth service soils provide—are two aspects of the same process. The fertility of soils—that is, their ability to supply nutrients to plants—is largely the result of the activities of diverse species of bacteria, fungi, algae, crustacea, mites, termites, springtails, millipedes, and worms, all of which, as groups, play important roles. Some bacteria are responsible for "fixing" nitrogen, a key element in proteins, by drawing it out of the atmosphere and converting it to forms usable by plants and, ultimately, human beings and other animals. Certain types of fungi play extremely important roles in supplying nutrients to many kinds of trees. Earthworms and ants act as "mechanical blenders," breaking up and mixing plant and microbial material and other matter (Jenny 1980). For example, as much as 10 metric tonnes of material may pass through the bodies of earthworms on a hectare of land each year, resulting in nutrient rich "casts" that enhance soil stability, aeration, and drainage (Lee 1985).

Finally, soils are a key factor in regulating the Earth's major element cycles—those of carbon, nitrogen, and sulfur. The amount of carbon and nitrogen stored in soils dwarfs that in vegetation, for example. Carbon in soils is nearly double (1.8 times) that in plant matter, and nitrogen in soils is about 18 times greater (Schlesinger 1991). Alterations in the carbon and nitrogen cycles may be costly over the long term, and in many cases, irreversible on a time scale of interest to

society. Increased fluxes of carbon to the atmosphere, such as occur when land is converted to agriculture or when wetlands are drained, contribute to the buildup of key greenhouse gases, namely carbon dioxide and methane, in the atmosphere (Schlesinger 1991). Changes in nitrogen fluxes caused by production and use of fertilizer, burning of wood and other biomass fuels, and clearing of tropical land lead to increasing atmospheric concentrations of nitrous oxide, another potent greenhouse gas that is also involved in the destruction of the stratospheric ozone shield. These and other changes in the nitrogen cycle also result in acid rain and excess nutrient inputs to freshwater systems, estuaries, and coastal marine waters. This nutrient influx causes eutrophication of aquatic ecosystems and contamination of drinking water sources—both surface and ground water— by high levels of nitrate-nitrogen (Vitousek et al. 1997).

Pollination

Animal pollination is required for the successful reproduction of most flowering plants. About 220,000 out of an estimated 240,000 species of plants for which the mode of pollination has been recorded require an animal such as a bee or hummingbird to accomplish this vital task. This includes both wild plants and about 70 percent of the agricultural crop species that feed the world. Over 100,000 different animal species—including bats, bees, beetles, birds, butterflies, and flies—are known to provide these free pollination services that assure the perpetuation of plants in our croplands, backyard gardens, rangelands, meadows and forests. In turn, the continued availability of these pollinators depends on the existence of a wide variety of habitat types needed for their feeding, successful breeding, and completion of their life cycles (Nabhan and Buchmann 1997).

One third of human food is derived from plants pollinated by wild pollinators. Without natural pollination services, yields of important crops would decline precipitously and many wild plant species would become extinct. In the United States alone, the agricultural value of wild, native pollinators—those sustained by natural habitats adjacent to farmlands— is estimated in the billions of dollars per year. Pollination by honey bees, originally imported from Europe, is extremely important as well, but these bees are presently in decline, enhancing the importance of pollinators from natural ecosystems. Management of the honey bee in the New World is currently threatened by the movement of, and hybridization with, an aggressive African strain of honey bee that was accidentally released in Brazil in 1956. Diseases of honey bee colonies are also causing a marked decline in the number of managed colonies. Meanwhile, the diversity of natural pollinators available to both wild and domesticated plants is diminishing: more than 60 genera of pollinators include species now considered to be threatened, endangered or extinct (Buchmann and Nabhan 1996).

Natural Pest Control Services

Humanity's competitors for food, timber, cotton, and other fibers are called pests, and they include numerous herbivorous insects, rodents, fungi, snails, nematodes, and viruses. These pests destroy an estimated 25 to 50 percent of the world's crops, either before or after harvest (Pimentel et al. 1989). In addition, numerous weeds compete directly with crops for water, light, and soil nutrients, further limiting yields.

Chemical pesticides, and the strategies by which they are applied to fight crop pests, can have harmful unintended consequences. First, pests can develop resistance, which means that higher and higher doses of pesticides must be applied or new chemicals developed periodically to achieve the same level of control. Resistance is now found in more than 500 insect and mite pests, over 100 weeds, and in about 150 plant pathogens (WRI 1994). Second, populations of the natural enemies of pests are decimated by heavy pesticide use. Natural predators are often more susceptible to synthetic poisons than are the pests because they have not had the same evolutionary experience with overcoming plant chemicals that the pests themselves have had. And natural predators also typically have much smaller population sizes than those of their prey. Destruction of predator populations leads to explosions in prey numbers, not only freeing target pests from natural controls but often "promoting" other non-pest species to pest status. In California in the 1970s, for instance, 24 of the 25 most important agricultural pests had been elevated to that status by the overuse of pesticides (NRC 1989). Third, exposure to pesticides and herbicides may pose serious health risks to humans and many other types of organisms; the recently discovered declines in human sperm counts may be attributable in part to such exposure (Colborn et al. 1996).

Fortunately, an estimated 99 percent of potential crop pests are controlled by natural enemies, including many birds, spiders, parasitic wasps and flies, lady bugs, fungi, viral diseases, and numerous other types of organisms (DeBach 1974). These natural biological control agents save farmers billions of dollars annually by protecting crops and reducing the need for chemical control (Naylor and Ehrlich 1997).

Seed Dispersal

Once a seed germinates, the resulting plant is usually rooted in place for the rest of its life. For plants, then, movement to new sites beyond the shadow of the parent is usually achieved through seed dispersal. Many seeds, such as those of the dandelion, are dispersed by wind. Some are dispersed by water, the most famous being the seafaring coconut. Many other seeds have evolved ways of getting around by using animals as their dispersal agents. These seeds may be packaged in sweet fruit to reward an animal for its dispersal services; some of these seeds even require passage through the gut of a bird or mammal before they can germinate. Others require burial—by, say, a forgetful jay or a squirrel which later leaves its cache uneaten—for eventual germination. Still others are

equipped with sticky or sharp, spiny surfaces designed to catch onto a passing animal and go for a long ride before dropping or being rubbed off. Without thousands of animal species acting as seed dispersers, many plants would fail to reproduce successfully. For instance, the whitebark pine (*Pinus albicaulis*), a tree found in the Rockies and Sierra Nevada - Cascade Mountains, cannot reproduce successfully without a bird called Clark's Nutcracker (*Nucifraga columbiana*), which chisels pine seeds out of the tightly closed cones and disperses and buries them; without this service, the cones do not open far enough to let the seeds fall out on their own. Animal seed dispersers play a central role in the structure and regeneration of many pine forests (Lanner 1996). Disruption of these complex services may leave large areas of forest devoid of seedlings and younger age classes of trees, and thus unable to recover swiftly from human impacts such as land clearing.

Aesthetic Beauty and Intellectual and Spiritual Stimulation

Many human beings have a deep appreciation of natural ecosystems. That is apparent in the art, religions, and traditions of diverse cultures, as well as in activities such as gardening and pet-keeping, nature photography and film-making, bird feeding and watching, hiking and camping, ecotouring and mountaineering, river-rafting and boating, fishing and hunting, and in a wide range of other activities. For many, nature is an unparalleled source of wonderment and inspiration, peace and beauty, fulfillment and rejuvenation (e.g., Kellert and Wilson).

THREATS TO ECOSYSTEM SERVICES

Ecosystem services are being impaired and destroyed by a wide variety of human activities. Foremost among the immediate threats are the continuing destruction of natural habitats and the invasion of non-native species that often accompanies such disruption; in marine systems, overfishing is a major threat. The most irreversible of human impacts on ecosystems is the loss of native biodiversity. A conservative estimate of the rate of species loss is about one per hour, which unfortunately exceeds the rate of evolution of new species by a factor of 10,000 or more (Wilson 1989; Lawton and May 1995). But complete extinction of species is only the final act in the process. The rate of loss of local populations of species—the populations that generate ecosystem services in specific localities and regions—is orders of magnitude higher (Daily and Ehrlich 1995; Hughes et al., in prep.). Destroying other life forms also disrupts the web of interactions that could help us discover the potential usefulness of specific plants and animals (Thompson 1994). Once a pollinator or a predacious insect is on the brink of extinction, for instance, it would be difficult to discover its potential utility to farmers.

Other imminent threats include the alteration of the Earth's carbon, nitrogen, and other biogeochemical cycles through the burning of fossil fuels and heavy use of nitrogen fertilizer; degradation of farmland through unsustainable agricultural practices; squandering of freshwater resources; toxification of land and waterways; and overharvesting of fisheries, managed forests, and other theoretically renewable systems.

These threats to ecosystem services are driven ultimately by two broad underlying forces. One is rapid, unsustainable growth in the scale of the human enterprise: in population size, in per-capita consumption, and also in the environmental impacts that technologies and institutions generate as they produce and supply those consumables (Ehrlich et al. 1977). The other underlying driver is the frequent mismatch between short-term, individual economic incentives and long-term, societal well-being. Ecosystem services are generally greatly undervalued, for a number of reasons: many are not traded or valued in the marketplace; many serve the public good rather than provide direct benefits to individual landowners; private property owners often have no way to benefit financially from the ecosystem services supplied to society by their land; and, in fact, economic subsidies often encourage the conversion of such lands to other, market-valued activities. Thus, people whose activities disrupt ecosystem services often do not pay directly for the cost of those lost services. Moreover, society often does not compensate landowners and others who do safeguard ecosystem services for the economic benefits they lose by foregoing more lucrative but destructive land uses. There is a critical need for policy measures that address these driving forces and embed the value of ecosystem services into decision making frameworks.

VALUATION OF ECOSYSTEM SERVICES

Human society would cease to exist in the absence of ecosystem services. Thus, their immense value to humanity is unquestionable. Yet quantifying the value of ecosystem services in specific localities, and measuring their worth against that of competing land uses is no simple task. When tradeoffs must be made in the allocation of land and other resources to competing human activities, the resolution often requires a measure of what is known as the marginal value. In the case of ecosystem services, for example, the question that might be posed would be: By how much would the flow of ecosystem services be augmented (or diminished) with the preservation (or destruction) of the next hectare of forest or wetland? Estimation of marginal values is complex (e.g., Bawa and Gadgil 1997; Daily 1997b). Often a qualitative comparison of relative values is sufficient— that is, which is greater, the economic benefits of a particular development project or the benefits supplied by the ecosystem that would be destroyed, measured over a time period of interest to people concerned about the well-being of their grandchildren?

There are, and will remain, many cases in which ecosystem service values are highly uncertain. Yet the pace of destruction of natural ecosystems, and the irreversibility of most such destruction on a time scale of interest to humanity, warrants substantial caution. Valuing a natural ecosystem, like valuing a human life, is fraught with difficulties. Just as societies have recognized fundamental human rights, however, it may be prudent to establish fundamental ecosystem protections even though uncertainty over economic values remains. New institutions and agreements at the international and subnational level will be needed to encourage fair participation in such protections (see, e.g., Heal 1994).

The tremendous expense and difficulty of replicating lost ecosystem services is perhaps best illustrated by the results of the first Biosphere 2 "mission," in which eight people lived inside a 3.15-acre closed ecosystem for two years. The system featured agricultural land and replicas of several natural ecosystems such as forests and even a miniature ocean. In spite of an investment of more than \$200 million in the design, construction, and operation of this model earth, it proved impossible to supply the material and physical needs of the eight Biospherians for the intended 2 years. Many unpleasant and unexpected problems arose, including a drop in atmospheric oxygen concentration to 14% (the level normally found at an elevation of 17,500 feet), high spikes in carbon dioxide concentrations, nitrous oxide concentrations high enough to impair the brain, an extremely high level of extinctions (including 19 of 25 vertebrate species and all pollinators brought into the enclosure, which would have ensured the eventual extinction of most of the plant species as well), overgrowth of aggressive vines and algal mats, and population explosions of crazy ants, cockroaches, and katydids. Even heroic personal efforts on the part of the Biospherians did not suffice to make the system viable and sustainable for either humans or many nonhuman species (Cohen and Tilman 1996).

MAJOR UNCERTAINTIES

Society would clearly profit by further investigation into some of the following broad research questions so that we might avoid on Biosphere 1, the earth, unpleasant surprises like those that plagued the Biosphere 2 project (Holdren 1991; Cohen and Tilman 1996; Daily 1997b):

- What is the relative impact of various human activities upon the supply of ecosystem services?
- What is the relationship between the condition of an ecosystem—that is, relatively pristine or heavily modified—and the quantity and quality of ecosystem services it supplies?
- To what extent do ecosystem services depend upon biodiversity at all levels, from genes to species to landscapes?

- To what extent have various ecosystem services already been impaired? And how are impairment and risk of future impairment distributed in various regions of the globe?
- How interdependent are different ecosystem services? How does exploiting or damaging one influence the functioning of others?
- To what extent, and over what time scale, are ecosystem services amenable to repair or restoration?
- How effectively, and at how large a scale, can existing or foreseeable human technologies substitute for ecosystem services? What would be the side effects of such substitutions?
- Given the current state of technology and the scale of the human enterprise, what proportion and spatial pattern of land must remain relatively undisturbed, locally, regionally, and globally, to sustain the delivery of essential ecosystem services?

CONCLUSIONS

The human economy depends upon the services performed "for free" by ecosystems. The ecosystem services supplied annually are worth many trillions of dollars. Economic development that destroys habitats and impairs services can create costs to humanity over the long term that may greatly exceed the short-term economic benefits of the development. These costs are generally hidden from traditional economic accounting, but are nonetheless real and are usually borne by society at large. Tragically, a short-term focus in land-use decisions often sets in motion potentially great costs to be borne by future generations. This suggests a need for policies that achieve a balance between sustaining ecosystem services and pursuing the worthy short-term goals of economic development.

REFERENCES

- Adams, R. McC. 1981. Heartland of Cities: Surveys of Ancient Settlement and Land Use on the Central Floodplain of the Euphrates, Chicago: University of Chicago Press.
- Alexander, S., S. Schneider, and K. Lagerquist. 1997. Ecosystem services: Interaction of Climate and Life. Pages 71-92 in G. Daily, editor. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, D.C.
- Allegre, C. and S. Schneider. 1994. The evolution of the earth. Scientific American 271: 44-51.
- Bawa, K. and M. Gadgil. 1997. Ecosystem services, subsistence economies and conservation of biodiversity. Pages 295-310 in G. Daily, editor. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, D.C.
- Bormann, F., G. Likens, D. Fisher, and R. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. Science 159: 882-884.

- Buchmann, S.L. and G.P. Nabhan. 1996. *The Forgotten Pollinators*. Island Press, Washington, D.C.
- Chanway, C. 1993. Biodiversity at risk: soil microflora. Pages 229-238 in M. A. Fenger, E. H. Miller, J. A. Johnson, and E. J. R. Williams, editors. *Our Living Legacy: Proceedings of a Symposium on Biological Diversity*. Royal British Columbia Museum, Victoria, Canada.
- Cohen, J.E. and D. Tilman. 1996. Biosphere 2 and biodiversity: The lessons so far. *Science* 274: 1150-1151.
- Colborn, T., D. Dumanoski, and J. P. Myers. 1996. *Our Stolen Future*. Dutton, New York.
- Daily, G.C. 1997a. Introduction: What are ecosystem services? Pages 1-10 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Daily, G.C. 1997b. Valuing and safeguarding Earth's life support systems. Pages 365-374 in G. Daily, editor. *Natures Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Daily, G.C., P.A. Matson, and P.M. Vitousek. 1997. Ecosystem services supplied by soil. Pages 113-132 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Daily, G.C. and P.R. Ehrlich. 1995. Population diversity and the biodiversity crisis. Pp. 41-51 in C. Perrings, K.G. Maler, C. Folke, C.S. Holling and B.O. Jansson (eds.), *Biodiversity Conservation: Problems and Policies*, Dordrecht, Kluwer Academic Press.
- DeBach, P. 1974. *Biological Control by Natural Enemies*. Cambridge University Press, London.
- Diamond, J. 1991. *The Rise and Fall of the Third Chimpanzee*. Radius, London.
- Dobson, A. 1995. Biodiversity and human health. *Trends in Ecology and Evolution* 10: 390-391.
- Dowling, H.F. 1977. *Fighting Infection*. Harvard Univ. Press, Cambridge, MA.
- Ehrlich, P.R. and A.H. Ehrlich. 1981. *Extinction*. Ballantine, New York.
- Ehrlich, P.R., A.H. Ehrlich, and J.P. Holdren. 1977. *Ecoscience: Population, Resources, Environment*. Freeman and Co., San Francisco.
- Ewel, K. 1997. Water quality improvement: evaluation of an ecosystem service. Pages 329-344 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Farnsworth, N.R., O. Akerele, A.S. Bingel, D.D. Soejarto, and Z.-G. Guo. 1985. Medicinal plants in therapy. *Bulletin of the World Health Organization* 63: 965-981.
- Felder, A. J. and D. M. Nickum. 1992. *The 1991 economic impact of sport fishing in the United States*. American Sportfishing Association, Alexandria, Virginia.
- FAO (United Nations Food and Agriculture Organization). 1990. *Soilless Culture for Horticultural Crop Production*. Rome: FAO.

- Grifo, F. and J. Rosenthal, editors. 1997. *Biodiversity and Human Health*. Island Press, Washington, D.C.
- Hall, D.O., F. Rosillo-Calle, R.H. Williams, and J. Woods. 1993. Biomass for energy: supply prospects. Pages 593-651 in T. Johansson, H. Kelly, A. Reddy, and R. Williams, editors. *Renewable Energy: Sources for Fuels and Electricity*. Island Press, Washington, D.C.
- Heal, G. 1994. Formation of international environmental agreements. Pages 301-332 in C. Carraro, editor, *Trade, Innovation, Environment*. Kluwer Academic Publishers, Dordrecht.
- Hillel, D. 1991. *Out of the Earth: Civilization and the Life of the Soil*. The Free Press, New York.
- Holdren, J. P. 1991. "Report of the planning meeting on ecological effects of human activities." National Research Council, 11-12 October, Irvine, California, mimeo.
- Holdren, J.P. and P.R. Ehrlich. 1974. Human population and the global environment. *American Scientist* 62: 282-292.
- Hughes, J.B., G.C. Daily, and P.R. Ehrlich. In prep. The importance, extent, and extinction rate of global population diversity.
- Ives, J. and B. Messerli. 1989. *The Himalayan Dilemma: Reconciling Development and Conservation*, London: Routledge.
- Jenny, H. 1980. *The Soil Resource*. Springer-Verlag, New York. Kaufman, L. and P. Dayton. 1997. Impacts of marine resource extraction on ecosystem services and sustainability. Pages 275-293 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Kellert, S.R. and E.O. Wilson, editors. 1993. *The Biophilia Hypothesis*. Island Press, Washington, D.C.
- Lanner, R.M. 1996. *Made for Eachother: A Symbiosis of Birds and Pines*. Oxford University Press, New York.
- Lawton, J. and R. May, editors. 1995. *Extinction Rates*. Oxford University Press, Oxford.
- Lee, K. 1985. *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press, New York.
- Leung, A.Y. and S. Foster. 1996. *Encyclopedia of Common Natural Ingredients Used in Food, Drugs, and Cosmetics*. John Wiley & Sons, Inc., New York.
- McCormick, K.D., M.A. Deyrup, E.S. Menges, S.R. Wallace, J. Meinwald, and T. Eisner. 1993. Relevance of chemistry to conservation of isolated populations: the case of volatile leaf components of *Dicerandra* mints. *Proc. Nat. Acad. Sci. USA* 90: 7701-7705.
- Myers, N. 1983. *A Wealth of Wild Species*. Westview Press, Boulder, CO.
- Myers, N. 1997. The world's forests and their ecosystem services. Pages 215-235 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Nabhan, G.P. and S.L. Buchmann. 1997. Pollination services: Biodiversity's direct link to world food stability. Pages 133-150 in G. Daily,

- editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- National Research Council (NRC). 1989. *Alternative Agriculture*. National Academy Press, Washington, D.C.
 - National Research Council (NRC). 1992. *Managing Global Genetic Resources: The U.S. National Plant Germplasm System*. National Academy Press, Washington, D.C.
 - Naylor, R. and P. Ehrlich. The value of natural pest control services in agriculture. Pages 151-174 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
 - Oldeman, L., V. van Engelen, and J. Pulles. 1990. "The extent of human-induced soil degradation, Annex 5" of L. R. Oldeman, R. T. A. Hakkeling, and W. G. Sombroek, *World Map of the Status of Human-Induced Soil Degradation: An Explanatory Note*, rev. 2d ed. Wageningen: International Soil Reference and Information Centre.
 - Overgaard-Nielsen, C. 1955. Studies on enchytraeidae 2: Field studies. *Natura Jutlandica* 4: 5-58.
 - Peterson, C.H. and J. Lubchenco. 1997. On the value of marine ecosystem services to society. Pages 177-194 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
 - Pimentel, D., C. Harvey, P. Resosudarmo, K. Sinclair, D. Kurz, M. McNair, S. Crist, L. Shpritz, L. Fitton, R. Saffouri, and R. Blair. 1995. "Environmental and economic costs of soil erosion and conservation benefits." *Science* 267: 1117-1123.
 - Pimentel, D., L. McLaughlin, A. Zepp, B. Lakitan, T. Kraus, P. Kleinman, F. Vancini, W. Roach, E. Graap, W. Keeton, and G. Selig. 1989. Environmental and economic impacts of reducing U.S. agricultural pesticide use. *Handbook of Pest Management in Agriculture* 4: 223-278.
 - Postel, S. and S. Carpenter. 1997. Freshwater ecosystem services. Pages 195-214 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
 - Prescott-Allen, R. and C. Prescott-Allen. 1990. How many plants feed the world? *Conservation Biology* 4: 365-374.
 - Principe, P.P. 1989. The economic significance of plants and their constituents as drugs. Pages 1-17 in H. Wagner, H. Hikino, and N.R. Farnsworth, editors. *Economic and Medicinal Plant Research*, Vol. 3, Academic Press, London.
 - Reid, W.V., S.A. Laird, C.A. Meyer, R. Gamez, A. Sittenfeld, D. Janzen, M. Gollin, and C. Juma. 1996. Biodiversity prospecting. Pages 142-173 in M. Balick, E. Elisabetsky, and S. Laird, editors. *Medicinal Resources of the Tropical Forest: Biodiversity and Its Importance to Human Health*. Columbia Univ. Press, New York.
 - Rouatt, J. and H. Katznelson. 1961. A study of bacteria on the root surface and in the rhizosphere soil of crop plants. *J. Applied Bacteriology* 24: 164-171.

- Sala, O.E. and J.M. Paruelo. 1997. Ecosystem services in grasslands. Pages 237-252 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Salati, E. 1987. The forest and the hydrological cycle. Pages 273-294 in R. Dickinson, editor. *The Geophysiology of Amazonia*. John Wiley and Sons, New York.
- Schlesinger, W. 1991. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego.
- Schneider, S. and P. Boston, editors. 1991. *Scientists on Gaia*. MIT Press, Boston.
- Schneider, S. and R. Londer. 1984. *The Coevolution of Climate and Life*. Sierra Club Books, San Francisco.
- Shiklomanov, I.A. 1993. World fresh water resources. Pp. 13-24 in P. Gleick, editor. *Water in Crisis: A Guide to the World's Fresh Water Resources*. Oxford University Press, New York.
- Shukla, J., C. Nobre, and P. Sellers. 1990. Amazon deforestation and climate change. *Science*. 247: 1322-1325.
- Tilman, D. 1997. Biodiversity and ecosystem functioning. Pages 93-112 in G. Daily, editor. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- Thompson, J.N. 1994. *The Coevolutionary Process*. Chicago Univ. Press, Chicago. United Nations Food and Agriculture Organization (UNFAO). 1993. *Marine Fisheries and the Law of the Sea: A Decade of Change*. Fisheries Circular No. 853, Rome.
- United Nations Food and Agriculture Organization (UNFAO). 1994. *FAO Yearbook of Fishery Statistics*. Volume 17.
- United States Department of Agriculture (USDA). 1993. *World Agriculture: Trends and Indicators, 1970-91*. Washington, DC: USDA.
- Vitousek, P., P. Ehrlich, A. Ehrlich, and P. Matson. 1986. Human appropriation of the products of photosynthesis. *BioScience* 36: 368-373.
- Vitousek, P., J. Aber, R. Howarth, G. Likens, P. Matson, D. Schindler, W. Schlesinger, and D. Tilman. 1997. Human alteration of the global nitrogen cycle: causes and consequences. *Issues in Ecology*, Volume 1, Spring 1997.
- Wilson, E.O. 1987. The little things that run the world: The importance and conservation of invertebrates. *Conservation Biology* 1: 344-346.
- Wilson, E.O. 1989. Threats to biodiversity. *Scientific American* Sept: 108-116.
- World Bank. 1991. *Agricultural Biotechnology: The Next Green Revolution?* World Bank Technical Paper no. 133. Washington, D.C.
- World Resources Institute (WRI). 1994. *World Resources: A Guide to the Global Environment*. Oxford University Press, Oxford.