Proc. Natl. Acad. Sci. USA
Vol. 93, pp. 2764–2769, April 1996
Ecology

Environmental services of biodiversity

NORMAN MYERS

Green College, Oxford University, United Kingdom OX3 8SZ

Contributed by Norman Myers, September 29, 1995

ABSTRACT Humans derive many utilitarian benefits from the environmental services of biotas and ecosystems. This is often advanced as a prime argument to support conservation of biodiversity. There is much to be said for this viewpoint, as is documented in this paper through a summary assessment of several categories of environmental services, including regulation of climate and biogeochemical cycles, hydrological functions, soil protection, crop pollination, pest control, recreation and ecotourism, and a number of miscellaneous services. It is shown that the services are indeed significant, whether in ecological or economic senses. Particularly important is the factor of ecosystem resilience, which appears to underpin many of the services. It should not be supposed, however, that environmental services stem necessarily and exclusively from biodiversity. While biodiversity often plays a key role, the services can also derive from biomass and other attributes of biotas. The paper concludes with a brief overview assessment of economic values at issue and an appraisal of the implications for conservation planning.

I. Introduction

Conservation biologists increasingly face the question, What is biodiversity good for? Naive as this may seem to some, it is a valid question. There is no longer enough room for a complete stock of biodiversity on an overcrowded planet with almost six billion humans and their multifarious activities, let alone a projected doubling of human numbers and a tripling or quadrupling of salient activities. So biodiversity must stake its claims for living space in competition with other causes. Generally speaking, biodiversity must urge the merits of its cause through what it contributes to human welfare, preferably doing it in the way that most appeals to political leaders and the general public, namely in economic terms.

In response to the question above, conservation biologists proclaim the many significant contributions of biodiversity to the human cause. There are two categories of contributions: material goods and environmental services. The first has been frequently and widely documented (1–4), principally in the form of new and improved foods, medicines and drugs, raw materials for industry, and sources of bioenergy. The second has been far less documented even though the issue was identified as unusually significant almost two decades ago (5) and even though its total value is surely far greater than that of the first (1, 6–9). The main reasons for this lamentable lacuna are that scientists find it much harder to demonstrate the precise nature of the services, and it is still harder to quantify them economically. Whereas the benefits of material goods tend to accrue to individuals, often as producers or consumers in the marketplace, the values of environmental services generally pertain to society, and hence they mostly remain unmarketed (10, 11).

This paper reviews our knowledge and understanding of the principal services at issue. The services are extremely diverse, and they occur in every last segment of the biosphere. So the paper is perforce restricted to an illustrative selection of the more significant services.

II. Conceptual Background

Biodiversity embraces the totality of life forms, from the planetary spectrum of species to subunits of species (races, populations) together with ecosystems and their ecological processes. The species component includes all plants, animals, and microorganisms, of which there are between 8 million and 30 million (conceivably 100 million) (12). The subspecies component includes populations, of which there could be many billions (13). Spanning both these main categories are various subdivisions, including community diversity, food web diversity, keystone diversity, and functional diversity.

Environmental services are also known as ecosystem services,* both terms reflecting environmental functions and ecological processes. They can be defined as any functional attribute of natural ecosystems that are demonstrably beneficial to humankind (15). They comprise the main indirect values of biodiversity, as opposed to direct values in the form of material goods such as timber, fish, plant-based pharmaceuticals, and germ-plasm infusions for major crops. They include generating and maintaining soils, converting solar energy into plant tissue, sustaining hydrological cycles, storing and cycling essential nutrients (notably in the form of nitrogen fixation), supplying clean air and water, absorbing and detoxifying pollutants, decomposing wastes, pollinating crops and other plants, controlling pests, running biogeochemical cycles (of such vital elements as carbon, nitrogen, phosphorus, and sulfur), controlling the gaseous mixture of the atmosphere (which helps to determine climate), and regulating weather and climate at both macro and micro levels. Thus they basically include three forms of processing, namely of minerals, energy, and water (16). In addition, biodiversity provides sites for research, recreation, tourism, and inspiration (1, 17, 18).

The bulk of this paper will be given over to describing and evaluating certain of these services. But first, a couple of caveats. It is far from true that all forms of biodiversity can contribute all environmental services or that similar forms of biodiversity can perform similar tasks with similar efficiency. How far do environmental services depend upon biodiversity *per se*? Recent research suggests that they are highly resilient to some loss of species and they can keep on supplying their services even in highly modified states. A sugarcane plantation may be more efficient at producing organic material than the natural vegetation it replaced, and a tree farm may be more capable of fixing atmospheric carbon than a natural forest. At the same time, many natural ecosystems with low biodiversity (e.g., tropical freshwater swamps) have a high capacity to fix carbon.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

*The term environmental services is preferred since it embraces the larger-scale and often more important services, such as the albedo stabilization supplied by the Amazonia and Zaire forests (14). These forest regions are too large to conform to the category of ecosystems as conventionally understood.

Similarly, the services supplied by one form of biodiversity in one locality may not necessarily be supplied by a similar form of biodiversity in another locality. Just because a wetland on the Louisiana coast performs a particular suite of functions, it cannot be assumed that a wetland on the Georgia coast will perform the same functions, still less an inland wetland in Massachusetts or California, and still less again a montane wetland in Sweden or a forest wetland in Thailand. Services tend to be quite site-specific. This makes it much more difficult for conservation biologists to demonstrate the intrinsic value of wetlands or any other biotopes.

Biodiversity plays two critical roles. (*i*) It provides the biospheric medium for energy and material flows, which in turn provide ecosystems with their functional properties; and (*ii*) it supports and fosters ecosystem resilience (17, 19–24). As biodiversity is depleted, there is usually a shift and often (though not always) a decline in the integrity of ecosystem processes that supply environmental services.

The second caveat is that we should distinguish between what can be called the ecologist's and the economist's mode of calculation of values at issue. The first favors estimating biodiversity's values "in themselves," i.e., the worth of a biodiversity attribute as manifested by its role in ecosystem workings (for example, the part played by forest cover in watershed functions). The second approach prefers to consider biodiversity's contributions as economic attributes, looking at the consequences of biodiversity decline for economic activities (both production and consumption) and assessing the resultant costs such as prevention of damage, compensatory alternatives, and substitutes (if any) (2, 11, 25). All this is a highly anthropocentric approach, and many ecologists consider that it severely underestimates total values at stake.

Both these approaches run the risk of viewing a segment of biodiversity—whether a species, a population, a gene reservoir, a biotope, or a biota—in isolation from its support system. A mammal species, a butterfly community, a wetland food web, or a forest ecosystem cannot exist except within the myriad ecological relationships and ecosystem processes (moisture supply, nutrient cycling, energy flow, and the like) of its environs, much if not most of which makes scant if any direct utilitarian contribution to human welfare. The only worthwhile approach is to conserve the lot—a strategy to be followed in fortunate circumstances such as when a keystone species serve as a flagship species too.

III. Assessment of Select Environmental Services

Environmental services are so abundant and diverse that I cannot do more here than look at an illustrative selection [for a comprehensive treatment from an ecological standpoint, see Ehrlich and Ehrlich (1), and from an economic standpoint, see Pearce and Moran (26)]. Note that while biodiversity plays a part in all these services, it may not always play a predominant or even a primary role, even though it almost always seems to play a significant role. In Instances 1–4 (below), the key contribution may be supplied by biomass or some other attribute of biotas and ecosystems (for further elaboration of this key question, see Section V below, *Biodiversity and Biomass*).

1. Climate. Biodiversity helps to maintain the gaseous composition of the atmosphere and thus to regulate climate. It also affects climate by cycling vast amounts of water. A leading example is provided by Amazonia, which contains two-thirds of all above-ground freshwater on Earth. At least half of Amazonia's moisture is retained within the forest ecosystem, being constantly transpired by plants before being precipitated back onto the forest, with a mean recycling time of 5.5 days (27).

There are other biodiversity/rainfall connections. In several parts of the humid tropics—the Panama Canal Zone, northwestern Costa Rica, southwestern Ivory Coast, montane Tanzania, southwestern India, northwestern Peninsular Malaysia, and parts of the Philippines among other areas—rainfall regimes have been disrupted if not depleted in the wake of deforestation (28).

2. Biogeochemical Cycles. The Earth's biotas are prime pumps in the major biogeochemical cycles (29–31). It is debatable, however, how far this function is impaired by loss of biodiversity in itself, rather than by loss of vegetation and other biomass (32, 33).

A notable illustration lies with the carbon cycle and, hence, with climate change in the form of global warming. Roughly half of global warming is due to build-up of anthropogenic carbon dioxide in the global atmosphere. More carbon dioxide is released than remains in the atmosphere, the rest being absorbed by the oceans and terrestrial biotas.

While vegetation can serve as a major sink of carbon dioxide, we do not know how much, nor how far, the function depends on biodiversity. Preliminary evidence shows that species-rich ecosystems can often (though not always) consume carbon dioxide at a faster rate than less diverse ecosystems; and in turn this suggests that biodiversity decline may promote the build-up of carbon dioxide (34). In addition, to the extent that species-rich ecosystems produce more biomass, they consume more carbon dioxide, thereby reducing the build-up of carbon dioxide.

The value of carbon storage in tropical forests as a counter to global warming is estimated to be in the order of $1000 to $3500 per hectare per year (35), depending upon the type of forest and primarily reflecting the amount of biomass in the forest (rather than the amount of biodiversity in forest communities—though the first is to some extent a function of the second). The value of the carbon storage service supplied by Brazilian Amazonia is estimated to be some $46 billion (36). It has been further estimated that replacing the carbon storage function of all tropical forests would cost $3.7 trillion (37). But note a strong qualifier: the forests supply the service by virtue of their biomass, in which biodiversity appears to play a vital though not predominant role.

3. Hydrological Functions. Plants play a part in hydrological cycles in addition to those cited in Item 1, by controlling water runoff. Thick and sturdy vegetation permits a slower and more regulated runoff, allowing water supplies to make a steadier and more substantive contribution to their ecosystems, instead of quickly running off into streams and rivers—possibly resulting in flood and drought regimes downstream. Excessive runoff causes soil erosion in catchment zones and siltation in valleyland water courses. Siltation of reservoirs costs the global economy some $6 billion a year in lost hydropower and irrigation water (37).

In the 120-km^2 Bacuit Bay with its 78-km^2 drainage basin on Palawan Island in the Philippines, logging on steep slopes has increased soil erosion 235 times above that for undisturbed forest, with a "silt smother" effect for the Bay's coral reef and its fisheries that reduced commercial revenues by almost half in the mid-1980s (38). The montane forest of the Rwanda Volcanoes Park, home to one of the last populations of the mountain gorilla, covers only about 1% of Rwanda but acts as the sponge that absorbs and metes out about 10% of agricultural water for that severely overpopulated nation (39). At the Korup Park in Cameroon, watershed functions (flood prevention, protection of fisheries, and soil conservation) have a net present value of $85 per hectare (40). In Java, siltation of reservoirs, irrigation systems and harbors levied damage costs worth $58 million in 1987, equivalent to 0.5% of agricultural gross domestic product (41).

Consider too the important though little recognized services performed by wetlands. These services include supply of freshwater for household needs, sewage treatment, cleansing of industrial wastes, habitats for commercial and sport fisheries, recreation sites, and storm protection (42). Their economic values can be sizeable (43). Louisiana wetlands are estimated to be worth \$6000–16,000 per hectare with an 8% discount rate or \$22,500–42,500 per hectare with a 3% discount rate. At the lowest value, the current annual rate of loss of these wetlands is levying costs of about \$600,000 per km^2 per year, and at the largest value, levying \$4.4 million (late 1980s values). The most valuable wetlands service by far is storm protection (44). Marshlands near Boston are valued at \$72,000 per hectare per year solely on the basis of their role in reducing flood damage (45).

Particularly important wetlands are to be found in estuaries. They feature rapid plant and algal growth that provides the start of food chains for local fisheries, and they serve as nurseries for the juvenile stages of many marine fish species. In the past 50 years, many U.S. estuaries have been severely damaged by industrial pollution, dumping of untreated residential sewage, and coastal development. The National Marine Fisheries Service estimates this damage has cost the nation more than \$200 million per year just in the lost productive value of commercial fish and sport fish (2).

4. Soil Protection. In similar style, vegetation and to some extent biodiversity protects soil cover. Soil erosion is a major problem in many parts of the world since it leads to (*i*) significant declines in soil fertility and, thus, in the productivity of croplands and pastures and (*ii*) sedimentation of rivers and other water bodies affecting downstream communities. Four-fifths of the world's agricultural soils are affected by erosion, and every year 75 billion tonnes (1 tonne = 1000 kg) of topsoil are washed or blown away, causing 80,000 km^2 to be lost to agriculture. In the past 200 years, the average topsoil depth in the United States has declined from 23 cm to 15 cm, costing the American consumer around \$300 per year through loss of nutrients and water and with total costs to the United States of \$44 billion. Worldwide costs of soil erosion are in the order of \$400 billion per year or equivalent to half of what the world spends on military activities (46).

5. Crop Pollination. About one-third of the human diet depends on insect-pollinated vegetables, legumes, and fruits. Wild bees and honey bees pollinate \$30 billion worth of 90 U.S. crops annually, plus many natural plant species. On a bright sunny day in upstate New York, bees can pollinate as many as one trillion blossoms. Honey bee numbers in the United States have dropped by about 20% during the period from mid-1990 to mid-1994, due to the introduction of two alien parasitic mites. As a result, almond growers in California, with a crop worth \$800 million a year, have had to import bees from as far away as Florida and South Dakota. Pollination is a service for which there is no technological substitute (47).

6. Pest Control. Around 35% of the world's crop production is lost to pests, of which there are at least 67,000 recognized species. Only about 300 species have been targeted by biological controls, and of these 120 species have been success stories. So there is much scope to draw on the vast stock of natural controls "out there" in the form of predators and parasites, plus host plant resistance (17, 48, 49).

7. Ecotourism. Biodiversity plays a vital part in the fast-growing sector of ecotourism. Each year people taking nature-related trips contribute to the national incomes of countries concerned a sum estimated to be at least \$500 billion, perhaps twice as much (50, 51). Much of the enjoyment of these ecotourists reflects the biodiversity they encounter.

In the late 1970s, a single lion in Kenya's Amboseli Park earned \$27,000 per year in tourist revenues, while an elephant herd earned \$610,000 per year (52). In 1994, whale watching in 65 countries and dependent territories attracted 5.4 million viewers and generated tourism revenues of \$504 million, with annual rates of increase of more than 10% and almost 17%, respectively. A pod of 16 Bryde's whales at Ogata in Japan would, according to very conservative estimates, earn at least \$41 million from whale watchers over the next 15 years (and be left alive), whereas if killed (as a one-shot affair) they would generate only \$4.3 million (53). In 1970, ecotourism in Costa Rica's Monteverde Cloud Forest Reserve generated revenues of \$4.5 million, or \$1250 per hectare—to be compared with \$30–100 per hectare for land outside the reserve (54). Florida's coral reefs are estimated to be worth \$1.6 billion a year in tourism revenues (55).

8. Miscellaneous Services. Now for a brief selection of some further services: The larvae of certain aquatic flies—notably mayflies, stone flies, caddis flies, and true flies—can be used to identify point sources of chemical contaminants in water bodies, especially with respect to molybdenum, manganese, and copper (56). Other species, such as earthworms and certain fish, birds, and mammals, serve as biological monitors of various kinds of widespread pollution. A number of wild plants, for instance the water hyacinth, act as first-rate depolluting agents in sewage lagoons. A few plant species can even register radiation, some of them more sensitively than a dosimeter (57).

A number of tree species (beech, elm, oak, sycamore, willow, and elder) in cities serve to clean up pollution, notably sulfur dioxide (58). Trees also act as air coolants. A 20-m shade tree can mitigate 900,000 BTUs (1 BTU = 1060 J) of heat, worth three tonnes of air conditioning a day at a cost of \$20 in the United States (early 1980s value) (59).

Certain animals, such as dogs, cats, horses, chimpanzees, and snakes, appear able to anticipate even slight earth tremors and, thus, to warn of impending earthquakes (60).

Many species act as research models. The woodpecker, with a neck built to withstand severe whiplash, has offered a blueprint for crash helmets. A species of chalcid wasp with unusual capacity for hovering has aided with the design of an improved helicopter. Squids, with nerve fibers 1000 times larger in cross-section than human nerve fibers, supply neuroscientists with crucial insights into the human nervous system.

For a lengthy listing of such miscellaneous items, see Myers (3).

IV. Ecosystem Resilience

Many of the services listed above are closely associated with the phenomenon of ecosystem resilience. If this resilience declines, the services can generally be expected to decline, too. This aspect is so important that, while it can be characterized as a service (or rather, as a kind of super-service), it warrants treatment on its own.

Resilience can be defined as the ability of ecosystems to resist stresses and shocks, to absorb disturbance, and to recover from disruptive change (many of these perturbations being due to human activity and especially economic activity) (19, 24, 61, 62). Or, to express the concept more formally, it connotes an equilibrium-theory idea to the effect that ecosystems with their cybernetic mechanisms display homeostatic attributes that allow them to maintain function in the face of stress-induced structural changes (15, 63). How far is ecosystem resilience dependent on biodiversity? If there is indeed a directly causative connection, this may turn out to be the number one service supplied by biodiversity insofar as all other services appear to depend on it to some degree (19, 64, 65).

There is some evidence that biodiversity can make an important contribution to ecosystem resilience (66–68). At the same time, there is much uncertainty about several associated factors (69): the range of species composition within which ecosystems and communities function (70); the part played by species richness (only one aspect of biodiversity) in ecosystem attributes such as trophic structures and successional stages (62); the contribution of dominant species such as keystone mutualists and critical-link species (71); the link between biodiversity and ecosystem scale (13); and the relationships among biodiversity, biomass, and ecosystem productivity (19) (for more on this last point, see Part V below). Moreover, each of these factors may operate differently when an ecosystem is at equilibrium or in transition (62). All this means that the environmental services supplied by biodiversity may be quite wide in scope, while localized in scale and particularized in effect (23, 72).

There is much controversy about the biodiversity/resilience relationship. In certain circumstances, biodiversity can enhance ecosystem performance overall (19, 62). For instance, more diverse plant communities tend to reveal greater primary productivity under conditions of laboratory experiment (34, 73); and the primary productivity of species-rich plant communities in grasslands is more resistant to, and recovers more fully from, major stresses such as droughts (24, 74–76). Then there is uncertainty about threshold effects (except that they are specially significant). At what point of biodiversity decline do ecosystems start to lose the self-organizing capacity and, hence, the resilience that apparently enables them to provide certain environmental services (67)? In terms of net primary productivity, evidence suggests that above a threshold number of species, there is no gain in function (16).

The biodiversity contribution to resilience extends of course to subunits of species. Populations differ in their genetic structure by virtue of their adaptation to environmental conditions and random chance. The genetic variability represented by geographically disparate populations helps assure the ability of an entire species to respond evolutionarily to environmental change (13, 77, 78). If, for example, there is rapid climatic change (as is likely to ensue through global warming), a species with many populations is more likely to include members genetically adapted to the new conditions than a species with a single population.

This behoves us to expand our purview of the mass extinction crisis underway and to consider a crunch question. Suppose, as is entirely likely, that within the coming few decades we lose 50% of all species and 90% of populations of surviving species. Which will entail the greatest repercussions for ecosystem resilience in a world undergoing environmental upheaval of altogether unprecedented scope and scale? This is a vital issue for conservation biologists—also political leaders, policy makers, the general public, and indeed anybody concerned about the future habitability of the biosphere.

Herein too lies the question of species redundancy. This postulates that many if not most species are not required for ordinary ecosystem functioning. As noted, ecosystem processes often appear to be quite resilient to biodiversity decline: they can keep on supplying environmental services after losing a good number of species and large numbers of populations (74). Plainly, then, there is much redundancy built into nature. Britain has lost the bear, the wolf, and other top carnivores, plus many herbivores and perhaps detritivores, with little if any apparent harm to its ecosystems (albeit thanks in many instances to compensatory management such as sport hunting and culling of deer). North America, Madagascar, and Australia have lost a large share of their vertebrate megafauna within the recent past, yet there is scant evidence of profound or pervasive ecosystem decay (but see ref. 79).

It is incorrect, then, to say that each species has its essential part to play in ecosystems, let alone that it is a mainstay of stability or resilience. It is also incorrect to say that we can lose lots of species with impunity. A cut-off stage would (eventually) arrive when there would be simply too few species to maintain basic ecosystem functions. Where is the "grey" zone where biodiversity decline starts to approach the threshold of irreversible ecosystem injury? Scientists have all too little idea, and so they would do well to recall the rivet popping analogy (1). Similarly pertinent is the notion that redundancy itself may well have a functional value for ecosystems, as a kind of "nature's insurance"—a benefit that generally becomes operative only within extended time frames (23, 24, 68). To this extent, we may eventually find that biodiversity contributes an environmental service of semiabsolute value in the sense of reducing severe risk but that it plays only a relatively significant role in supplying the many other services listed.

In conclusion to this review of ecosystem resilience and of biodiversity's part in it, recall that the issue is so beset with uncertainty of multiple sorts that we shall never be scientifically assured as to how far biodiversity limits can be pressed before unacceptable risks are encountered. Final knowledge comes only with a post mortem. Note the warning of that biodiversity doyen, Edward O. Wilson (80):

> "If enough species are extinguished, will ecosystems collapse and will the extinction of most other species follow soon afterwards? The only answer anyone can give is: Possibly. By the time we find out, however, it might be too late. One planet, one experiment."

V. Biodiversity and Biomass

Much of Part IV has brought up a basic issue: environmental services often appear to depend not only or not so much on biodiversity as on biomass. When a patch of natural forest in the humid tropics is eliminated in favor of a commercial pine plantation or even a tea crop (dozens of plant species replaced by one), the new vegetation can supply certain of the same ecological functions, notably protection of soil cover and hydrologial systems (81). Similarly, it is not only biodiversity that enables plants to exploit energy from the sun. Photosynthesis can often be generated most productively (though perhaps with less long-term stability) by a monoculture of, e.g., sugarcane. So it is important not to confuse biodiversity with biomass—or, for that matter, associated factors such as community make-up and vegetation structure.

Plants cycle moisture from the soil. A single rainforest tree can, during a lifetime of 100 years, return at least 10 million liters of water to the atmosphere (1). But a succession of 12,000 corn stalks occupying 0.1 hectare (roughly the same area as taken up by a rainforest tree) for a few months each year would, in the case of the United States and during the same century, transfer 0.5 million liters per year and 50 million liters in 100 years—though the corn would need massive inputs of synthetic fertilizer and other agronomic inputs to do it (46).

Similarly, a carbon sink can be maintained by a tract of rainforest or a plantation of eucalyptus trees—though a plantation would probably provide less cycling of minerals and other soil nutrients, be more vulnerable to pest outbreaks, and supply next to nothing in the way of "genetic library" services. The estimated 20,000 species of ants number somewhere between one trillion and 10 trillion individuals, with a biomass as much as all humankind; in certain localities they can make up 25% of the animal biomass, and in sectors of the Amazonia forest they constitute more than four times the biomass of all land vertebrates combined (82). We can still ask, however, whether ants' multifarious activities could not be performed more or less as well with an equal amount of biomass containing far fewer species.

VI. Some Economic Dimensions

It is the aim of this paper to demonstrate the scope and scale of environmental services and their values, rather than to engage in a comprehensive assessment of their values in economic terms. Of course it helps to have some idea of how far the economic values are significant, and so the paper presents a few illustrative instances of values in question.

More revealing, however, is an indication—however preliminary and exploratory—of the economic values overall implicit in the environmental services supplied by some particular ecosystem or region. Note, then, that the annual value of nonmarketed environmental services provided primarily by wetlands, forests, and agricultural areas in the state of Georgia have been estimated to be worth $2.6 billion in 1982 dollars—a sum to be compared with the annual value of the state's marketed agricultural products, $2.8 billion, and marketed timber products, $4.5 billion (83). In the state of Oregon, environmental services in the form of amenity alone are estimated to be worth at least $500 per citizen per year (84).

On a larger scale, consider the cost of Biosphere 2, being the man-made technosphere in the Arizona desert that (marginally) regulated life-support systems for eight Biospherians over 2 years: about $150 million, or $9 million per person per year. These same services are provided to the rest of us by natural processes, at no cost. But if we were charged at the rate levied by Biosphere 2, the total bill for all Earthospherians would come to $3 quintillion for the current generation alone (85).

VII. Conclusion

First, this paper demonstrates that (*i*) the environmental services of biodiversity are certainly significant, probably much more so than the direct benefits of biodiversity in the form of material goods; and (*ii*) all too little is known about the nature, scope, and scale of these services, whether in environmental or economic senses. This places a premium on research to increase our understanding—a challenge made all the more pressing by the expansion of the human niche and all that entails for progressively increasing pressures on biodiversity's habitats and life-support systems.

It might not be of much profit, however, to engage in more, and more detailed, documentation of the services, even though no more than a start on gathering data and other forms of information has been made. The critical track ahead lies not so much with knowledge as with understanding. A far greater analysis of basic key questions is needed, such as: how does biodiversity generate environmental services; how much biodiversity is needed to do the job; and how far does the relationship depend on local circumstances, especially site conditions (which may change over time)? On top of these questions and others already recognized, there are surely other vital questions that have not even been identified and defined.

Herein lies the biggest challenge of all, to determine a comprehensive answer to the point posed at the start of this article, What is biodiversity good for? At present rates of research and analysis, responses to that question may eventually be found only by discovering what has been lost after much biodiversity together with its environmental services has been eliminated.

A second conclusion is that conservation biologists should feel more inclined to simply reject the question, What is biodiversity good for? There will not be anywhere near a sufficient answer within a time frame to conclusively persuade political leaders, policy makers, and the public (let alone the professional skeptics). Rather, the uniqueness and irreversibility arguments should be invoked and thus the burden of proof should be thrown on the doubters, requiring them to demonstrate that biodiversity is generally worth so little that it can be dispensed with if human welfare demands as much through, e.g., agricultural encroachment on wildland habitats. True, there is vast uncertainty about what biodiversity contributes to the human cause. But due to the asymmetry of evaluation, the doubters are effectively saying they are completely certain that we, and our descendants for millions of years (until evolution restores the loss), can manage well enough without large quantities of biodiversity.

I assert, above all, that biodiversity conservation is complementary to, rather than competitive with, other pursuits of human well-being. The time has come when biodiversity cannot be safeguarded primarily in protected areas. For one thing, there is not nearly enough of them in the right places, and most of them are too small—and there is poor chance that many more can be established in an increasingly crowded world. For another thing, one-third of protected areas in the tropics (the most vital zone from the biodiversity standpoint) are already being encroached upon by expanding agriculture, and this trend is likely to accelerate given the burgeoning numbers of land-hungry peasants. For still another and yet more significant thing, several of the best managed parks and reserves are being overtaken by acid rain; similarly, no protected area can ever be shielded from UV-B radiation and global warming. Within a few decades, indeed, there may be no more protected areas [to cite McNeely (86)]:

> "either because they have been over-taken by land-hungry peasants or grandscale pollution, or because we have finally found a way to manage all our landscapes that the needs of biodiversity are taken care of automatically."

This all means that biodiversity can ultimately be saved only by saving the biosphere as well. Thus the following things must be undertaken on all kinds of other good grounds: stem acid rain, push back the deserts, replant the forests, restore topsoil, reverse ozone-layer depletion, stabilize climate, etc. (also of course halt population growth, reduce overconsumption, cut back on global inequities, etc.). In this writer's view, it is far more important to focus on ways to meet these imperatives than to engage in finer-grain assessment of environmental services.

Emphatic thanks to David Duthie and Stuart Pimm for their unusually helpful comments on an early draft of this paper. This article has been written with funding through the Pew Fellows Programme.

1. Ehrlich, P. R. & Ehrlich, A. H. (1992) *Ambio* **21,** 219–226.
2. McNeely, J. A. (1988) *Economics and Biological Conservation: Developing and Using Economic Incentives to Conserve Biological Resources* (Int. Union for Conservation of Nature and Natural Resources, Gland, Switzerland).
3. Myers, N. (1983) *A Wealth of Wild Species* (Westview, Boulder, CO).
4. Oldfield, M. L. (1989) *The Value of Conserving Genetic Resources* (Sinauer, Sunderland, MA).
5. Westman, W. E. (1977) *Science* **197,** 960–964.
6. Bishop, R. C. (1987) in *Valuing Wildlife: Economic and Social Perspectives*, eds. Decker, D. J. & Goff, D. R. (Westview, Boulder, CO), pp. 24–34.
7. di Castri, F. & Younis, T. (1990) *Ecosystem Function of Biodiversity* (Int. Union Biol. Sci., Paris), Biol. Int. Special Issue 22.
8. Green, C. H. & Tunstall, S. M. (1991) *J. Environ. Manage.* **33,** 123–141.
9. Risser, P. G. (1995) *Conserv. Biol.* **9,** 742–746.
10. Barbier, E. B., Burgess, J. C. & Folke, C. (1994) *Paradise Lost? The Ecological Economics of Biodiversity* (Earthscan, London).
11. Brown, K., Pearce, D., Perrings, C. & Swanson, T. (1993) *Economics and the Conservation of Global Biological Diversity* (Global Environment Facility, The World Bank, Washington, DC).
12. Ehrlich, P. R. & Wilson, E. O. (1991) *Science* **253,** 758–762.
13. Ehrlich, P. R. & Daily, G. C. (1993) *Ambio* **22,** 64–68.
14. Gash, J. H. C. & Shuttleworth, W. J. (1992) in *Tropical Forests and Climate*, ed. Myers, N. (Kluwer Academic, Dordrecht, The Netherlands), pp. 123–134.
15. Cairns, J. & Pratt, J. R. (1995) in *Evaluating and Monitoring the Health of Large-Scale Ecosystems*, eds. Rapport, D. J., Gaudet, C. L. & Calow, P. (Springer, Berlin), pp. 63–76.
16. Perrings, C. (1987) *Economy and Environment: A Theoretical Essay on the Interdependence of Economic and Environmental Systems* (Cambridge Univ. Press, Cambridge, U.K.).
17. Baskin, Y. (1994) *BioScience* **44,** 657–666.
18. Cairns, J. & Niederlehner, B. R. (1994) *Environ. Health Perspect.* **102,** 936–939.
19. Schulze, E.-D. & Mooney, H. A., eds. (1994) *Biodiversity and Ecosystem Function* (Springer, New York), Study Ed.

20. Ehrlich, P. R. & Roughgarden, J. (1987) *The Science of Ecology* (Macmillan, New York).
21. Folke, C. & Kaberger, T., eds. (1991) *Linking the Natural Environment and the Economy* (Kluwer Academic, Dordrecht, The Netherlands).
22. Holling, C. S. (1986) in *Sustainable Development of the Biosphere*, eds. Clark, W. C. & Munn, R. E. (Cambridge Univ. Press, Cambridge, U.K.).
23. Perrings, C. (1995) in *The Economics and Ecology of Biodiversity Decline: The Forces Driving Global Change*, ed. Swanson, T. M. (Cambridge Univ. Press, Cambridge, U.K.), pp. 69–77.
24. Walker, B. H. (1992) *Conserv. Biol.* **6,** 18–23.
25. Aylward, B. & Barbier, E. B. (1992) *Biodiversity Conserv.* **1,** 34–50.
26. Pearce, D. & Moran, D. (1994) *The Economic Value of Biodiversity* (Earthscan, London).
27. Salati, E. & Nobre, C. A. (1992) in *Tropical Forests and Climate*, ed. Myers, N. (Kluwer Academic, Dordrecht, The Netherlands), pp. 177–196.
28. Meher-Homji, V. M. (1992) in *Tropical Forests and Climate*, ed. Myers, N. (Kluwer Academic, Dordrecht, The Netherlands), pp. 163–173.
29. Odum, E. P. (1993) *Ecology and Our Endangered Life-Support Systems* (Sinauer, Sunderland, MA).
30. Ricklefs, R. E. (1987) *Science* **235,** 167–171.
31. Schlesinger, W. H. (1991) *Biogeochemistry: An Analysis of Global Change* (Academic, San Diego).
32. Kareiva, P. M., Kingsolver, J. G. & Huey, R. B., eds. (1993) *Biotic Interactions and Global Change* (Sinaeur, Sunderland, MA).
33. Vitousek, P. M. & Hooper, D. U. (1994) in *Biodiversity and Ecosystem Function*, eds. Schulze, E.-D. & Mooney, H. A. (Springer, New York), pp. 3–14.
34. Naeem, S., Tompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M. (1994) *Nature (London)* **368,** 734–737.
35. Pearce, D. & Moran, D. (1995) *The Economic Consequences of Biodiversity Loss* (Centre for Social and Economic Research on the Global Environment, University College, London).
36. Gutierrez, B. & Pearce, D. W. (1992) *Estimating the Environmental Benefits of the Amazon Forest: An International Evaluation Exercise* (Centre for Social and Economic Research on the Global Environment, University College, London).
37. Panayotou, T. & Ashton, P. S. (1992) *Not By Timber Alone* (Earthscan, London).
38. Hodgson, G. & Dixon, J. A. (1988) *Logging Versus Fisheries and Tourism in Palawan* (East-West Environment and Policy Inst. East-West Center, Honolulu).
39. McNeely, J. A. & Miller, K. R. (1984) *National Parks, Conservation and Development: The Role of Protected Areas in Sustaining Society* (Smithsonian Inst. Press, Washington, DC).
40. Ruitenbeek, J. (1989) *Social Cost-Benefit Analysis of the Korup Project, Cameroon* (World Wide Fund for Nature-U.K., Godalming, U.K.).
41. Magrath, W. & Arens, P. (1989) *The Costs of Soil Erosion on Java: A Natural Resource Accounting Approach* (The World Bank, Washington, DC).
42. Mitsch, W. J. & Gosselink, J. G. (1993) *Wetlands* (Reinhold, New York), 2nd Ed.
43. Folke, C. (1991) in *Linking the Natural Environment and the Economy*, eds. Folke, C. & Kaberger, T. (Kluwer, Dordrecht, The Netherlands), pp. 141–171.
44. Costanza, R., Farber, S. C. & Maxwell, J. (1989) *Ecol. Econ.* **1,** 335–361.
45. Hair, J. D. (1988) *The Economics of Conserving Wetlands: A Widening Circle* (Natl. Wildlife Fed., Washington, DC).
46. Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R. & Blair, R. (1995) *Science* **267,** 1117–1122.
47. Pimentel, D., Stachow, U., Takacs, D. A., Brubaker, H. W., Dumas, A. R., Meaney, J. J., O'Neil, J. A. S., Onsi, D. E. & Corzilius, D. B. (1992) *BioScience* **42,** 354–362.
48. Pimentel, D. (1991) *Crop Prot.* **10,** 243–253.
49. Gillis, A. M. (1992) *BioScience* **42,** 482–485.
50. Eagles, P. F. J., Buse, S. D. & Hvengaard, G. T., eds. (1993) *The Ecotourism Society Annotated Bibliography* (Ecotourism Soc., Bennington, VT).
51. Whelan, T., ed. (1991) *Nature Tourism: Managing for the Environment* (Island Press, Washington, DC).
52. Western, D. & Henry, W. (1979) *BioScience* **29,** 414–418.
53. Hoyt, E. (1995) *The Worldwide Value and Extent of Whale Watching, 1995* (Whale and Dolphin Conserv. Soc., Bath, U.K.).
54. Tobias, D. & Mendelsohn, R. (1991) *Ambio* **20,** 91–93.
55. Adams, J. (1995) *Ecotourism: Conservation Tool or Threat?* (World Wildlife Fund-US, Washington, DC).
56. Root, M. (1990) *BioScience* **40,** 83–86.
57. Mansfield, T. A., ed. (1976) *Effects of Air Pollutants on Plants* (Cambridge Univ. Press, Cambridge, U.K.).
58. Roberts, B. R. (1979) *Trees as Biological Filters* (U.S. Dept. Agriculture, Delaware, OH).
59. Dove, M. R. (1982) cited in Cairns, J. & Niederlehner, B. R. (1994) *Environ. Health Perspect.* **102,** 936–939.
60. Kerr, R. A. (1980) *Science* **208,** 695–696.
61. Ehrlich, P. R. (1986) *The Machinery of Nature* (Simon & Schuster, New York).
62. Pimm, S. L. (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities* (Univ. Chicago Press, Chicago).
63. Odum, E. P. (1985) *BioScience* **35,** 419–422.
64. Perrings, C., Maler, K.-G., Folke, C., Holling, C. S. & Jansson, B. O., eds. (1995b) *Biodiversity Loss: Ecological and Economic Issues* (Cambridge Univ. Press, Cambridge, U.K.).
65. Ricklefs, R. E. & Schluter, D., eds. (1993) *Species Diversity in Ecological Communities* (Univ. Chicago Press, Chicago).
66. Jones, C. G. & Lawton, J. H., eds. (1995) *Linking Species and Ecosystems* (Chapman & Hall, London).
67. Pimm, S. L. (1994) in *Biodiversity and Ecosystem Function*, eds. Schulze, E.-D. & Mooney, H. A. (Springer, New York), pp. 347–360.
68. Walker, B. (1995) *Conserv. Biol.* **9,** 747–752.
69. Perrings, C. & Opschoor, H. (1994) *Environ. Resource Econ.* **4,** 1–11.
70. Solbrig, O. T. (1991) *Environment* **33,** 10–23.
71. Mills, L. S., Soule, M. E. & Doak, D. F. (1993) *BioScience* **43,** 219–224.
72. Common, M. & Perrings, C. (1992) *Ecol. Econ.* **6,** 9–15.
73. Kareiva, P. (1994) *Nature (London)* **368,** 686–687.
74. Lawton, J. H. & Brown, V. K. (1994) in *Biodiversity and Ecosystem Function*, eds. Schulze, E.-D. & Mooney, H. A. (Springer, New York), pp. 255–270.
75. Tilman, D. & Downing, J. A. (1994) *Nature (London)* **376,** 363–365.
76. Walker, B. H. (1993) *Ambio* **22,** 80–87.
77. Caro, T. M. & Laurenson, M. K. (1994) *Science* **263,** 485–486.
78. Rawls, K., Ballou, J. D. & Brownwell, R. L. (1993) *Biol. Conserv.* **25,** 209–215.
79. Owen-Smith, N. (1988) *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge Univ. Press, Cambridge, U.K.).
80. Wilson, E. O. (1992) *The Diversity of Life* (Harvard Univ. Press, Cambridge, MA).
81. Myers, N. (1992) *The Primary Source* (Norton, New York).
82. Wilson, E. O. (1995) *Naturalist* (Allen Lane, London).
83. Turner, M. G., Odum, E. P., Costanza, R. & Springer, T. M. (1988) *Environ. Manage.* **12,** 209–217.
84. Durning, A. T. (1992) *How Much is Enough?* (Worldwatch Inst., Washington, DC).
85. Avise, J. C. (1994) *Conserv. Biol.* **8,** 327–329.
86. McNeely, J. A. (1990) *Environment* **(Jan/Feb),** 16–20 and 36–41.