Essay

Biodiversity Loss Threatens Human Well-Being

Sandra Díaz*, **Joseph Fargione, F. Stuart Chapin III, David Tilman**

The diversity of life on Earth is dramatically affected by human alterations of ecosystems [1]. Compelling evidence now shows that the reverse is also true: biodiversity in the broad sense affects the properties of ecosystems and, therefore, the benefits that humans obtain from them. In this article, we provide a synthesis of the most crucial messages emerging from the latest scientific literature and international assessments of the role of biodiversity in ecosystem services and human well-being.

Human societies have been built on biodiversity. Many activities indispensable for human subsistence lead to biodiversity loss, and this trend is likely to continue in the future. We clearly benefit from the diversity of organisms that we have learned to use for medicines, food, fibers, and other renewable resources. In addition, biodiversity has always been an integral part of the human experience, and there are many moral reasons to preserve it for its own sake. What has been less recognized is that biodiversity also influences human well-being, including the access to water and basic materials for a satisfactory life, and security in the face of environmental change, through its effects on the ecosystem processes that lie at the core of the Earth's most vital life support systems (Figure 1).

Three recent publications from the Millennium Ecosystem Assessment [2–4], an initiative involving more than 1,500 scientists from all over the world [5], provide an updated picture of the fundamental messages and key challenges regarding biodiversity at the global scale. Chief among them are: (a) human-induced changes in land cover at the global scale lead to clear losers and winners among species in biotic communities; (b) these changes have large impacts on ecosystem

processes and, thus, human well-being; and (c) such consequences will be felt disproportionately by the poor, who are most vulnerable to the loss of ecosystem services.

What We Do Know: Functional Traits Matter Most

Biodiversity in the broad sense is the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system (Figure 2). Biodiversity influences ecosystem services, that is, the benefits provided by ecosystems to humans, that contribute to making human life both possible and worth living [4] (Box 1). As well as the direct provision of numerous organisms that are important for human material and cultural life (Figure 1, path 1), biodiversity has well-established or putative effects on a number of ecosystem services mediated by ecosystem processes (Figure 1, path 2). Examples of these services are pollination and seed dispersal of useful plants, regulation of climatic conditions suitable to humans and the animals and plants they consider important, the control of agricultural pests and diseases, and the regulation of human health. Also, by affecting ecosystem processes such as biomass production by plants, nutrient and water cycling, and soil formation and retention, biodiversity indirectly supports the production of food, fiber, potable water, shelter, and medicines. The links between biodiversity and ecosystem services have been gaining increasing attention in the scientific literature of the past few years [2–4,6]. However, not until now has there been an effort to summarize those components of biodiversity that do, or should, matter the most for the provision of these services, and the underlying mechanisms explaining those links (Table 1; see also [3]).

A few key messages can be drawn from existing theory and empirical

studies. The first is that the number and strength of mechanistic connections between biodiversity and ecosystem processes and services clearly justify the protection of the biotic integrity of existing and restored ecosystems and its inclusion in the design of managed ecosystems. All components of biodiversity, from genetic diversity to the spatial arrangement of landscape units, may play a role in the long-term provision of at least some ecosystem services. However, some of these components are more important than others in influencing specific ecosystem services. The evidence available indicates that it is functional composition—that is, the identity, abundance, and range of species traits—that appears to cause the effects of biodiversity on many ecosystem services. At least among species within the same trophic level (e.g., plants), rarer species are likely to have small effects at any given point in time. Thus, in natural systems, if we are to preserve the services that ecosystems provide to humans, we should focus on preserving or restoring

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Essays articulate a specific perspective on a topic of broad interest to scientists.

Box 1. From Ecosystem Processes to Human Well-Being

Ecosystem processes are intrinsic processes and fluxes whereby an ecosystem maintains its integrity (such as primary productivity, trophic transfer from plants to animals, decomposition and nutrient cycling, evapotranspiration, etc.). They exist independently from human valuation, and their magnitude and rate can be established regardless of the cultural, economic, and social values and interests of different human groups (Figure 1, Ecosystem Processes box).
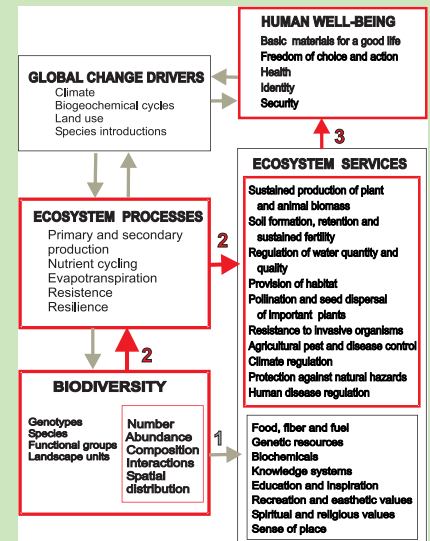
Ecosystem services are the benefits provided by ecosystems that contribute to making human life both possible and worth living. Ecosystem services are context-dependent; that is, the same ecosystem process can produce an ecosystem service that is highly valued by one society or stakeholder group but not highly valued by other societies or groups. Some ecosystem services involve the direct provision of material and non-material goods and are associated directly with the presence of particular species of plants and animals—for example, food, timber, medicines, and ritual materials (Figure 1, path 1 and bottom sub-box of Ecosystem Services box). Other ecosystem services arise, either directly or indirectly, from the continued functioning of ecosystem processes. For example, the service of formation, retention, and sustained fertility of soils necessary for the production of plants and animals considered important by different human societies depends on the ecosystem processes of decomposition, nutrient cycling by soil microbiota, and the retention of water and soil particles by a well-developed root network (Figure 1, path 2 and top sub-box in red of Ecosystem Services box). Some authors (e.g., [30]) have advocated a stricter definition of ecosystem services as components of nature that are directly enjoyed, consumed, or used in order to maintain or enhance human well-being. Although such an approach can be useful when it comes to ecosystem service accounting, our emphasis here is conceptual, and therefore we prefer to use the broader, widely accepted definitions and classification adopted by the Millennium Ecosystem Assessment [4]. This is because some ecosystem services (e.g., food provision) can be quantified in units that are easily comprehensible by policy makers and the general public. Others—for example, the services that regulate and support the production of tradable goods—are more difficult to quantify. If a criterion based on economic accounting is applied too strictly, there is a risk that ecosystem service assessment could be biased toward services that are easily quantifiable, but not necessarily the most critical ones [29].

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Figure 1. Biodiversity Is Both a Response Variable Affected by Global Change Drivers and a Factor That Affects Human Well-Being

Links developed in this article are indicated in red. In the biodiversity box, the hierarchical components of biodiversity (genotypes, species, functional groups, and landscape units) each have the characteristics listed in the sub-box and explained in Figure 2 (number, relative abundance, composition, spatial distribution, and interactions involved in "vertical" diversity).
Modified from [3,4].

Human well-being is a human experience that includes the basic materials for a good life, freedom of choice and action, health, good social relationships, a sense of cultural identity, and a sense of security. The sense of well-being is strongly dependent on the specific cultural, geographical, and historical context in which different human societies develop, and is determined by cultural-socio-economic processes as well as by the provision of ecosystem services. However, the well-being of the vast majority of human societies is based more or less directly on the sustained delivery of fundamental ecosystem services, such as the production of food, fuel, and shelter, the regulation of the quality and quantity of water supply, the control of natural hazards, etc. (see Figure 1, path 3).

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their biotic integrity in terms of species composition, relative abundance, functional organization, and species numbers (whether inherently species-poor or species-rich), rather than on simply maximizing the number of species present.

Another key message is that, precisely because ecosystem processes depend on the presence and abundance of organisms with particular functional traits, there is wide variation in how ecosystem services—that in turn depend on ecosystem processes—respond to changes in species number as particular species are lost from or get established in the system. So, to the question of how biodiversity matters to ecosystem services, we have to reply that it depends on what organisms there are. Daunting? Certainly, but

not hopeless. We know from recent assessments [1,2,7,8] that global biodiversity loss is not occurring at random. As a consequence of global change drivers, such as climate, biological invasions, and especially land use, not only is the total number of species on the planet decreasing, but there are also losers and winners. On average, the organisms that are losing out have longer lifespans, bigger bodies, poorer dispersal capacities, more specialized resource use, lower reproductive rates, and other traits that make them more susceptible to human activities such as nutrient loading, harvesting, and biomass removal by burning, livestock grazing, ploughing, clear-felling, etc. A small number of species with the opposite characteristics are becoming increasingly dominant

around the world (Figure 3). Because there are well-established links between functional traits of locally abundant organisms and ecosystem processes, especially for plants [9–12], it may become possible to identify changes in ecosystem processes and in ecosystem services that depend on them under different biodiversity scenarios.

What We Do Not Know: Cascades, Surprises, and Megadiversity Hot-Spots

Some ecosystem services show a saturating relationship to species number—that is, the ecosystem-service response to additional species is large at low number of species and becomes asymptotic beyond a certain number of species. We seldom know what this threshold number is, but we suspect

it differs among ecosystems, trophic levels, and services. The experimental evidence indicates that, in the case of primary production (e.g., for plant-based agricultural products), nutrient retention (which can reduce nutrient pollution and sustain production in the long term), and resistance to invasions (which incur damage and control costs in agricultural and other settings) by temperate, herbaceous communities, responses often do not show further significant increases beyond about ten plant species per square meter [3,13]. But in order to achieve this number in a single square meter, a much higher number of species is needed at the landscape level [14]. What about slow-growing natural communities, or communities that consist of plant species with more contrasting biology? What about communities that typically include many more species—for example, the megadiverse forest hot-spots of the Amazon and Borneo, where species number can exceed 100 tree species per hectare [15]? To what extent are all those species essential for the maintenance of different ecosystem processes and services? Ecological theory [16] and traditional knowledge [17,18] suggest that a large number of resident species per functional group, including those species that are rare, may act as 'insurance' that buffers ecosystem processes and their derived services in the face of changes in the physical and biological environment (e.g., precipitation, temperature, pathogens), but these ideas have yet to be tested experimentally, and no manipulative experiment has been performed in any megadiversity hot-spot.

Most of the links between biodiversity and ecosystem services summarized in Table 1 emerged from theory and manipulative experiments, involved biodiversity within a single trophic level (usually plants), and operated mostly at the level of local communities. However, the most dramatic examples of effects of small changes in biodiversity on ecosystem services have occurred at the landscape level and have involved alterations of food-web diversity through indirect interactions and trophic cascades. Most of these have been "natural experiments," that is, the unintended consequence of intentional or accidental removal or addition of certain predator,

pathogen, herbivore, or plant species to ecosystems. These "ecological surprises" usually involve disproportionately large, unexpected, irreversible, and negative alterations of ecosystem processes, often with repercussions at the level of ecosystem services, with large environmental, economic, and cultural losses. Examples include the cascading effects of decreases in sea otter population that led to coastal erosion in the North Pacific [19], and a marked decrease in grassland productivity and nutritional quality in the Aleutian islands as a consequence of decreased nutrient flux from the sea by the introduction of Arctic foxes [20] (see [3] for a comprehensive list of examples). The vast literature on biological invasions and their ecological and socio-economic impacts [21] further illustrates this point. Ecological surprises are difficult to predict, since they usually involve novel interactions among species. They most often result from introductions of predators, herbivores, pathogens

Number

Relative abundance

Composition

Range of functional traits

Spatial distribution

Vertical diversity (related to food web structure)

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Figure 2. The Different Components of Biodiversity

All of these components can be affected by human intervention (arrows), and in turn have repercussions for ecosystem properties and services. Symbols represent individuals or biomass units. Symbols of different shades represent different genotypes, phenotypes, or species.

and diseases, although cases involving introduced plants are also known. They do not depend linearly on species number or on well-established links between the functional traits of the species in question and putative ecosystem processes or services [3,22].

Uneven Impacts: Biodiversity and Vulnerable Peoples

People who rely most directly on ecosystem services, such as subsistence farmers, the rural poor, and traditional societies, face the most serious and immediate risks from biodiversity loss. First, they are the ones who rely the most on the "safety net" provided by the biodiversity of natural ecosystems in terms of food security and sustained access to medicinal products, fuel, construction materials, and protection from natural hazards such as storms and floods [4]. In many cases the provision of services to the most privileged sectors of society is subsidized but leaves the most vulnerable to pay most of the cost of biodiversity losses. These include, for example, subsistence farmers in the face of industrial agriculture [23] and subsistence fishermen in the face of intensive commercial fishing and aquaculture [24]. Second, because of their low economic and political power, the less privileged sectors cannot substitute purchased goods and services for the lost ecosystem benefits and they typically have little influence on national policy. When the quality of water deteriorates as a result of fertilizer and pesticide loading by industrial agriculture, the poor are unable to purchase safe water. When protein and vitamins from local sources, such as hunting and fruit, decrease as a result of habitat loss, the rich can still purchase them, whereas the poor cannot. When the capacity of natural ecosystems to buffer the effects of storms and floods is lost because of coastal development [25], it is usually the people who cannot flee—for example, subsistence fishermen—who suffer the most. In summary, the loss of biodiversity-dependent ecosystem services is likely to accentuate inequality and marginalization of the most vulnerable sectors of society, by decreasing their access to basic materials for a healthy life and by reducing their freedom of choice and action. Economic development that does not consider effects on these
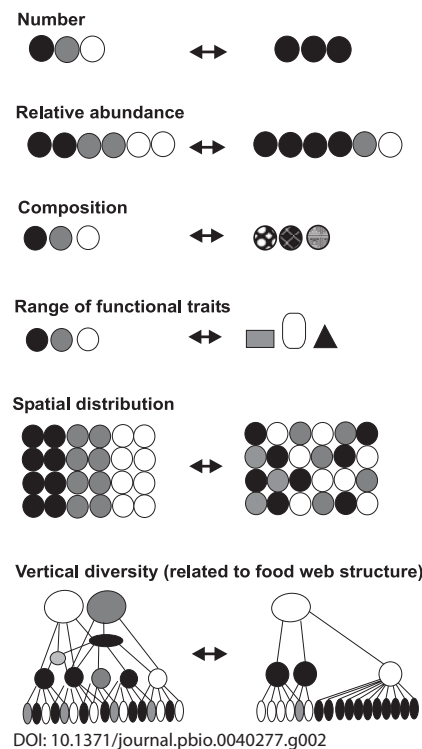
Table 1. Biodiversity Components Affect Ecosystem Services in Multiple and Complex Ways

| Ecosystem Services	Main Components of Diversity Involved and Mechanisms That Produce the Effect
Amount of biomass produced by plants considered important by humans	*** Functional composition—Faster-growing, bigger, more locally adapted plants produce more biomass, irrespective of the number of species present; in species-poor systems, coexisting plants with different resource use strategies or that facilitate each other's performance may take up more resources.
	** Number of species—Within a constant resource and disturbance regime, a large species pool is more likely to contain groups of complementary or facilitating species and highly productive species, both of which could lead to higher productivity of the community.
Stability of biomass production by plants considered important by humans	*** Genetic diversity—Large genetic variability within a crop species buffers production against losses due to diseases and environmental change.
	*** Number of species—Cultivation of more than one species in the same plot or landscape maintains production over a broader range of conditions.
	*** Functional composition—Life history characteristics and resource use strategy of dominant plants determine the capacity of ecosystem processes to remain unchanged or return to their initial state in the face of perturbations.
Preservation of the fertility of soils that sustain the production of plants and animals considered important by humans	*** Functional composition—Fast-growing, nutrient-rich plants enhance soil fertility; dense root systems prevent soil erosion.
Regulation of quantity and quality of water available to humans, domestic animals, and crops	*** Arrangement and size of landscape units—Intact riparian corridors and extensive areas with dense vegetation cover reduce erosion and improve water quality.
	*** Functional composition—Vegetation dominated by large, fast-growing, big-leafed, deep-rooted plants has high transpiration rate, reducing stream flow.
Pollination essential for the immediate production of fruits by, and the perpetuation of, important plant species	*** Functional composition of pollinator assemblage—Loss of specialized pollinators leads to genetic impoverishment and lower number and quality of fruits.
	** Number of species of pollinator assemblage—Lower number of pollinator species leads to genetic impoverishment of plant species.
	** Arrangement and size of landscape units—Large and/or well-connected landscape units allow movement of pollinators among plants of the same species, thus maintaining plant genetic pool.
Resistance to invasive organisms that have negative ecological, economic, and/or cultural impacts	*** Functional composition—Some key native species are very competitive or can act as biological controls to the spread of aliens.
	*** Arrangement of landscape units—Landscape corridors (e.g., roads, rivers, and extensive crops) can facilitate the spread of aliens; size and nature of suitable corridors are likely to be different for different organisms.
	** Number of species—All else being equal, species-rich communities are more likely to contain highly competitive species and to contain less unused resources, and therefore be more resistant to invasions.
Pest and disease control in agricultural systems	*** Genetic diversity of crops—High intraspecific genetic diversity reduces density of hosts for specialist pests and, thus, their ability to spread.
	** Number of crop, weed, and invertebrate species—High number of species acts similarly as genetic diversity and also increases habitat for natural enemies of pest species.
	** Spatial distribution of landscape units—Natural vegetation patches intermingled with crops provide habitat for natural enemies of insect pests.
Regulation through biophysical feedbacks of climatic conditions suitable to humans and the animals and plants they consider important	*** Arrangement and size of landscape units—Size and spatial arrangement of landscape units over large areas influence local-to-regional climate by lateral movement of air masses of different temperature and moisture; the threshold for effect is patch size of about 10 km diameter, depending on wind speed and topography.
	** Functional composition—Height, structural diversity, architecture, and phenology modify albedo, heat absorption, and mechanical turbulence, thus changing local air temperature and circulation patterns.
Regulation through carbon sequestration in the biosphere of climatic conditions suitable to humans and the animals and plants they consider important	*** Arrangement and size of landscape units—Carbon loss is higher at forest edges, therefore as forest fragments decline in size or area/perimeter ratio, a larger proportion of the total landscape is losing carbon.
	** Functional composition—Small, fast-growing, fast-decomposing, short-lived plants retain less carbon in their biomass than large, slow-growing, slow-decomposing, long-lived plants.
	* Number of species—High number of species can slow down the spread of pests and pathogens, which are important agents of carbon loss from ecosystems.
Protection against natural hazards (storms, floods, hurricanes, fires) that cause damage to humans and the animal production systems that they depend on	*** Arrangement and size of landscape units—Large patches of structurally complex vegetation or small, close-by patches are likely to offer more shelter to nearby ecosystems, and buffer them against flooding, sea intrusion, and wind.
	*** Functional composition—Deep-rooted plants are less susceptible to uprooting by hurricanes; extensive, mat-forming, superficial root systems protect soil against erosion by floods and storms; deciduous canopy types decrease flammability.

Asterisks indicate importance and/or degree or certainty (*** > ** > *) of the link between the ecosystem service in question and different components of biodiversity. Biodiversity components refer to plant assemblages unless otherwise specified. The putative mechanisms have been empirically tested in some cases, but remain speculative in others (modified from [3]). The list of ecosystem services is illustrative, rather than exhaustive.

ecosystem services may decrease the quality of life of these vulnerable populations, even if other segments of society benefit. Biodiversity change is therefore inextricably linked to poverty, the largest threat to the future of humanity identified by the United Nations. This is a sobering conclusion for those who argue that biodiversity is simply an intellectual preoccupation of those whose basic needs and aspirations are fulfilled.
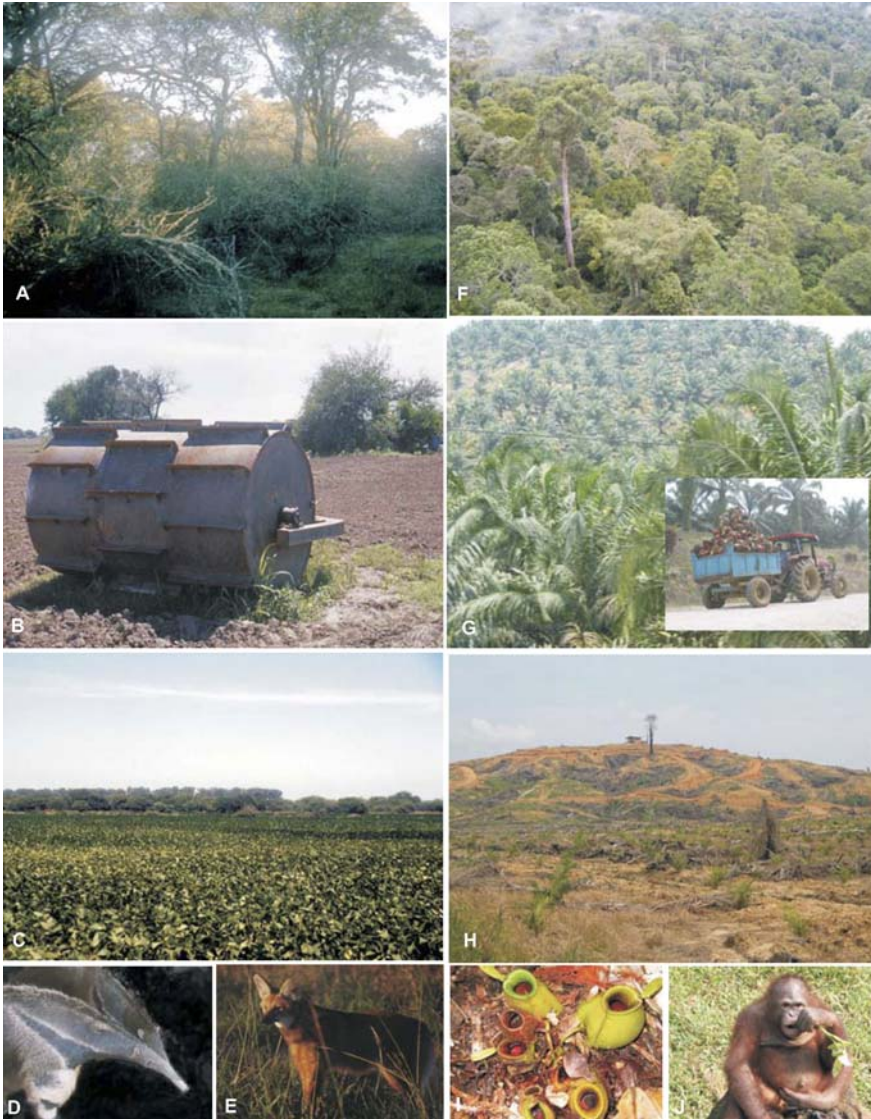
Figure 3. Lost Ecosystem Services and Vanishing Ecological Roles

Forest ecosystems in the tropics and subtropics are being quickly replaced by industrial crops and plantations. This provides large amounts of goods for national and international markets, but results in the loss of crucial ecosystem services mediated by ecological processes. In Argentina and Bolivia, the Chaco thorn forest (A) is being felled at a rate considered among the highest in the world (B), to give way to soybean cultivation (C). In Borneo, the Dypterocarp forest, one of the species-richest in the world (F), is being replaced by oil palm plantations (G). These changes are irreversible for all practical purposes (H). Many animal and plant populations have been dramatically reduced by changing land use patterns, to the point that they could be considered functionally extinct, such as the maned wolf (D) and the giant anteater in the Chaco plains (E), and the orangutan (I) and several species of pitcher plants (J) in the Bornean rainforest.
Photos by Sandra Díaz, except (A and C), courtesy by Marcelo R. Zak.

Future Directions

Most of the concrete actions to slow down biodiversity loss fall under the domain of policy making by governments and the civil society. However, the scientific community still needs to fill crucial knowledge gaps. First, we need to know more about the links between biodiversity and ecosystem services in species-rich ecosystems dominated by long-lived plants. Second, if we are to anticipate and avoid undesirable ecological surprises, better models and more empirical evidence are needed on the links between ecosystem services and interactions among different trophic levels. Third, we need to reinforce the systematic screening for functional traits of organisms likely to have ecosystem-level consequences. In this sense, our knowledge of how the presence and local abundance of organisms (especially plants) bearing certain attributes affect ecosystem processes has made considerable progress in the past few years. However, we know much less of how the range of responses to environmental change among species affecting the same ecosystem function contributes to the preservation of ecosystem processes and services in the face of environmental change and uncertainty [16,26]. This is directly relevant to risk assessment of the sustained provision of ecosystem services. Fourth, experimental designs for studying links between biodiversity and ecosystem processes and services need to not only meet statistical criteria but also mimic biotic configurations that appear in real ecosystems as a result of common land-use practices (e.g., primary forest versus monospecific plantations versus enrichment planting, or grazing-timber agroforestry systems versus a diverse grazing megafauna versus a single grazer such as cattle). In pursuing this, traditional knowledge systems and common management practices provide a valuable source of inspiration to develop new designs and testable hypotheses [27,28]. Finally, in order to assist policy decisions and negotiation among different local, national, and international stakeholders, considerable advance is needed in the evaluation and accounting of ecosystem services [29,30]. The challenge here is to find ways to identify and monitor services that are as concrete as possible, but at the same time not alienate the view of less powerful social actors or bias the analysis against services that are difficult to quantify or grasp.

The Bottom Line

By affecting the magnitude, pace, and temporal continuity by which energy and materials are circulated through ecosystems, biodiversity in the broad sense influences the provision of ecosystem services. The most dramatic changes in ecosystem services are likely to come from altered functional compositions of communities and from the loss, within the same trophic level, of locally abundant species rather than from the loss of already rare species. Based on the available evidence, we cannot define a level of biodiversity loss that is safe, and we still do not have satisfactory models to

account for ecological surprises. Direct effects of drivers of biodiversity loss (eutrophication, burning, soil erosion and flooding, etc.) on ecosystem processes and services are often more dramatic than those mediated by biodiversity change. Nevertheless, there is compelling evidence that the tapestry of life, rather than responding passively to global environmental change, actively mediates changes in the Earth's life-support systems. Its degradation is threatening the fulfillment of basic needs and aspiration of humanity as a whole, but especially, and most immediately, those of the most disadvantaged segments of society. ∎

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References

1. Baillie JEM, Hilton-Taylor C, Stuart SN (2004) IUCN Red List of Threatened Species: A Global Species Assessment. Gland (Switzerland): IUCN.
2. Mace G, Masundire H, Baillie J, Ricketts T, Brooks T, et al. (2005) Biodiversity. In: Hassan R, Scholes R, Ash N, editors. Ecosystems and human well-being: Current state and trends: Findings of the Condition and Trends Working Group. Washington (D. C.): Island Press. pp. 77–122.
3. Díaz S, Tilman D, Fargione J, Chapin FI, Dirzo R, et al. (2005) Biodiversity regulation of ecosystem services. In: Hassan R, Scholes R, Ash N, editors. Ecosystems and human well-being: Current state and trends: Findings of the Condition and Trends Working Group. Washington (D. C.): Island Press. pp. 297–329.
4. Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: Biodiversity synthesis. Washington (D. C.): World Resources Institute. 86 p.
5. Stokstad E (2005) Ecology: Taking the pulse of earth's life-support systems. Science 308: 41–43.
6. Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? Ecol Lett 8: 468–479.
7. Kotiaho JS, Kaitala V, Komonen A, Paivinen J (2005) Predicting the risk of extinction from shared ecological characteristics. Proc Natl Acad Sci U S A 102: 1963–1967.
8. McKinney M, Lockwood J (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14: 450–453.
9. Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. Chichester (United Kingdom); New York: John Wiley & Sons. 417 p.
10. Eviner VT, Chapin FS (2003) Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. In: Futuyma DJ, editor. Annual review of ecology evolution and systematics, volume 34. Palo Alto (California): Annual Reviews. pp. 455–485.
11. Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, et al. (2004) The plant traits that drive ecosystems: Evidence from three continents. J Veg Sci 15: 295–304.
12. Garnier E, Cortez J, Billès G, Navas ML, Roumet C, et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85: 2630–2637.
13. Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75: 3–35.
14. Tilman D (1999) Diversity and production in European grasslands. Science 286: 1099–1100.
15. Phillips OL, Hall P, Gentry AH, Sawyer SA, Vasquez R (1994) Dynamics and species richness of tropical rain-forests. Proc Natl Acad Sci U S A 91: 2805–2809.
16. Elmqvist T, Folke C, Nystrom M, Peterson G, Bengtsson J, et al. (2003) Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1: 488–494.
17. Trenbath B (1999) Multispecies cropping systems in India: Predictions of their productivity, stability, resilience and ecological sustainability. Agroforestry Systems 45: 81–107.
18. Altieri M (2004) Linking ecologists and traditional farmers in the search for sustainable agriculture. Frontiers in Ecology and the Environment 2: 35–42.
19. Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473–476.
20. Maron JL, Estes JA, Croll DA, Danner EM, Elmendorf SC, et al. (2006) An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecol Monogr 76: 3–24.
21. Mooney HA, Mack RN, McNeely J, Neville LE, Schei PJ, et al. (2005) Invasive alien species: A new synthesis. Washington (D. C.): Island Press. 368 p.
22. Walker B, Meyers JA (2004) Thresholds in ecological and social-ecological systems: A developing database. Ecology and Society 9. Available: http://www.ecologyandsociety.org/vol9/iss2/art3. Accessed 23 June 2006.
23. Lambin EF, Geist HJ, Lepers E (2003) Dynamics of land-use and land-cover change in tropical regions. Annual Review of Environment and Resources 28: 205–241.
24. Naylor RL, Goldburg RJ, Primavera JH, Kautsky N, Beveridge MCM, et al. (2000) Effect of aquaculture on world fish supplies. Nature 405: 1017–1024.
25. Danielsen F, Sorensen MK, Olwig MF, Selvam V, Parish F, et al. (2005) The Asian tsunami: A protective role for coastal vegetation. Science 310: 643.
26. Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct Ecol 16: 545–556.
27. Díaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. Trends Ecol Evol 18: 140–146.
28. Scherer-Lorenzen M, Potvin C, Koricheva J, Bornik Z, Hector A, et al. (2005) The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen M, Körner C, Schulze ED, editors. The functional significance of forest diversity. Berlin: Springer-Verlag. pp. 377–389.
29. DeFries R, Pagiola S, Adamowicz W, Resit Akçakaya H, Arcenas A, et al. (2005) Analytical approaches for assessing ecosystem conditions and human well-being. In: Hassan R, Scholes R, Ash N, editors. Ecosystems and human well-being Current state and trends: Findings of the Condition and Trends Working Group. Washington (D. C.): Island Press. pp. 37–71.
30. Boyd J, Banzhaf S (2006) What are ecosystem services? The need for standardized environmental accounting units. Washington (D. C): Resources for the Future.

Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions

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The threats to the future of biodiversity are many and well known. They include habitat conversion, environmental toxification, climate change, and direct exploitation of wildlife, among others. Moreover, the projected addition of 2.6 billion people by mid-century will almost certainly have a greater environmental impact than that of the last 2.6 billion. Collectively, these trends portend a grim future for biodiversity under a business-as-usual scenario. These threats and their interactions are formidable, but we review seven strategies that, if implemented soundly and scaled up dramatically, would preserve a substantial portion of global biodiversity. These are actions to stabilize the human population and reduce its material consumption, the deployment of endowment funds and other strategies to ensure the efficacy and permanence of conservation areas, steps to make human-dominated landscapes hospitable to biodiversity, measures to account for the economic costs of habitat degradation, the ecological reclamation of degraded lands and repatriation of extirpated species, the education and empowerment of people in the rural tropics, and the fundamental transformation of human attitudes about nature. Like the carbon "stabilization wedges" outlined by Pacala and Socolow [Pacala S, Socolow R (2004) Stabilization wedges: Solving the climate problem for the next 50 years with current technologies. *Science* 305:968–972] (1), the science and technologies needed to effect this vision already exist. The remaining challenges are largely social, political, and economic. Although academic conservation biology still has an important role to play in developing technical tools and knowledge, success at this juncture hinges more on a massive mobilization of effort to do things that have traditionally been outside the scope of the discipline.

biodiversity loss | conservation trust funds | global warming | national parks | population extinction

The fate of biological diversity for the next 10 million years will almost certainly be determined during the next 50–100 years by the activities of a single species. That species, *Homo sapiens*, is ≈200,000 years old. It has been fabulously successful by ecological standards: it boasts as-yet-unchecked population growth and a cosmopolitan distribution, and it has vanquished its predators, competitors, and some of its parasites. The fossil record suggests that the typical mammal species persists for approximately one million years (2), which puts *Homo sapiens* in mid-adolescence. This is a fitting coincidence, because *Homo sapiens* is now behaving in ways reminiscent of a spoiled teenager. Narcissistic and presupposing our own immortality, we mistreat the ecosystems that produced us and support us, mindless of the consequences.

The state of biodiversity today is a reflection of that abuse, but the reflection is hazy because we know neither the total number of populations or species nor how many have gone extinct. Our best information is on the rate and extent of habitat destruction and degradation. For example, we know from long-term monitoring that coral cover in Jamaican reef ecosystems declined from >50% to <5% between the late 1970s and 1994 (3). From remote-sensing studies, we know that the rate of selective logging in the Brazilian Amazon ranged from 12,000 to 20,000 km²/year

between 1999 and 2002 (4) and that the rate of deforestation in the Peruvian Amazon averaged 645 km²/year from 1999 to 2005 (5). Likewise, we know from global mapping studies that nearly 50% of all temperate grasslands, tropical dry forests, and temperate broadleaf forests have been converted to human-dominated uses worldwide, whereas only 4–10% of those biome types are formally protected (6).

Of the total number of species on Earth, we still cannot say much more than that it is likely to be "of the general order of 10^7" (7). Estimates of species extinction rates—often based on estimates of habitat loss in conjunction with the species–area relationship—are similarly imprecise (8, 9) and are sensitive to multiple assumptions (e.g., refs. 10 and 11). The number of animal and plant extinctions certified since 1600 is only slightly greater than 1,000 (8), but our pitiful knowledge of biodiversity's extent and the inherently inconspicuous nature of extinction ensures that this figure is a small fraction of the true number. Although no scientific consensus is forthcoming on the exact rate of extinction for any region or group of organisms, much less for global biodiversity, there is a consensus that current extinction rates vastly exceed background ones, perhaps by two to three orders of magnitude (12, 13).

Although species loss occupies an overwhelming proportion of the literature, genetically distinct populations are also an important component of biodiversity. Estimates of population diversity and extinction rates are even more uncertain than those for species, but even these crude estimates are alarming: of perhaps one to seven billion populations worldwide, 16 million may be extinguished each year in tropical forests alone (14). Trends in key parameters of well studied populations are consistent with this picture of decline. Amphibian populations have declined locally and globally in recent years (15, 16), and many mammal species worldwide exhibit range-size contractions indicative of heavy population loss (17).

When we were first asked to prepare a paper addressing the question "Where does biodiversity go from here?" a variety of cynical answers leapt to mind. The principal threats to biodiversity—direct overexploitation of organisms, habitat destruction and degradation, environmental toxification, climate change, and biological invasions, among others—have been known for decades. Yet despite a ballooning number of publications about biodiversity and its plight, there has been dispiritingly little progress in stanching the losses—so little that some commentators have characterized applied ecology as "an ever-more sophisticated refinement of the obituary of nature" (18).

As conservation-oriented scientists, we are responsible for biodiversity. Its loss is our failure.

We draw on the literature to sketch a brief and incomplete answer to the question posed to us, assuming that society continues business as usual. Because that outlook is bleaker than we are willing to accept, we then outline a more hopeful set of answers. These amount to a portfolio of strategies for combating biodiversity loss.

Business as Usual: Where Does Biodiversity Go from Here?

There are ≈6.7 billion people in the world as we write this, a number that is projected to grow (according to a mid-range forecast) to 9.3 billion by 2050 (19). The continued growth of the human population displaces biodiversity directly, as land is developed to create living room. In one recent example, Venezuelan president Hugo Chavez aims to translocate 100,000 people into a brand new city in El Avila National Park to alleviate overcrowding in Caracas (20). Providing a huge global populace with the resources necessary for survival (much less comfort) also displaces biodiversity. A recent spatially explicit analysis showed that humanity already appropriates nearly a quarter of global terrestrial net primary productivity, and up to 80% in large regional swaths (21).

Supplying the consumption of the next 2.6 billion people will almost certainly have a greater environmental impact than supplying the last 2.6 billion added since 1975. Our species has already plucked the lowest-hanging resources and converted the richest lands. To maintain the pace, metals will have to be won from ever-poorer ores, and oil, natural gas, and water will need to be obtained from ever-deeper wells and transported farther—all requiring accelerating energy use. So-called "marginal lands," often the last holdouts of biodiversity, are the final frontier, awaiting conversion into more human biomass. Whenever biodiversity preservation poses a threat to human livelihood, comfort, or convenience, the politically expedient choice is usually to liquidate the natural capital. In sum, every increment in the human population accelerates competition with other organisms for Earth's primary production. And, of course, not only do the present poor need more consumption, the present rich also demand it—as certainly will the newcomers. This is all in the face of signs that average per capita consumption is already unsustainable in developed regions (22), indicating a stark tradeoff between today's consumption and the basic human rights of future generations.

A major byproduct of human consumption is the toxification of Earth's ecosystems. Human agriculture and fossil-fuel combustion have multiplied the emission and deposition of nitrogen in recent decades, with negative consequences for biodiversity in grasslands (23) and aquatic ecosystem (24). Widely used herbicides such as atrazine and glyphosate harm amphibians (25, 26), potentially contributing to global amphibian decline, and the use of antiinflammatory drugs such as diclofenac and ibuprofen to treat livestock in India has ravaged scavenging birds, for which cattle carcasses are a major food source (27, 28).

Anthropogenic climate change stems from a special case of toxification: carbon pollution. Many biological impacts of global heating are evident, as animals and plants undergo changes in phenology, distribution, and local abundance (29). More alarming, anthropogenic heating has already been directly implicated in several extinctions (30) and seems likely to precipitate others. In the oceans, heating is already reducing the extent and altering the structure of coral reefs via breakdown of the coral–algal symbiosis (31). Moreover, rising CO_2 concentrations are lowering oceanic pH, with potentially disastrous consequences for coral reefs and other marine ecosystems (32, 33).

Direct exploitation of wildlife species by human beings takes a variety of forms, from subsistence hunting (34) to the harvesting of wild plants and animals for conversion into luxury goods and pets (35, 36). Large mammals and fish suffer disproportionately from direct human predation. Many of these vertebrates (e.g., apex carnivores, large ungulates, etc.) are strongly interacting species in their native ecosystems (37–40), and overharvesting them may have destabilizing effects on biodiversity and ecological processes such as seed dispersal, nutrient cycling, and even primary production. In oceans, top piscivores suffer disproportionately as fleets fish down the food web (41). Industrialized fisheries have often devastated community biomass of predatory fish within a few decades (42), with even sharper declines common among the apex predators (43).

Nonnative species introduced by people into naive ecosystems have occasionally wrought havoc on local biodiversity via predation, competition, and the disruption of co-evolved interactions. Biotic interchange is likely to increase with increasing mobility in an increasingly globalized world; under business as usual, biogeography will be increasingly homogeneous.

A cryptic yet critical threat to biodiversity is the loss of future evolutionary potential. Extinction of genetically distinct populations, decreases in effective population sizes, and homogenization of habitat types are all likely to have negative effects on future biodiversity (13, 44). The positive relationship between speciation rate and habitat area (45) indicates that decreases in species geographic ranges will diminish future speciation rates, which in turn will impoverish future diversity (46). Speciation of large vertebrates, which are highly mobile and require large habitats, may cease entirely (13), and biodisparity—the range of morphological and physiological variety on Earth—will decrease as phylogenetically distinct, species-poor branches are pruned from the tree of life (47).

Loss of microevolutionary potential will also limit the capacity of populations to adapt to changing environmental conditions, highlighting another important point: The drivers of biodiversity loss will often act synergistically in imperiling populations and species. Habitat loss and fragmentation compound the effects of climate change, as species are unable to track their thermal niches spatially (48). The interactions among logging, fire, and climate change threaten to transform the Amazon rainforest into savanna (49, 50). Such positive feedbacks seem to be a rule, rather than an exception, and they make it impossible to generate precise estimates of future biodiversity.

In short, although there are many uncertainties about the trajectories of individual populations and species, we know where biodiversity will go from here in the absence of a rapid, transformative intervention: up in smoke; toward the poles and under water; into crops and livestock; onto the table and into yet more human biomass; into fuel tanks; into furniture, pet stores, and home remedies for impotence; out of the way of more cities and suburbs; into distant memory and history books. As biodiversity recedes, we also lose the stories that go with it and many ways of relating to the world in which we evolved.

We now consider what might happen if humanity changes the way it does business. Ours is not a comprehensive treatment of this issue. The Millennium Ecosystem Assessment (51) contains a thorough and colorful summary of the state of biodiversity, and it provides important (and necessarily overarching) recommendations for softening human impact on ecosystems—things like increasing governmental accountability, eliminating environmentally malign subsidies, and reducing greenhouse-gas emissions. However, the breadth and complexity of these objectives, and the considerable political clout required to enact them, can engender the misconception that only governments can determine where biodiversity goes from here. That misconception, in turn, is a recipe for paralysis among concerned individuals. Therefore, we try to focus more narrowly on seven more-or-less concrete sets of actions that individuals or small groups have already set in motion. If implemented more broadly and scaled

up dramatically, these actions would collectively enable a different, more appealing fate for biodiversity.

Although each of the following strategies is being used somewhere, none is yet realizing its full potential. Some may not be achievable in all times and places, but none is exclusive of any other. Most of these strategies are familiar to most people in the conservation community; the notion that they are all "correct" ways to conserve biodiversity is perhaps less so. Indeed, squabbles over strategy are endemic within the conservation community, perhaps because different strategies are seen as competing for funding and for primacy in the scholarly idea-scape. The alacrity with which international conservation nongovernmental organizations have "branded" themselves (52) and the sometimes absurdly acrimonious exchanges between conservation academics seem to manifest a widespread "either–or" belief that there are absolutely right and wrong ways to protect biodiversity (53). Ostrom *et al.* (54), in a recent PNAS Special Feature, wrote of the need "to go beyond relying on abstract cure-all proposals for solving complex problems related to achieving sustainable social–ecological systems." By emphasizing a portfolio of partial solutions, we hope to reinforce the idea that maximizing future biodiversity will require a plurality of approaches in creative admixtures that are tailored to local realities. Each place needs a different mixture.

Business as Unusual: Where Else Might Biodiversity Go from Here?

Into a Less Peopled, Less Hostile Planet. The human impact on biodiversity is a product of three root factors, summarized in the heuristic I=PAT identity (55). The overall *I*mpact (encompassing all of the drivers of biodiversity loss discussed above) is the product of *P*opulation size, per capita *A*ffluence, and the *T*echnologies (and socioeconomic–political systems) used to generate affluence. "Affluence" in this context is simply per capita consumption, and "socioeconomic–political systems" refer to the strictures that regulate technology use.

Tangible steps to reduce any of these factors will lessen their product and help produce a more hospitable future for biodiversity. A current example that integrates all three factors is the drive to produce biofuel (*T*) to satisfy the expanding energy consumption (*A*) of a growing population (*P*). Unchecked biofuel production has the potential to destroy all moist-tropical biodiversity that lacks conservation status. Biologically impoverished monocultures of oil palm, soybeans, and sugarcane for biodiesel and ethanol are devouring swaths of Brazilian Amazon and Cerrado, Indonesian, and Malaysian tropical rainforests and other vast reservoirs of biodiversity (56, 57). However, the production of biofuels from native grassland perennials on agriculturally degraded lands has the potential to reduce carbon emissions without displacing food production or converting native habitats (58). In this case, an innovative *T*echnological adjustment would reduce overall *I*mpact. Likewise, simple shifts in socioeconomic–political systems—instituting high-occupancy vehicle lanes to reduce carbon emissions, for example, or demanding high-seas ballast water exchange for cargo ships to reduce species introductions—would do a great deal.

Although population growth has slowed or is slowing in many developed countries, it remains high in many developing regions. Much is known about how to hasten the transition to a stable and then declining world population. Education and employment—for women especially—along with access to contraception and safe abortions are the most important components (59). Less is known about how to prevent overconsumption of natural resources (22). Mass media are a powerful tool for raising environmental awareness and influencing attitudes toward consumption, as demonstrated by Al Gore and his documentary film *An Inconvenient Truth*. To this end, we should exploit the media to the fullest possible extent. Although more environmentally benign technologies will also help, the battle will not be won without a transformative collective decision by consumers that less can be more. For example, although an 80% shift from beef and pork to farmed fish and poultry could enable displacement of up to 22% of U.S. gasoline consumption with low-impact, high-diversity biofuel (D. Tilman, personal communication), such a shift will not happen without hundreds of millions of conscious decisions that a sustainable economy is worth more than the taste of bacon cheeseburgers.

Into Perpetuity via Endowments for Conserved Areas. As many conservation biologists have noted, formally protected areas are not realizing their full potential, being too few, too small, too far apart, too expensive to establish and maintain, and/or too poorly administered (60, 61). These pitfalls notwithstanding, nature parks and other conservation areas are central to the future of biodiversity (62).

The outstanding national parks of North America and Australia demonstrate that well fed voter/taxpayers, whatever their environmental shortcomings, are at least willing and able to support biological preserves; people in poorer countries, the argument goes, cannot necessarily afford that luxury. Of the various forms of revenue used to support protected areas in poor countries, conservation trust funds—specifically, endowment funds intended to last in perpetuity—are the most promising. Unlike taxes, user fees, and debt swaps, endowments provide sustained funding and are relatively resilient to political whims and fluctuations in the demand for ecotourism (63). As of 2000, conservation trust funds had been established in more than 40 countries, and nine developing nations boasted endowments of US$10 million or more (63).

Spergel (63) argues that conservation trust funds should be additional to existing government funding, but this may not always be the case. Consider the following initiative being considered in Costa Rica. It is called Paz Con la Naturaleza—Peace with Nature—and it aims, among other things, to generate $500 million to endow the country's entire conserved-area system. Crucially, this would relieve Costa Rican taxpayers of the burden of financing conservation. Under the plan, $100 million would be spent to consolidate the existing national park system—25% of the country—into 11 large conservation areas (ref. 64 and D. H. Janzen, personal communication). The remaining $400 million would be invested outside the country in a university-like endowment; $20 million of annual revenue from that endowment would be divided among the conservation areas and used to cover operating costs, with any remaining income plowed back into the fund for growth. Although the financing would operate at a national and international scale, the plan calls for decentralized local administration of the individual conservation areas. This plan, with an endowment as its centerpiece, simultaneously redresses most of the frequently cited shortcomings of conservation areas: it aims to make them bigger, closer together, better administered, and essentially free to their users (aside from the opportunity cost of the land use).

It is an ambitious goal, to be sure. The price tag is steep by traditional conservation standards, but with many U.S. research universities boasting endowments in the multiple billions of dollars, $500 million to conserve 25% of a nation and 4% of global biodiversity forever—creating the world's first explicitly green country in the process—seems like a bargain. It remains to be seen whether the plan can be implemented in small, stable, "green" Costa Rica, much less anywhere else; we will not know until money is pledged. In any event, perpetual endowment funds have tremendous potential in conservation (e.g., as a source of revenue for restoration and other projects: refs. 63 and 65) and will generally increase the "localization" and longevity of conservation initiatives by tying funds to long-term programs in particular areas.

Into Human-Modified Landscapes, as Best It Can. Unbroken tracts of conserved wild area, if they exist, will always be the greatest reservoirs of biodiversity and the most interesting places to visit. But under certain conditions, human-dominated pastoral and agricultural landscapes can also harbor an appreciable amount of biodiversity (66–68). Simple and inexpensive management techniques, such as maintaining living hedges around agricultural plots (69) and preserving remnant trees in pasture (70), can often buttress the biodiversity of these areas.

There are many compelling reasons to conserve countryside biodiversity. One is that most human-dominated landscapes will not revert to wildness anytime soon; enabling wild populations to persist in these areas is the best plausible outcome for biodiversity. Another is that habitat types vary in their tolerance of human activity. Whereas tropical forests are quite sensitive to burning, wood chopping, and hunting, tropical savannas are relatively resilient to anthropogenic disturbance. In many parts of Africa, much or most wildlife occurs outside of nationally protected areas (68), and wildlife can coexist alongside limited livestock populations (71). That people also share this space does not necessarily diminish its conservation value. Moreover, maintaining nonconserved areas in biodiversity-friendly ways aids migration and dispersal between protected areas, a process that will become even more important as climate change rearranges species' distributions (48, 72). Finally, maximizing biodiversity in areas where humans are active in their daily lives increases the frequency of interactions between human and nonhuman organisms, which enhances the potential for ecosystem-service delivery and bioliteracy development (see *Onto the Cultural Radar Screen*). Economic incentives (or legal strictures) can be developed to encourage (or require) biodiversity-friendly use of privately held lands (73, 74).

Biodiversity maximization in human-dominated landscapes does not in any respect reduce the need for large conserved wildlands. How to allocate conservation resources among these two different frameworks is a local problem, and answers will vary depending on such factors as the habitat types involved, local land-use history, the state of the region's government and protected-area system, and the availability and price of land for purchase. As in most other respects, Britain is different from Kenya is different from Amazonia. The challenges in planning for conservation in human-dominated landscapes are perhaps most pronounced in fragmented tropical forest–pasture–field mosaics, because tropical-forest biodiversity is so great and the alternate landscape states are so dramatically different from the baseline. One uncertainty is whether the apparently high conservation value of these mosaics (e.g., refs. 66 and 75) will be sustained over centuries, or whether it will ultimately succumb to the "extinction debt" (76, 77). A related concern is that the diversity of interspecific interactions in human-dominated landscapes will decline more quickly and less perceptibly than the diversity of populations or species and that this will eventually lead to additional population and species loss. A 300-year-old canopy tree species in a Brazilian pasture may serve as a roost for a diversity of birds, epiphytes, and other organisms. But if its pollinator or seed disperser has been lost or will not venture into the pasture (78), or if its seeds will not germinate in a pasture, or if its seedling crop will be devastated by pasture-tolerant seedling predators, then it is among the living dead (76): it will not replace itself, and, when it goes, so go the other species that used it.

Toward a (Protected) Role Within the Global Economy. Ecotourism has long been one of the most potent forces favoring conservation and will continue to be so. Ecotourists are consumers of services that nature provides (beauty, adventure, life lists, etc.), and they obligingly pay for these services in many ways (paying for park entry fees, rooms at hotels, vehicle repairs at the local mechanic, etc.).

But ecotourism is exceptional in these respects. The biosphere provides a steady stream of other direct and indirect benefits to humanity for which nobody pays. The last decade has seen "ecosystem services" transformed from an abstract academic concept (79) into an applied research program and a powerful policy tool (51, 80). These services include, but are not limited to, providing raw materials, natural water filtration, carbon sequestration and storage in forests, flood and erosion mitigation by plant communities, and pollination of crops by wild animals (80). Ecosystems, in addition to being reservoirs of biological diversity and an integral part of our planetary and cultural heritage, are capital assets.

The global economy does not in any serious way account for the value of ecosystem services. The perversity of this situation is obvious. The costs, both in the traditional economic sense and in terms of human health and well being, of losing these services would be immense: many economic institutions would either collapse outright or require technological surrogates vastly more expensive than simply conserving the relevant ecosystems. The archetypal example of an ecosystem service in action is the conservation of the Catskill watershed, which has (thus far) spared the city of New York the $8 billion cost of building a water-filtration plant. Elsewhere, there are indications that mangroves and other coastal vegetation might have protected some coastal villages from the devastating Asian tsunami of 2004 (81). Recent population crashes of honey bees (*Apis mellifera*) have threatened an approximately $15 billion crop-pollinating industry in the United States, highlighting the importance of conserving diverse native-bee communities (82, 83). These case studies are small components of a total-biosphere value that is, effectively, infinite (84).

The idea that economic growth is independent of environmental health, and that humanity can therefore indefinitely expand its physical economy, is a dangerous delusion. The problem is that although we know that individual ecosystem services are valuable, we rarely know precisely how valuable. And although quantitatively estimating the dollar value of individual services can be an eye-opening exercise, the effort required makes doing so prohibitive for every ecosystem (to say nothing of the futility of trying to add up to infinity). The challenges, then, are to provoke society to acknowledge ecosystem-service values (even though approximate or only qualitative) and to maintain service provision by protecting service sources.

In addition to the individual efforts of a growing number of academics and practitioners, innovative programs are emerging to tackle these twin challenges at large scales. The Natural Capital Project is an international collaboration involving Stanford University, The Nature Conservancy, and World Wildlife Fund that aims to integrate ecosystem-service values into land-use and policy decisions (85). By developing new decision-support tools—including software to quantify and map the value of ecosystem services across landscapes and seascapes—and applying them in several demonstration sites across the world, the project hopes to promote more forward-thinking land-use decisions.

In some cases, protecting ecosystem services (or even engineering them) may not enhance biodiversity conservation (86, 87), but it may be useful for other anthropocentric reasons. We should be frank about that when pondering how to justify and finance our operations. We should also think about how increased valuation of ecosystem services might spill over into other sectors of the economy: If we rely on an ecosystem to do a job, are we putting a human being out of work, and might that person retaliate against the service-providing ecosystem?

Finally, we must recognize that, for whatever reason, demand

for particular ecosystem services will wax and wane, but that the sources of the services must not be allowed to wax and wane in sync. As proponents and critics of market-based conservation approaches both point out, complete commodification of ecosystems is not the goal. Yes, ecosystem services have enormous value in traditional economic terms for their role in sustaining and enriching human life, and efforts to ascertain these values are important. No, ecosystems and their biodiversity cannot compete on the open market as service providers alone (88). To subject ecosystems to all of the same demands and risks that commodities and corporations face in capitalist economies would be to ensure their eventual diminution and demise.

Globalization intensifies this hazard. In a globalized, demodularized world, goods and services can often be imported and outsourced more cheaply than they can be obtained locally—and this includes goods and services provided by ecosystems. "Endemic" ecosystem services, which cannot be supplanted by goods and services from distant sources, will likely be the most effective allies to biodiversity in the future.

Into Ecologically Reclaimed and Restored Habitats. Experience has shown not only that science can inform more rapid, more effective restoration of local habitats (89), but also that contiguous ecosystems can be built from scattered pieces at large scales (90). This process has several names—restoration, rewilding, renaturalization—and provides a constructive, creative counterpoint to the stop-loss approach of traditional conservation. Thus, the future of biodiversity is not just what we can save of what is left, but also what we can create from what is left (see also ref. 91). As Young (92) put it, "The conservation mindset is one of loss on a relatively short time horizon, whereas the restoration mindset is one of long-term recovery."

Successes abound. The regeneration of tropical forest in Guanacaste Province, northwestern Costa Rica (90, 93), is particularly heartening for several reasons: it involves restoration of multiple habitat types; it is large-scale yet local and decentralized; and it was achieved by using a portfolio of innovative mechanisms and via broad collaboration among scientists, businesspeople, politicians, and the local community. The result has been the regeneration and conservation of 700 km^2 of tropical dry forest along with abutting chunks of rain and montane forest. In poverty-stricken Niger on the fringe of the Sahara, farmers have helped hold off desertification in many areas by nurturing saplings in their fields rather than removing them—and they have begun to reap benefits from this greening of the countryside (94). In the oceans, researchers have had some success transplanting live coral fragments onto degraded reefs (95). Likewise, efforts to rebuild damaged watersheds and wetlands have been a major focus of scientific restoration ecology (e.g., ref. 96), with important implications for the availability of potable water.

Large animals are particularly extinction-prone, at both the population and species levels. They are also often particularly important to ecological dynamics. Returning megafaunal species to what remains of their historical ranges (97) can yield a number of overlapping benefits: the return of these charismatic species undoes population extinctions, makes habitats more interesting and exciting, and can restore ecological interactions with appealing system-wide consequences. The repatriation of wolves to Yellowstone National Park in 1995 not only titillated tourists but also revived a multispecies trophic interaction involving elk, beavers, and trees, which has rejuvenated the region's riparian ecosystems (98, 99).

These examples and others illustrate that ecological restoration has a critical role in determining where biodiversity goes from here; we hope for enormous and rapid expansion of such revival efforts, even if the ultimate ecological goals take centuries to achieve. The only caveat is that many projects branded as "restoration" may be only weakly beneficial or neutral for biodiversity (100). Tree plantations are not forests.

Into the Fabric of Local Communities. For various reasons, conservation programs in developing regions are likely to fail when they are imposed from the top down by outsiders/foreigners (101). That realization has spurred interest in (*i*) involving local communities in conservation planning and (*ii*) fostering their desire and capacity to help achieve conservation goals. In some ways, these can be seen as short- and long-term components of the same strategy. Earning local support for a conservation initiative is needed to get the ball rolling; building local capacity ensures that the ball keeps rolling once the outsiders leave.

Community involvement in conservation planning and protected-area establishment/maintenance can take a variety of forms (102, 103) and is the subject of a gargantuan literature. At its most straightforward, it involves dialogue and follow-up with local stakeholders to establish what kinds of compensation (broadly construed) would sweeten the prospect of restrictions on habitat use, but more nuanced and sophisticated schemes have also been used (104, 105).

Local capacity building can also operate at multiple scales. Education is clearly central to this goal, from providing on-the-ground biodiversity training in parataxonomy (106, 107) to training professional national park staffs to facilitating advanced degrees for local students via scholarships and other mechanisms (52). But even more basic contributions (local-language publications and extension efforts, computer and telecommunications access, etc.) can be extremely beneficial.

As conservationists increasingly realize, programs along these lines should attend every tropical conservation effort. Such programs are crucial—not only for the long-term success of the given conservation effort, but also for the augmentation and transmission of biodiversity knowledge. Efforts to "engage" local communities in conservation and land management can and have gone awry, and there are often important tradeoffs between conservation and development (88). None of this alters the fact that, without local acceptance of biodiversity and the rationale for its conservation, any gains will be ephemeral.

Onto the Cultural Radar Screen. For decades, conservationists have appealed to aesthetics as a principal reason to conserve wild areas and species. But beauty is in the eye of the beholder, and the 13-billion-plus beholding eyes of the world are drawn to many things that are hostile to biodiversity: large families, tractors, treasure, pavement, goats, and Cadillacs, to name a few. The processes of economic and infrastructural development help to divorce people from the natural world. Moreover, although outdoor recreation and ecotourism are still important parts of many lives in rich countries, biophilic impulses seem increasingly swamped by other stimuli. In the United States, the rise of electronic media has coincided with a 20-year downturn in National Park visitation, after 50 years of steady increase (108). Recent findings indicate that similar declines in contact with nature are common to developed nations worldwide (109).

Such trends will not be reversed and the biodiversity crisis will not be resolved until nature can rival virtual reality as a source of entertainment, intrigue, and inspiration. Janzen (110, 111) offers a compelling analogy: as books are uninteresting and useless to an illiterate person, so is biodiversity uninteresting and useless to a bioilliterate person. People keep what they use, and increasing bioliteracy would enable more people to find uses for biodiversity. Demand for ecotourism and perceived "existence values" would increase and, with them, biodiversity-sustaining revenues. In a world of stingy appropriations for conservation, we have a wonderful academic literature on how to maximize returns on conservation investments (112). But we have spent comparatively little effort figuring out ways to create

a world of biodiversity fanatics and conservation voters, where conservation resources would presumably flow more freely.

The earlier in the developmental process comes exposure to nature, the better the odds of inspiring devotion to biodiversity and its conservation. It is a rare conservationist who did not encounter nature as a child. Every one of us can go to elementary schools to show pictures of animals and plants and tell funny stories about ecology. The teachers will be happy to have us. More ambitious people might think about how to finance and institutionalize school field trips to natural areas. Those of us who work in the tropics can do these things there, too.

Clearly, we can also use other strategies. One method is to appropriate the very technologies that are currently enforcing the divide between people and biodiversity. Biodiversity is increasingly on the World Wide Web via projects such as the Encyclopedia of Life (www.eol.org) and Wikispecies (http://species.wikimedia.org). But we can do more. We can upload science and nature shorts to YouTube and contribute our knowledge to Wikipedia and its offshoots. We can post our lectures online (113). We can work to add ecological dimensions to online virtual-reality platforms and video games like Second Life, which currently has 10 million registered accounts. These are obvious ideas; many more are possible. There is hope here: Online sales have helped to revitalize classical music (114), which is like biodiversity in that its devotees have long been predicting and lamenting its demise.

Some have argued that the key to widespread biodiversity appreciation is the ability to know immediately what is what in nature. Janzen (110) believes that this requires a comprehensive library of DNA barcodes (115) along with a handheld, nanotechnological, field-portable sequencing device. We are hopeful about this dream, as well as any other means of achieving the same end.

Profound social transformations are not impossible or "unrealistic." Shifts happen. They have happened in our lifetimes. We all know these terms: segregation, Iron Curtain, apartheid. "Anthropogenic extinction" belongs on that list. More than anything else, the long-term future of biodiversity will be determined by our success or failure in helping to precipitate such an overhaul in popular perceptions of nature and what it means.

Concluding Thoughts

A substantial amount of biodiversity—enough to preserve many functional ecosystems and to satisfy the desire felt by many to coexist with our only known living companions in the universe—can be saved via the pluralistic deployment of the seven sets of actions that are discussed above and that have been discussed for years in countless other corners of academia.

The subheadings sound ambitious, but the actions they comprise are demonstrably doable. As with the atmospheric "stabilization wedges" of Pacala and Socolow (1), each of the strategies above has passed beyond the laboratory bench and demonstration phase, but none has yet been implemented on a large-enough scale or in conjunction with enough of the others. Part of the reason for this shortfall is that most of us in the academic community who are familiar with all of these ideas do not see implementing them as part of our job description.

Where Does Conservation Biology Go from Here? Academic ecological papers are often tinseled with one or two sentences about the applied significance of the science (116), which accomplishes little. The selective pressures of academia, as currently set up, promote this practice by insisting on work that is at once scientifically transformative and socially beneficial. Yet many of the most useful things that we can do for biodiversity—like talking to kindergartners—are not at the cutting edge of science. Thus, we are implicitly encouraged to deck our papers with references to the urgent biodiversity crisis while quietly opting out of the grittier work. (We do not excuse ourselves from this indictment.)

This phenomenon is the very definition of the Ivory Tower, but it need not apply here. It is up to us. We can maintain the status quo, which has not yet enabled us to stop or even slow biodiversity loss. Alternatively, we can go a few steps down from our cathedral by systematically rewarding (or even mandating) a certain tithe to society and incorporating it into our system for evaluating one another. Each institution seems free to make its own decision on this front. Major funding bodies, such as the U.S. National Science Foundation, rightly insist that applicants explain both the intellectual importance and the "broader impacts" of their science. However, we suspect that scientists face more accountability to the former than to the latter. Closer scrutiny of the delivery of societal benefits promised from previous grants would likely prompt an increase in tithing.

Where Does Humanity Go from Here? Where the human juggernaut goes from here will depend in many ways on where biodiversity goes. In this article we have tried to suggest one hopeful answer: from here, humanity goes to grips with biodiversity as a part of society that we accept, accommodate, need, use, pay for, puzzle over, admire, and enjoy. The alternative future is much uglier, but we still have time to reject it.

1. Pacala S, Socolow R (2004) Stabilization wedges: Solving the climate problem for the next 50 years with current technologies. *Science* 305:968–972.
2. Martin RD (1993) Primate origins: Plugging the gaps. *Nature* 363:223–234.
3. Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
4. Asner GP, *et al.* (2005) Selective logging in the Brazilian Amazon. *Science* 310:480–482.
5. Oliveira PJC, *et al.* (2007) Land-use allocation protects the Peruvian Amazon. *Science* 317:1233–1236.
6. Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol Lett* 8:23–29.
7. May RM (1988) How many species are there on Earth? *Science* 241:1441–1449.
8. May RM, Lawton JH, Stork NE (1995) in *Extinction Rates*, eds Lawton JH, May RM (Oxford Univ Press, Oxford), pp 1–24.
9. Balmford A, Green RE, Jenkins M (2003) Measuring the changing state of nature. *Trends Ecol Evol* 18:326–330.
10. Regan HM, Lupia R, Drinnan AN, Burgman MA (2001) The currency and tempo of extinction. *Am Nat* 157:1–10.
11. Seabloom EW, Dobson AP, Stoms DM (2002) Extinction rates under nonrandom patterns of habitat loss. *Proc Natl Acad Sci USA* 99:11229–11234.
12. Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science* 269:347–350.
13. Woodruff DS (2001) Declines of biomes and biotas and the future of evolution. *Proc Natl Acad Sci USA* 98:5471–5476.
14. Hughes JB, Daily GC, Ehrlich PR (1997) Population diversity: Its extent and extinction. *Science* 278:689–692.
15. Houlahan JE, Findlay CS, Schmidt BR, Meyer AH, Kuzmin SL (2000) Quantitative evidence for global amphibian population declines. *Nature* 404:752–755.
16. Rachowicz LJ, *et al.* (2006) Emerging infectious disease as a proximate cause of amphibian mass mortality. *Ecology* 87:1671–1683.
17. Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. *Science* 296:904–907.
18. Jackson JBC (2007) Economic incentives, social norms, and the crisis of fisheries. *Ecol Res* 22:16–18.
19. Population Reference Bureau (2007) *2007 World Population Data Sheet* (Population Reference Bureau, Washington, DC).

20. Forero J (November 12, 2007) Venezuela's Chavez attempts new city. *Morning Edition* (National Public Radio, Washington, DC).

21. Haberl H, *et al.* (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proc Natl Acad Sci USA* 104:12942–12945.

22. Ehrlich PR, Goulder LH (2007) Is current consumption excessive? A general framework and some indications for the United States. *Conserv Biol* 21:1145–1154.

23. Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science* 303:1876–1879.

24. Carpenter SR, *et al.* (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol Appl* 8:559–568.

25. Hayes TB, *et al.* (2002) Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. *Proc Natl Acad Sci USA* 99:5476–5480.

26. Relyea RA (2005) The lethal impact of roundup on aquatic and terrestrial amphibians. *Ecol Appl* 15:1118–1124.

27. Oaks JL, *et al.* (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427:630–633.

28. Cuthbert R, Parry-Jones J, Green RE, Pain DJ (2007) NSAIDs and scavenging birds: Potential impacts beyond Asia's critically endangered vultures. *Biol Lett* 3:90–93.

29. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669.

30. Pounds JA, *et al.* (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–167.

31. Hughes TP, *et al.* (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.

32. Orr JC, *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686.

33. Hoegh-Guldberg O, *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.

34. Brashares JS, *et al.* (2004) Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* 306:1180–1183.

35. Root TL, Bishop KD, Ehrlich PR, Schneider SH, Ehrlich AH (2006) Conservation of southeast Asian birds: The role of bird markets and avian flu. *Environ Awareness* 29:57–65.

36. O'Brien S, *et al.* (2003) Decline of the Madagascar radiated tortoise *Geochelone radiata* due to overexploitation. *Oryx* 37:338–343.

37. Terborgh J, *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.

38. Ripple WJ, Beschta RL (2007) Hardwood tree decline following large carnivore loss on the Great Plains, USA. *Front Ecol Environ* 5:241–246.

39. Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc Natl Acad Sci USA* 104:193–197.

40. Palmer TM, *et al.* (2008) Breakdown of an ant-plant mutualism follows the loss of large mammals from an African savanna. *Science* 319:192–195.

41. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860–863.

42. Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283.

43. Baum JK, Myers RA (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol Lett* 7:135–145.

44. Myers N, Knoll AH (2001) The biotic crisis and the future of evolution. *Proc Natl Acad Sci USA* 98:5389–5392.

45. Losos JB, Schluter D (2000) Analysis of an evolutionary species-area relationship. *Nature* 408:847–850.

46. Rosenzweig ML (2001) Loss of speciation rate will impoverish future diversity. *Proc Natl Acad Sci USA* 98:5404–5410.

47. Jablonski D (1995) in *Extinction Rates*, eds Lawton JH, May RM (Oxford Univ Press, Oxford), pp 25–44.

48. Travis JMJ (2003) Climate change and habitat destruction: A deadly anthropogenic cocktail. *Proc Biol Sci* 270:467–473.

49. Oyama MD, Nobre CA (2003) A new climate-vegetation equilibrium state for tropical South America. *Geophys Res Lett* 30.

50. Terborgh J (2007) The green vs. the brown Amazon. *NY Rev Books* LIV:33–35.

51. Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis* (Island, Washington, DC).

52. Rodriguez JP, *et al.* (2007) Globalization of conservation: A view from the south. *Science* 317:755–756.

53. Wiens J (2007) The dangers of black-and-white conservation. *Conserv Biol* 21:1371–1372.

54. Ostrom E, Janssen MA, Anderies JM (2007) Going beyond panaceas. *Proc Natl Acad Sci USA* 104:15176–15178.

55. Ehrlich PR, Holdren JP (1971) Impact of population growth. *Science* 171:1212–1217.

56. Fearnside PM (2001) Soybean cultivation as a threat to the environment in Brazil. *Environ Conserv* 28:23–38.

57. Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. *Conserv Biol* 19:707–713.

58. Tilman D, Hill J, Lehman C (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314:1598–1600.

59. Rindfuss RR, Bumpass L, St. John C (1980) Education and fertility: Implications for the roles women occupy. *Am Sociol Rev* 45:431–447.

60. Noss RF, Cooperrider AY (1994) *Saving Nature's Legacy: Protecting and Restoring Biodiversity* (Island, Washington, DC).

61. Kareiva P (2006) Conservation biology: Beyond marine protected areas. *Curr Biol* 16:533–535.

62. Terborgh J, van Schaik C (2002) in *Making Parks Work: Strategies for Preserving Tropical Nature*, eds Terborgh J, van Schaik C, Davenport L, Rao M (Island, Washington, DC), pp 3–14.

63. Spergel B (2002) in *Making Parks Work: Strategies for Preserving Tropical Nature*, eds Terborgh J, van Schaik C, Davenport L, Rao M (Island, Washington, DC), pp 364–382.

64. Dalton R (2006) Biodiversity: Cashing in on the rich coast. *Nature* 441:567–569.

65. Schuyt K (2005) in *Forest Restoration in Landscapes: Beyond Planting Trees*, eds Mansourian S, Vallauri D, Dudley N (Springer, New York), pp 161–165.

66. Daily GC, Ehrlich PR, Sanchez-Azofeifa GA (2001) Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol Appl* 11:1–13.

67. Pimentel D, *et al.* (1992) Conserving biological diversity in agricultural-forestry systems: Most biological diversity exists in human-managed ecosystems. *BioScience* 42:354–362.

68. Western D (1989) in *Conservation for the Twenty-First Century*, eds Western D, Pearl MM (Oxford Univ Press, Oxford), pp 158–165.

69. Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *J Appl Ecol* 39:157–176.

70. Luck GW, Daily GC (2003) Tropical countryside bird assemblages: Richness, composition, and foraging differ by landscape context. *Ecol Appl* 13:235–247.

71. Georgiadis NJ, Olwero JGN, Ojwang G, Romanach SS (2007) Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biol Conserv* 137:461–472.

72. Ricketts TH (2001) The matrix matters: Effective isolation in fragmented landscapes. *Am Nat* 158:87–99.

73. Stoneham G, Chaudhri V, Ha A, Strappazzon L (2003) Auctions for conservation contracts: An empirical examination of Victoria's BushTender trial. *Austr J Agric Resource Econ* 47:477–500.

74. Farrier D (1995) Conserving biodiversity on private land: Incentives for management or compensation for lost expectations? *Harvard Environ Law Rev* 19:303–408.

75. Mayfield MM, Daily GC (2005) Countryside biogeography of neotropical herbaceous and shrubby plants. *Ecol Appl* 15:423–439.

76. Janzen DH (1986) The future of tropical ecology. *Annu Rev Ecol Syst* 17:305–324.

77. Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66.

78. Cordeiro NJ, Howe HF (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc Natl Acad Sci USA* 100:14052–14056.

79. Ehrlich PR, Mooney HA (1983) Extinction, substitution, and ecosystem services. *BioScience* 33:248–254.

80. Daily GC (1997) *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington, DC).

81. Danielsen F, *et al.* (2005) The Asian tsunami: A protective role for coastal vegetation. *Science* 310:643–643.

82. Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99:16812–16816.

83. Winfree R, Williams NM, Dushoff J, Kremen C (2007) Native bees provide insurance against ongoing honey bee losses. *Ecol Lett* 10:1105–1113.

84. Dasgupta P, Levin S, Lubchenco J (2000) Economic pathways to ecological sustainability. *BioScience* 50:339–345.

85. Aldhous P, Holmes B (2007) Innovate or watch them die. *New Scientist* 195:6–8.

86. Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. *PLoS Biol* 4:2138–2152.

87. Turner WR, *et al.* (2007) Global conservation of biodiversity and ecosystem services. *BioScience* 57:868–873.

88. Chan KMA, *et al.* (2007) When agendas collide: Human welfare and biological conservation. *Conserv Biol* 21:59–68.

89. Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecol Lett* 8:662–673.

90. Janzen DH (2000) in *Norway/UN Conference on the Ecosystem Approach for Sustainable Use of Biological Diversity* (Norwegian Directorate for Nature Research, Trondheim, Norway), pp 122–132.

91. Soule ME, Terborgh J (1999) Conserving nature at regional and continental scales: A scientific program for North America. *BioScience* 49:809–817.

92. Young TP (2000) Restoration ecology and conservation biology. *Biol Conserv* 92:73–83.

93. Janzen DH (2002) in *Handbook of Ecological Restoration, Volume 2: Restoration in Practice*, eds Perrow MR, Davy AJ (Cambridge Univ Press, Cambridge, UK), pp 559–583.

94. Polgreen L (February 11, 2007) In Niger, trees and crops turn back the desert. *NY Times*, World Section, www.nytimes.com/2007/02/11/world/africa/11uiger.html.

95. Guzman HM (1991) Restoration of coral reefs in Pacific Costa Rica. *Conserv Biol* 5:189–195.

96. Mitsch WJ, Wilson RF (1996) Improving the success of wetland creation and restoration with know-how, time, and self-design. *Ecol Appl* 6:77–83.

97. Donlan CJ, *et al.* (2006) Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *Am Nat* 168:660–681.

98. Ripple WJ, Beschta RL (2007) Restoring Yellowstone's aspen with wolves. *Biol Conserv* 138:514–519.

99. Wolf EC, Cooper DJ, Hobbs NT (2007) Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecol Appl* 17:1572–1587.

100. Zedler JB, Callaway JC (1999) Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restor Ecol* 7:69–73.

101. Chapin M (2004) A challenge to conservationists. *World Watch Mag* 2004:17–31.

102. Western D, Wright MA (1994) *Natural Connections: Perspectives in Community-Based Conservation* (Island, Washington, DC).

103. Borgerhoff Mulder M, Coppolillo P (2005) *Conservation: Linking Ecology, Economics and Culture* (Princeton Univ Press, Princeton).

104. Berkes F (2007) Community-based conservation in a globalized world. *Proc Natl Acad Sci USA* 104:15188–15193.

105. Kremen C, *et al.* (1999) Designing the Masoala National Park in Madagascar based on biological and socioeconomic data. *Conserv Biol* 13:1055–1068.

106. Sheil D, Lawrence A (2004) Tropical biologists, local people and conservation: New opportunities for collaboration. *Trends Ecol Evol* 19:634–638.

107. Janzen DH (2004) Setting up tropical biodiversity for conservation through non-damaging use: Participation by parataxonomists. *J Appl Ecol* 41:181–187.

108. Pergams ORW, Zaradic PA (2006) Is love of nature in the US becoming love of electronic media? 16-year downtrend in national park visits explained by watching movies, playing video games, internet use, and oil prices. *J Environ Manag* 80:387–393.

109. Pergams ORW, Zaradic PA (2008) Evidence for a fundamental and pervasive shift away from nature-based recreation. *Proc Natl Acad Sci USA* 105:2295–2300.

110. Janzen DH (2004) Now is the time. *Phil Trans R Soc London B* 359:731–732.

111. Janzen DH (2005) in *Plant Conservation: A Natural History Approach*, eds Krupnick G, Kress J (Univ of Chicago Press, Chicago), pp ix–xiii.

112. Wilson KA, *et al.* (2007) Conserving biodiversity efficiently: What to do, where, and when. *PLoS Biol* 5:e223.

113. Rimer S (December 19, 2007) At 71, physics professor is a web star. *NY Times*, Education Section http://www.nytimes.com/2007/12/19/education/19physics.html.

114. Kozinn A (May 28, 2006) Check the numbers: Rumors of classical music's demise are dead wrong. *NY Times*, Arts Section http://www.nytimes.com/2006/05/28/arts/music/28kozi.html.

115. Janzen DH, *et al.* (2005) Wedding biodiversity inventory of a large and complex Lepidoptera fauna with DNA barcoding. *Philos Trans R Soc London B* 360:1835–1845.

116. Marris E (2007) What to let go. *Nature* 450:152–155.

between ORC binding and nucleosome turnover, suggesting that turnover facilitates ORC binding. In contrast, other chromatin features that would be expected for open or dynamic chromatin, including nucleosome density, mononucleosome/oligonucleosome ratio (a measure of micrococcal nuclease accessibility), H2Av (an H2A.Z histone variant enriched in active chromatin), and salt-soluble nucleosomes, show little if any dependence on ORC abundance (Fig. 3, H to P). Our findings support the hypothesis that replication origins are determined by chromatin, not by sequence features (20, 21). The better quantitative correspondence of ORC to CATCH-IT data than to other chromatin measurements implies that the ORC occupies DNA that is made accessible by nucleosome turnover. In support of this interpretation, we note that very similar correspondences are seen when CATCH-IT data are aligned with GAF sites (fig. S9) and that GAF directs nucleosome turnover in vivo (22, 23).

Our direct strategy for measuring the kinetics of nucleosome turnover does not rely on transgenes or antibodies but rather uses native histones and generic reagents. Thus, CATCH-IT provides a general tool for studying activities that influence nucleosome turnover. With use of CATCH-IT, we found direct evidence that epigenetic maintenance involves nucleosome turnover, a process that erases histone modifications (10).

The fact that EZ is responsible for di- and trimethylation of H3K27, but the nucleosomes that it modifies turn over faster than a cell cycle, argues against proposals that histone modifications required for cellular memory themselves transmit epigenetic information (24). Rather, by simply increasing or decreasing accessibility of DNA to sequence-specific binding proteins, regulated nucleosome turnover may perpetuate active or silent gene expression states and facilitate initiation of replication.

References and Notes

1. S. Henikoff, *Nat. Rev. Genet.* **9**, 15 (2008).
2. Y. Mito, J. G. Henikoff, S. Henikoff, *Nat. Genet.* **37**, 1090 (2005).
3. Y. Mito, J. G. Henikoff, S. Henikoff, *Science* **315**, 1408 (2007).
4. U. Braunschweig, G. J. Hogan, L. Pagie, B. van Steensel, *EMBO J.* **28**, 3635 (2009).
5. C. M. Chow et al., *EMBO Rep.* **6**, 354 (2005).
6. C. Wirbelauer, O. Bell, D. Schübeler, *Genes Dev.* **19**, 1761 (2005).
7. C. Jin et al., *Nat. Genet.* **41**, 941 (2009).
8. S. L. Ooi, J. G. Henikoff, S. Henikoff, *Nucleic Acids Res.* **38**, e26 (2010).
9. A. Jamai, R. M. Imoberdorf, M. Strubin, *Mol. Cell* **25**, 345 (2007).
10. M. F. Dion et al., *Science* **315**, 1405 (2007).
11. A. Rufiange, P.-E. Jacques, W. Bhat, F. Robert, A. Nourani, *Mol. Cell* **27**, 393 (2007).
12. Materials and methods are available as supporting material on *Science* Online.
13. J. A. Prescher, C. R. Bertozzi, *Nat. Chem. Biol.* **1**, 13 (2005).
14. D. C. Dieterich, A. J. Link, J. Graumann, D. A. Tirrell, E. M. Schuman, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 9482 (2006).
15. K. Yamasu, T. Senshu, *J. Biochem.* **107**, 15 (1990).
16. Y. B. Schwartz et al., *Nat. Genet.* **38**, 700 (2006).
17. N. Nègre et al., *PLoS Genet.* **6**, e1000814 (2010).
18. S. Henikoff, J. G. Henikoff, A. Sakai, G. B. Loeb, K. Ahmad, *Genome Res.* **19**, 460 (2009).
19. B. P. Duncker, I. N. Chesnokov, B. J. McConkey, *Genome Biol.* **10**, 214 (2009).
20. H. K. Macalpine, R. Gordan, S. K. Powell, A. J. Hartemink, D. M. Macalpine, *Genome Res.* **20**, 201 (2010).
21. D. M. Gilbert, *Nat. Rev. Mol. Cell Biol.* **5**, 848 (2004).
22. T. Nakayama, K. Nishioka, Y. X. Dong, T. Shimojima, S. Hirose, *Genes Dev.* **21**, 552 (2007).
23. S. J. Petesch, J. T. Lis, *Cell* **134**, 74 (2008).
24. K. H. Hansen et al., *Nat. Cell Biol.* **10**, 1291 (2008).
25. We thank T. Furuyama for suggesting this approach, members of our lab for helpful discussions, and the Hutchinson Center Genomics Shared Resource for microarray processing. This work was supported by NIH grant 1R21DA025758 to S.H. and NIH Postdoctoral Fellowship 1F32GM083449 to R.B.D. All data sets can be found in GEO: GSE19788.

Global Biodiversity: Indicators of Recent Declines

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In 2002, world leaders committed, through the Convention on Biological Diversity, to achieve a significant reduction in the rate of biodiversity loss by 2010. We compiled 31 indicators to report on progress toward this target. Most indicators of the state of biodiversity (covering species' population trends, extinction risk, habitat extent and condition, and community composition) showed declines, with no significant recent reductions in rate, whereas indicators of pressures on biodiversity (including resource consumption, invasive alien species, nitrogen pollution, overexploitation, and climate change impacts) showed increases. Despite some local successes and increasing responses (including extent and biodiversity coverage of protected areas, sustainable forest management, policy responses to invasive alien species, and biodiversity-related aid), the rate of biodiversity loss does not appear to be slowing.

In 2002, world leaders committed, through the Convention on Biological Diversity (CBD), "to achieve by 2010 a significant reduction of the current rate of biodiversity loss" (1), and this "2010 target" has been incorporated into the United Nations Millennium Development Goals in recognition of the impact of biodiversity loss on human well-being (2). The CBD created a framework of indicators to measure biodiversity loss at the level of genes, populations, species, and ecosystems (3, 4). Although a minority have been published individually (5), hitherto they have not been synthesized to provide an integrated outcome. Despite suggestions that the target is unlikely to be (6–8), or has not been (4, 9, 10), met, we test this empirically using a broad suite of biodiversity indicators.

To evaluate achievement of the 2010 target, we (i) determined the trend, and timing and direction of significant inflections in trend for individual indicators (11) and (ii) calculated aggregated indices relating to the state of biodiversity, pressures upon it, policy and management responses, and the state of benefits (ecosystem services) that people derive from biodiversity, using the best available sources. To calculate aggregate indices, we first scaled each of 24 indicators (out of 31) with available trend information to a value of 1 in the first year with data from 1970 onward (only eight indicators had earlier trends) and calculated annual proportional change from this first year. Then we used a generalized additive modeling framework (5, 12, 13) and determined significant inflections (12). Although absolute values are difficult to interpret because they aggregate different elements of biodiversity, this approach permits a synthetic interpretation of rate changes across the elements measured: For example, the aggregated state index should show positive inflections if biodiversity loss has been significantly reduced.

Our analyses suggest that biodiversity has continued to decline over the past four decades, with most (8 out of 10) state indicators showing negative trends (Fig. 1 and Table 1). There have been declines in population trends of (i) vertebrates [13] and (ii) habitat specialist birds; (iii) shorebird populations worldwide; extent of (iv) forest [14, 15]; (v) mangroves; (vi) seagrass beds; and (vii) the condition of coral reefs. None show

significant recent reductions in the rate of decline (Table 1), which is either fluctuating (i), stable (ii), based on too few data to test significance (iii to vi), or stable after a deceleration two decades ago (vii). Two indicators, freshwater quality and trophic integrity in the marine ecosystem, show stable and marginally improving trends, respectively, which are likely explained by geographic biases in data availability for the former and spatial expansion of fisheries for the latter [5]. Aggregated trends across state indicators have declined, with no significant recent reduction in rate: The most recent inflection in the index (in 1972) was negative (Fig. 2). Because there were fewer indicators with trend data in the 1970s, we recalculated the index from 1980, which also showed accelerating biodiversity loss: The most recent inflection (2004) was negative. Finally, aggregated species' extinction risk (i.e., biodiversity loss at the species level) has accelerated: The International Union for Conservation of Nature (IUCN) Red List Index (RLI), measuring rate of change [16, 17], shows negative trends.

The majority of indicators of pressures on biodiversity show increasing trends over recent decades (Fig. 1 and Table 1), with increases in (i) aggregate human consumption of the planet's ecological assets, (ii) deposition of reactive nitrogen, (iii) number of alien species in Europe, (iv) proportion of fish stocks overharvested, and (v) impact of climate change on European bird population trends [18]. In no case was there a significant reduction in the rate of increase (Table 1), which was stable (i, iii, and v), fluctuating (iv), or based on too few data to test significance (ii), although growth in global nitrogen deposition may have slowed, and this may explain why the most recent inflection in aggregated trends (in 2006) was negative (Fig. 2) [5]. Global trends for habitat fragmentation are unavailable, but it is probably increasing; for example, 80% of remaining Atlantic Forest fragments are <0.5 km^2 in size [19], and 59% of large river systems are moderately or strongly fragmented by dams and reservoirs [20].

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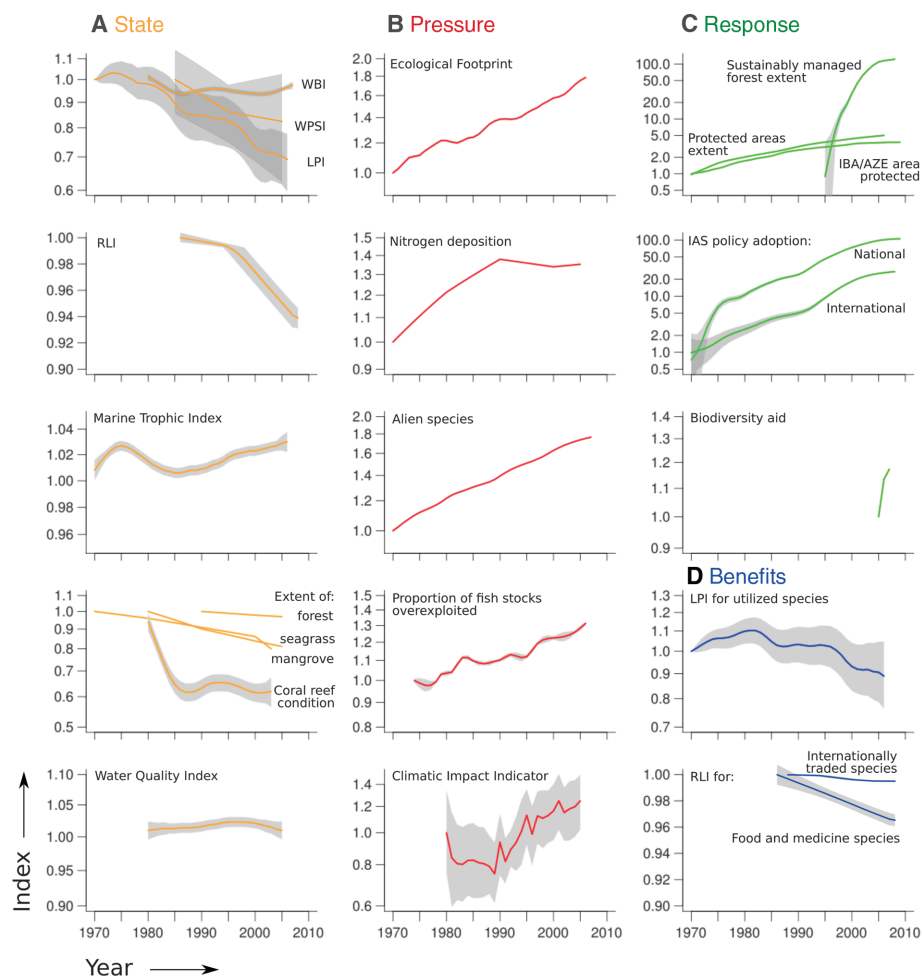

Fig. 1. Indicator trends for (**A**) the state of biodiversity, (**B**) pressures upon it, (**C**) responses to address its loss, and (**D**) the benefits humans derive from it. Data scaled to 1 in 1970 (or for first year of data if >1970), modeled (if >13 data points; see Table 1), and plotted on a logarithmic ordinate axis. Shading shows 95% confidence intervals except where unavailable (i.e., mangrove, seagrass, and forest extent, nitrogen deposition, and biodiversity aid). WBI, Wild Bird Index; WPSI, Waterbird Population Status Index; LPI, Living Planet Index; RLI, Red List Index; IBA, Important Bird Area; AZE, Alliance for Zero Extinction site; IAS, invasive alien species.

Table 1. Summary of global biodiversity indicator trends.

Indicator	Data availability (years)†	% Change since 1970‡	Mean annual % change§					Trends in rate of change‖
			1970s	1980s	1990s	2000s	Since 1970	
State								
Living Planet Index (LPI) (mean population trends of vertebrates)	1970–2006	−31*	−0.2	−1.4	−1.4	−0.9	−1.0	F
Wild Bird Index [mean population trends of habitat specialists in Europe and North America, disaggregated for terrestrial (t) and wetland (w) species]	1980–2007	−2.6*		−0.6	−0.2	+0.6	−0.1	S
		−16*(t)		−1.3	−0.7	+0.3	−0.7	D 1982–2007
		+40*(w)		+1.1	+1.3	+1.1	+1.2	S
Waterbird Population Status Index (% shorebird populations increasing, stable, or decreasing)	1985–2005†	−33		−1.4	−2.0	−2.4	−2.0	A?
Red List Index (RLI) (extinction risk of mammals, birds, amphibians, and corals)	1986–2008	−6.1*		−0.1	−0.2	−0.5	−0.3	A
Marine Trophic Index (shift in fishing catch from top predators to lower trophic levels)	1950–2006	+3.0*	+0.1	−0.1	+0.1	+0.1	+0.1	S
Forest extent	1990–2005†	−3.1			−0.2	−0.2	−0.2	S?
Mangrove extent	1980–2005†	−19		−1.0	−0.7	−0.7	−0.8	S?
Seagrass extent	1930–2003†	−20	−0.4	−0.5	−0.5	−2.4	−0.7	A?
Coral reef condition (live hard coral cover)	1980–2004	−38*		−3.9	−0.3	+0.2	−1.8	D 1985–1988
Water Quality Index (physical/chemical quality of freshwater)	1980–2005	0		+0.1	+0.0	−0.2	+0	S
Number of state indicators declining			**2/3**	**8/9**	**8/10**	**7/10**	**8/10**	
Pressures								
Ecological footprint (humanity's aggregate resource-consumption)	1961–2006	+78*	+2.0	+1.3	+1.3	+2.1	+1.6	S
Nitrogen deposition rate (annual reactive N deposited)	1850–2005†	+35	+2.0	+1.3	−0.3	+0.2	+0.9	D?
No. alien species in Europe (Mediterranean marine, mammal, and freshwater)	1970–2007	+76*	+2.0	+1.4	+1.6	+1.1	+1.5	S
Exploitation of fish stocks (% overexploited, fully exploited, or depleted)	1974–2006	+31*	+0.6	+0.6	+1.1	+1.2	+0.9	F
Climatic Impact Indicator (degree to which European bird population trends have responded in the direction expected from climate change)	1980–2005	+23*		−0.8	+3.2	+1.2	+1.2	S
Number of pressure indicators increasing			**4/4**	**4/5**	**4/5**	**5/5**	**5/5**	
Responses								
Extent of Protected Areas (PAs)	1888–2006	+400*	+7.6	+4.5	+3.4	+2.4	+4.7	S
Coverage by PAs of Important Bird Areas and Alliance for Zero Extinction sites	1888–2009	+360*	+5.6	+4.6	+2.6	+0.8	+3.4	D 1999–2008
Area of forest under sustainable management (FSC certified)	1995–2008	+12,000*			+100	+20	+46	D 2006
International IAS policy adoption (no. signatories to conventions with provision for tackling IAS)	1952–2008	+2700*	+10	+6.9	+14	+5.1	+9.1	S
National IAS policy adoption (% countries with relevant legislation)	1964–2009	+10,000*	+30	+8.7	+12	+4.1	+13	D 2004–2009
Official development assistance (US$ per year provided in support of CBD)	2005–2007†	+17				+8.4	+8.3	D?
Number of response indicators increasing			**4/4**	**4/4**	**5/5**	**6/6**	**6/6**	
Benefits								
LPI for utilized vertebrate populations	1970–2006	−15*	+1.0	−0.3	−1.3	−1.7	−0.4	A 1972–2006
RLI for species used for food and medicine	1986–2008	−3.5*		−0.2	−0.2	−0.2	−0.2	A
RLI for bird species in international trade	1988–2008	−0.5*		−0.01	−0.03	−0.02	−0.03	A
Number of benefits indicators declining			**0/1**	**3/3**	**3/3**	**3/3**	**3/3**	

*Significant trends (*P* < 0.05).   †Identifies indicators with insufficient data to test significance of post-1970 trends, usually because annual estimates are unavailable.   ‡Since earliest date with data if this is post-1970.   §Because the indicators measure different parameters, some comparisons of mean annual % change between indicators are less meaningful than comparisons between decades for the same indicator.   ‖Rate of change decelerating (D), accelerating (A), stable (S, i.e., no years with significant changes), fluctuating (F, i.e., a sequence of significant positive and negative changes), or with too few data points to test significance (?); years indicate periods in which second derivatives differed significantly from zero (*P* < 0.05).

All indicators of policy and management responses show increasing trends (Fig. 1 and Table 1), with increases in (i) extent of protected areas (PAs) (Table 2); (ii) coverage by PAs of two subsets of Key Biodiversity Areas (*21*) [39% of the area of 10,993 Important Bird Areas and 42% of the area of 561 Alliance for Zero Extinction sites (*22*) by 2009]; (iii) area of sustainably managed forests [1.6 million km^2 under Forest Stewardship Council (FSC) certification by 2007]; (iv) proportion of eligible countries signing international agreements relevant to tackling invasive alien species (IAS) [reaching 82% by 2008 (*23*)]; (v) proportion of countries with national legislation to control and/or limit the spread and impact of IAS [reaching 55% by 2009 (*23*)]; and (vi) biodiversity-related aid (reaching US$3.13 billion in 2007). The rate of increase was stable (i and iv), slowing (ii, iii, and v), or based on too few data to test significance (vi) (Table 1). The last three inflections in aggregated trends (2002, 2004, and 2008) were all negative (Fig. 2), indicating that the rate of improvement has slowed. Two other indicators have only baseline estimates: Management effectiveness was "sound" for 22% of PAs ("basic" for 65% and "clearly inadequate" for 13%), and the proportion of genetic diversity for 200 to 300 important crop species conserved ex situ in gene banks was estimated to be 70% (*24*).

Only three indicators address trends in the benefits humans derive from biodiversity (Fig. 1 and Table 1): (i) population trends of utilized vertebrates have declined by 15% since 1970, and aggregate species' extinction risk has increased

Fig. 2. Aggregated indices of (**A**) the state of biodiversity based on nine indicators of species' population trends, habitat extent and condition, and community composition; (**B**) pressures on biodiversity based on five indicators of ecological footprint, nitrogen deposition, numbers of alien species, overexploitation, and climatic impacts; and (**C**) responses for biodiversity based on six indicators of protected area extent and biodiversity coverage, policy responses to invasive alien species, sustainable forest management, and biodiversity-related aid. Values in 1970 set to 1. Shading shows 95% confidence intervals derived from 1000 bootstraps. Significant positive/upward (open circles) and negative/downward (filled circles) inflections are indicated.
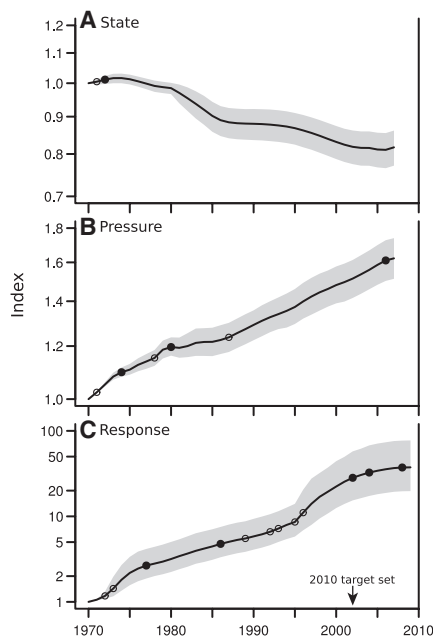
Table 2. Examples of successes and positive trends relevant to the 2010 target (*5*).

Indicator	Successes and positive trends
	State
Living Planet Index of Palearctic vertebrate populations	Increased by 43% since 1970 (e.g., Eurasian beaver and common buzzard)
Waterbird populations in North America and Europe	Increased by 44% since 1980 owing to wetland protection and sustainable management (but populations remain below historic levels).
Species downlisted on the IUCN Red List	Species qualifying for downlisting to lower categories of extinction risk owing to successful conservation action include 33 birds since 1988 (e.g., Lear's macaw), 25 mammals since 1996 (e.g., European bison), and 5 amphibians since 1980 (e.g., Mallorcan midwife toad).
Wild Bird Index and Red List Index for species listed on the European Union Birds Directive	Annex 1–listed species' population trends have improved in EU countries (*27*) and extinction risk reduced (RLI increased 0.46% during 1994–2004) owing to designation of Special Protected Areas and implementation of Species Action Plans under the directive (e.g., white-tailed eagle).
Extinctions prevented	At least 16 bird species extinctions were prevented by conservation actions during 1994–2004, e.g., black stilt (*28*).
Water Quality Index in Asia	Improved by 7.4% since 1970.
	Pressures
Deforestation in Amazonian Brazil	Slowed from 2.8 million ha in 2003–2004 to 1.3 million ha in 2007–2008, but it is uncertain to what extent this was driven by improved enforcement of legislation versus reduced demand owing to economic slowdown.
	Responses
National biodiversity strategies and action plans (NBSAPs)	87% of countries have now developed NBSAPs and therefore have outlined coherent plans for tackling biodiversity loss at the national scale.
Protected areas (PAs)	Nearly 133,000 PAs designated, now covering 25.8 million km^2: 12% of the terrestrial surface (but only 0.5% of oceans and 5.9% of territorial seas), e.g., Juruena National Park, Brazil, designated in 2006, covering 19,700 km^2 of Amazon/cerrado habitat.
Invasive alien species (IAS) policy, eradication, and control	82% of eligible countries have signed international agreements relevant to preventing the spread and promoting the control/eradication of IAS. Successful eradications/control of IAS include pigs on Clipperton Atoll, France (benefiting seabirds and land crabs), cats, goats and sheep on Natividad, Mexico (benefiting black-vented shearwater), and red fox in southwest Australia (benefiting western brush wallaby).
Official development assistance for biodiversity	Increased to at least US$3.13 billion in 2007.

at an accelerating rate (as shown by the RLI) for (ii) mammals, birds, and amphibian species used for food and medicine (with 23 to 36% of such species threatened with extinction) and (iii) birds that are internationally traded (principally for the pet trade; 8% threatened). Trends are not yet available for plants and other important utilized animal groups. Three other indicators, which lack trend data, show (iv) 21% of domesticated animal breeds are at risk of extinction (and 9% are already extinct); (v) languages spoken by fewer than 1000 people (22% of the current 6900 languages) have lost speakers over the past 40 years and are in danger of disappearing within this century (loss of linguistic diversity being a proxy for loss of indigenous biodiversity knowledge); and (vi) more than 100 million poor people live in remote areas within threatened ecoregions and are therefore likely to be particularly dependent upon biodiversity and the ecosystem services it provides.

Indicator development has progressed substantially since the 2010 target was set. However, there are considerable gaps and heterogeneity in geographic, taxonomic, and temporal coverage of existing indicators, with fewer data for developing countries, for nonvertebrates, and from before 1980 and after 2005 (4, 5, 25). Interlinkages between indicators and the degree to which they are representative are incompletely understood. In addition, there are gaps for several key aspects of state, pressures, responses, and especially benefits (4, 5, 7, 26).

Despite these challenges, there are sufficient data on key dimensions of biodiversity to conclude that at the global scale it is highly unlikely that the 2010 target has been met. Neither individual nor aggregated indicators of the state of biodiversity showed significant reductions in their rates of decline, apart from coral reef condition, for which there has been no further deceleration in decline since the mid-1980s. Furthermore, all pressure indicators showed increasing trends, with none significantly decelerating. Some local system-specific exceptions with positive trends for particular populations, taxa, and habitats (Table 2) suggest that, with political will and adequate resources, biodiversity loss can be reduced or reversed. More generally, individual and aggregated response indicators showed increasing trends, albeit at a decelerating rate (and with little direct information on whether such actions are effective). Overall, efforts to stem biodiversity loss have clearly been inadequate, with a growing mismatch between increasing pressures and slowing responses.

Our results show that, despite a few encouraging achievements, efforts to address the loss of biodiversity need to be substantially strengthened by reversing detrimental policies, fully integrating biodiversity into broad-scale land-use planning, incorporating its economic value adequately into decision making, and sufficiently targeting, funding and implementing policies that tackle biodiversity loss, among other measures. Sustained investment in coherent global biodiversity monitoring and in-

dicators is essential to track and improve the effectiveness of these responses.

References and Notes

1. Secretariat of the Convention on Biological Diversity, *Handbook of the Convention on Biological Diversity* (Earthscan, London, 2003).
2. United Nations, Millennium Development Goals Indicators (http://unstats.un.org/unsd/mdg/Host.aspx?Content=Indicators/OfficialList.htm, 2008).
3. Convention on Biological Diversity, Framework for monitoring implementation of the achievement of the 2010 target and integration of targets into the thematic programmes of work, COP 8 Decision VIII/15 (www.cbd.int/decisions, 2006).
4. M. Walpole et al., *Science* 325, 1503 (2009).
5. Further information is available as supporting material on *Science* Online.
6. H. M. Pereira, H. David Cooper, *Trends Ecol. Evol.* 21, 123 (2006).
7. G. M. Mace, J. E. M. Baillie, *Conserv. Biol.* 21, 1406 (2007).
8. J. D. Sachs et al., *Science* 325, 1502 (2009).
9. N. Gilbert, *Nature* 462, 263 (2009).
10. H. Mooney, G. Mace, *Science* 325, 1474 (2009).
11. L. Soldaat, H. Visser, M. van Roomen, A. van Strien, *J. Ornithol.* 148, (S2), 351 (2007).
12. R. M. Fewster, S. T. Buckland, G. M. Siriwardena, S. R. Baillie, J. D. Wilson, *Ecology* 81, 1970 (2000).
13. B. Collen et al., *Conserv. Biol.* 23, 317 (2009).
14. Food and Agriculture Organization, *Global Forest Resources Assessment* 2005 (FAO, Rome, 2006).
15. M. C. Hansen et al., *Proc. Natl. Acad. Sci. U.S.A.* 105, 9439 (2008).
16. S. H. M. Butchart et al., *PLoS ONE* 2, e140 (2007).
17. J. C. Vié, C. Hilton-Taylor, S. N. Stuart, Eds., *Wildlife in a Changing World* (IUCN, Gland, Switzerland, 2008).
18. R. D. Gregory et al., *PLoS ONE* 4, e4678 (2009).
19. M. C. Ribeiro, J. P. Metzger, A. C. Martensen, F. Ponzoni, M. Hirota, *Biol. Conserv.* 142, 1141 (2009).
20. C. Nilsson, C. A. Reidy, M. Dynesius, C. Revenga, *Science* 308, 405 (2005).
21. G. Eken et al., *Bioscience* 54, 1110 (2004).
22. T. H. Ricketts et al., *Proc. Natl. Acad. Sci. U.S.A.* 102, 18497 (2005).
23. M. A. McGeoch et al., *Divers. Distrib.* 16, 95 (2010).
24. SCBD, *The Convention on Biological Diversity Plant Conservation Reports* (SCBD, Montreal, 2009).
25. B. Collen, M. Ram, T. Zamin, L. McRae, *Trop. Conserv. Sci.* 1, 75 (2008).
26. A. Balmford, P. Crane, A. Dobson, R. E. Green, G. M. Mace, *Philos. Trans. R. Soc. London Ser. B* 360, 221 (2005).
27. P. F. Donald et al., *Science* 317, 810 (2007).
28. S. H. M. Butchart, A. J. Stattersfield, N. J. Collar, *Oryx* 40, 266 (2006).
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Plectasin, a Fungal Defensin, Targets the Bacterial Cell Wall Precursor Lipid II

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Host defense peptides such as defensins are components of innate immunity and have retained antibiotic activity throughout evolution. Their activity is thought to be due to amphipathic structures, which enable binding and disruption of microbial cytoplasmic membranes. Contrary to this, we show that plectasin, a fungal defensin, acts by directly binding the bacterial cell-wall precursor Lipid II. A wide range of genetic and biochemical approaches identify cell-wall biosynthesis as the pathway targeted by plectasin. In vitro assays for cell-wall synthesis identified Lipid II as the specific cellular target. Consistently, binding studies confirmed the formation of an equimolar stoichiometric complex between Lipid II and plectasin. Furthermore, key residues in plectasin involved in complex formation were identified using nuclear magnetic resonance spectroscopy and computational modeling.

Plectasin is a 40–amino acid residue fungal defensin produced by the saprophytic ascomycete *Pseudoplectania nigrella* (1).

Plectasin shares primary structural features with defensins from spiders, scorpions, dragonflies and mussels and folds into a cystine-stabilized alpha-

ECOLOGY

Biodiversity Conservation and the Millennium Development Goals

Any near-term gains in reducing extreme poverty will be maintained only if environmental sustainability is also achieved.

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The Millennium Development Goals (MDGs) are designed to inspire efforts to improve people's lives by, among other priorities, halving extreme poverty by 2015 (1). Analogously, concern about global decline in biodiversity and degradation of ecosystem services (2) gave rise in 1992 to the Convention on Biological Diversity (CBD). The CBD target "to achieve by 2010 a significant reduction of the current rate of biodiversity loss" was incorporated into the MDGs in 2002. Our lack of progress toward the 2010 target (3, 4) could undermine achievement of the MDGs and poverty reduction in the long term. With increasing global challenges, such as population growth, climate change, and overconsumption of ecosystem services, we need further integration of the poverty alleviation and biodiversity conservation agendas.

The links between poverty and the environment are, unsurprisingly, complex (5, 6) (Fig. 1). Some attempts have been made to identify a relation between development and biodiversity, but these have yielded mixed results (5). Action is urgently needed to identify and quantify the links between biodiversity and ecosystem services on the one hand, and poverty reduction on the other, while taking into account the global, regional, and local drivers of biodiversity loss in poor areas.

Tackling the root causes of both biodiversity loss and poverty can lead to complementary positive results. For example, reducing population pressure by promoting voluntary reductions in fertility in impoverished regions could support conservation of biodiversity and faster poverty alleviation (7). However, there

may be complex trade-offs, especially in the short term. Trade liberalization, for instance, might increase the supply of food commodities and could reduce prices in food-importing countries, which would remove some pressure on these countries' natural habitats. But reductions in trade barriers might also lead to increased production in food-exporting countries where commercial agriculture could increase vulnerability to deforestation, pests, diseases, and/or natural disasters, and might reduce the availability of ecosystem services (8, 9). Nevertheless, countervailing efforts to maintain biodiversity must be sensitive to human needs if they are to retain public support (10).

The scientific and development policy communities should focus on jointly articulating and addressing the critical research questions that, when answered, will help ensure that poverty alleviation and conservation efforts produce win-win outcomes, or at least minimize harm to either agenda. To ensure greater synergies, we suggest the following actions. Attention must focus on constructing and meeting a new biodiversity target for the remaining MDG period and beyond. The next target should be more specific, similarly time-limited, reasonably achievable, and should address the consequences of biodiversity loss globally and for the most vulnerable people and societies.

It should be supported by a small set of indicators (11) that measure trends in the state of biodiversity and ecosystem services, drivers of biodiversity loss and activities to safeguard biodiversity.

We need evidence-based interventions that can address both poverty reduction and environmental sustainability. In agriculture, for instance, we can use existing land more efficiently; we can pursue development that protects or enhances biodiversity; and we can improve productivity in ways that maintain ecosystem services, through institutional changes to secure better access to seeds, markets, and expertise, combined with adaptive applications of technologies (12). Similarly, finance and technology for adaptation, disaster management, and reduced emissions from deforestation and forest degradation (13) are particularly important in helping developing countries deal with climate change.

Future projects should explicitly monitor the impact poverty alleviation efforts have on ecosystems and their services; similarly, conservationists must better document the impact their interventions have on the poor. Ideally, interdisciplinary science that helps to identify the most cost-effective solutions will ensure that future environment and development projects are implemented, not just simultaneously, but in an integrated fashion.

Poverty alleviation and biodiversity agendas need to be jointly presented to policymakers. Establishment of a proposed Intergovernmental Platform on Biodiversity and Ecosystem Services to complement the existing Intergovernmental Panel on Climate
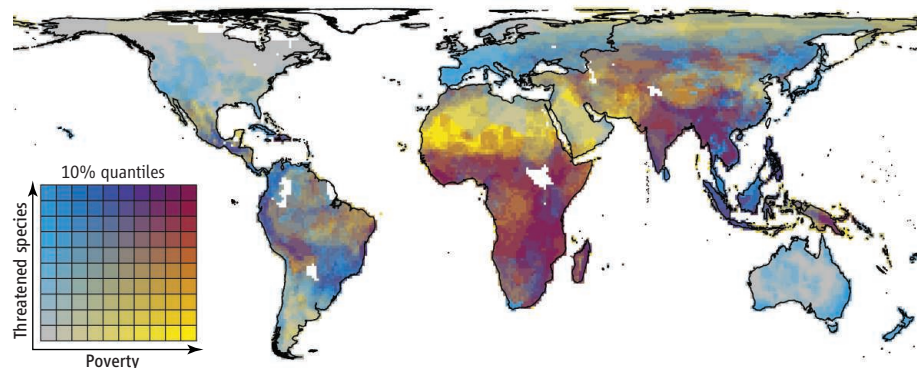
[1]Columbia University. [2]Zoological Society of London. [3]University of Cambridge. [4]University of Sheffield. [5]IUCN. [6]Imperial College London. [7]House of Commons, London. [8]University of Oxford. [9]Royal Society for The Protection of Birds. [10]Natural History Museum London. [11]Imperial College London. [12]University College London. [13]GLOBE International, London. [14]International Institute for Environment and Development, London. [15]University East Anglia. [16]United Nations Environment Programme World Conservation Monitoring Centre. [17]Department for Environment, Food and Rural Affairs, London.

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Fig. 1. Map of poverty and potential biodiversity loss, showing the level of poverty (proxied by the log rate of human infant mortality) combined with the log number of threatened species of mammals, birds, and amphibians per one-degree grid square (Behrmann equal-area projection). White areas represent missing data. Data from (14) and (15).

Change may provide a means to enhance the quality and timeliness of the interactions between scientists and policy-makers at national scales and above. The GLOBE International Commission on Land Use Change and Ecosystems, made up of senior legislators from the G8+5 and several developing countries, provides another opportunity to bring policy-makers and scientists together. Similar initiatives will also be needed at the subnational scale.

The United Nations will convene a summit in 2010 to consider the second 5-year review of the MDGs and to catalyze action ahead of the 2015 MDG target year. We must advise policy-makers and civil society organizations on the most critical initiatives needed to achieve the MDGs while preserving biodiversity and ecosystem services.

References and Notes

1. U.N. Millennium Project, *Investing in Development: A Practical Plan to Achieve the Millennium Development Goals* (Earthscan, New York, 2005).
2. G. M. Mace, H. Masundire, J. E. M. Baillie, in *Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group* (Millennium Ecosystem Assessment Series, Island Press, Washington, DC, vol. 1, 2005), chap. 4.
3. B. Collen *et al.*, *Conserv. Biol.* **23**, 317 (2009).
4. G. M. Mace, J. E. M. Baillie, *Conserv. Biol.* **21**, 1406 (2007).
5. S. Dasgupta, B. Laplante, H. Wang, D. Wheeler, *J. Econ. Perspect.* **16**, 147 (2002).
6. P. Dasgupta, in *Handbook of Environmental Economics: Environmental Degradation and Institutional Responses*, K.-G. Maler, J. R. Vincent, Eds. (Elsevier, London, 2003), pp. 192–240.
7. M. Q. Dao, *J. Stud. Econ. Econometr.* **32**, 47 (2008).
8. J. D. Sachs, *The End of Poverty: Economic Possibilities for Our Time* (Penguin, New York, 2005).
9. R. E. Green, S. J. Cornell, P. W. Scharlemann, A. Balmford, *Science* **307**, 550 (2005).
10. W. M. Adams, J. Hutton, *Conserv. Soc.* **5**, 147 (2007).
11. M. Walpole *et al.*, *Science* **325**, 1503 (2009).
12. W. M. Adams *et al.*, *Science* **306**, 1146 (2004).
13. B. Strassburg, R. K. Turner, B. Fisher, R. Schaeffer, A. Lovett, *Glob. Environ. Change* **19**, 265 (2009).
14. Poverty maps, http://sedac.ciesin.columbia.edu/povmap.
15. R. Grenyer *et al.*, *Nature* **444**, 93 (2006).

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ECOLOGY

Tracking Progress Toward the 2010 Biodiversity Target and Beyond

Biodiversity indicators used by policy-makers are underdeveloped and underinvested.

Matt Walpole,[1]*† Rosamunde E. A. Almond,[1] Charles Besançon,[1] Stuart H. M. Butchart,[2] Diarmid Campbell-Lendrum,[3] Geneviève M. Carr,[4,5] Ben Collen,[6] Linda Collette,[7] Nick C. Davidson,[8] Ehsan Dulloo,[9] Asghar M. Fazel,[1] James N. Galloway,[10] Michael Gill,[11] Tessa Goverse,[12] Marc Hockings,[13] Danna J. Leaman,[14] David H. W. Morgan,[15] Carmen Revenga,[16] Carrie J. Rickwood,[5,17] Frederik Schutyser,[18] Sarah Simons,[19] Alison J. Stattersfield,[2] Tristan D. Tyrrell,[1] Jean-Christophe Vié,[20] Mark Zimsky[21]

In response to global declines in biodiversity, some 190 countries have pledged, under the Convention on Biological Diversity (CBD), to reduce the rate of biodiversity loss by 2010 (*1*, *2*). Moreover, this target has recently been incorporated into the Millennium Development Goals in recognition of the impact of biodiversity loss on human well-being (*3*). Timely information on where and in what ways the target has or has not been met, as well as the likely direction of future trends, depends on a rigorous, relevant, and comprehensive suite of biodiversity indicators with which to track changes over time, to assess the impacts of policy and management responses, and to identify priorities for action. How far have we come in meeting these needs, and is it sufficient?

In 2006, the CBD adopted a framework of 22 cross-disciplinary headline indicators with which to measure progress toward the target at a global level (*4*, *5*). Countries are being encouraged to report progress at the national level using this framework, which is also being applied in regional initiatives such as "Streamlining European Biodiversity Indicators" (SEBI 2010). Other global multilateral environmental agreements, including the Ramsar Convention on Wetlands, the Convention on Migratory Species, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora, are also adopting and adapting relevant subsets of the indicators.

However, with 2010 fast approaching, the indicator set is by no means complete. This is unsurprising given the short time since the framework was agreed upon. Of the 22 headline indicators, 5 are not being developed at a global scale, and there will be none to measure the status of access and benefit sharing, one of the three objectives of the CBD. The remainder has been subdivided into 29 actual measures, of which only 9 can be considered well-developed, with established methodologies, reasonable global coverage (all continents except Antarctica, tropical and temperate regions, and developed and developing countries), and sufficient time-series data (at least three data points spanning at least 10 years) to demonstrate changes over time [(Table 1) and supporting online material (SOM)].

Even for these well-developed global indicators, there are challenges in terms of data availability, consistency, and relevance. Some indicators are only weak proxies for biodiversity, because the urgent need for indicators has often meant relying on existing measures designed for purposes other than tracking biodiversity change. For example, forest cover may be an acceptable proxy for timber stocks, but says less about the condition of forest biodiversity. Likewise, protected area coverage signals government commitments but does not in itself measure effectiveness in reducing biodiversity loss. These subtleties are beginning to be explored but require further effort.

Patchy data are another challenge, including gaps in data submissions for indicators compiled from national reports (*6–9*) and incomplete taxonomic and geographic coverage of indicators compiled directly from data. The most well developed direct measures of biodiversity are species indicators, such as the IUCN Red List Index (RLI) (*10*) and the Living Planet Index (LPI) (*11*). They are being used to inform and underpin a variety of other indica-

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2. G. M. Mace, H. Masundire, J. E. M. Baillie, in *Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group* (Millennium Ecosystem Assessment Series, Island Press, Washington, DC, vol. 1, 2005), chap. 4.
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tors (see SOM). Nevertheless, in the RLI, only a small number of taxonomic groups have been fully assessed, whereas, in the LPI, tropical species are poorly represented (*12*). Efforts are being made to improve representation in both of these indicators, including through a sampled RLI approach (*13*).

Information on genetic- or ecosystem-level changes in biodiversity is much patchier. Despite the promise of remote sensing and the increasing quality and availability of satellite imagery, translating this into meaningful metrics of change for freshwater systems, drylands, coastal and marine habitats, and other ecosystem types has proved challenging to date. Local and regional studies are available (*14*), but they are yet to be applied

globally. Likewise, indicators of genetic biodiversity are slowly being compiled for domesticated and cultivated varieties but not yet for wild relatives.

For the indicators that are under development, the race is now on to ensure adequate coverage and sufficient time-series data by 2010. Although progress has undoubtedly been made, for some, such as trends in genetic diversity and ecosystem fragmentation, a baseline and established methodology may be the most that can be expected. Some of these indicators require input from a range of disciplines not traditionally associated with biodiversity science, such as geophysics, economics, sociology, anthropology, agronomy, and health. The scientific community must be encouraged to engage in the development of these indicators and to provide case studies demonstrating how and why biodiversity losses have been reduced.

Whatever the indicators tell us, it is widely held that the target cannot and will not be achieved in its entirety (*16*). Although the current indicators will provide a partial story about both achievements and failures, there are gaps and missing linkages in the framework that mean it may not be sufficient to communicate the urgency of the message, to hold politicians to account, or to inform them of how best to act.

In October 2010, the Conference of the Parties (COP) to the CBD will review progress and agree on a new set of targets and a revised indicator framework. Whatever shape these targets take, the lessons for indicator development are clear. Indicators must be closely linked to the targets, but also to each other. We believe that a revised framework comprising a small set of headline indicators in four focal areas (pressures–threats, status–trends, benefits–services, and actions–responses) with underlying measures that are causally linked, will make it clearer to policy-makers how biodiversity loss affects people and how actions to reduce threats make a difference.

Continued investment must be made in the existing indicators to improve taxonomic, geographic, and temporal coverage, alongside support to develop measures at the finer (genetic) and broader (ecosystem) scales. Indicators of

the biodiversity impacts of a wider range of threats, including climate change, should be incorporated. Critically, indicators must be developed to fill a major gap regarding the effect of biodiversity change on the provision of ecosystem services. A balance must be found between developing too large and confusing an array of individual measures versus relying on a few aggregate indices that appear compelling but that mask complexity and can be misinterpreted. Quality-control efforts are needed to ensure that indicators are sufficiently scientifically rigorous, free of bias, and sensitive enough to detect meaningful change (*16*).

Indicators cannot be developed in the absence of reliable biodiversity data. Systematic global biodiversity monitoring (*17*, *18*) would help, but this must be balanced with significant indicator capacity development at the national level. Better national indicators, developed as part of an inclusive international process, will enable better global syntheses beyond 2010. The scientific community must engage and encourage governments in this regard.

References and Notes
1. In 2002, the COP to the CBD agreed "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at global, regional, and national level as a contribution to poverty alleviation and to the benefit of all life on Earth" (*2*).
2. "Strategic Plan for the Convention on Biological Diversity" [Decision VI/26 of the COP to the CBD at the Sixth Meeting (COP 6), 2002]; available at www.cbd.int/decisions/.
3. Millennium Development Goals Indicators, http://unstats.un.org/unsd/mdg/Host.aspx?Content=Indicators/OfficialList.htm.
4. A. Balmford *et al.*, *Science* **307**, 212 (2005).
5. "Framework for monitoring implementation of the achievement of the 2010 target and integration of targets into the thematic programmes of work" (Decision VIII/15, COP 8, 2006); available at www.cbd.int/decisions/.
6. G. M. Carr, C. J. Rickwood, *Water Quality Index for Biodiversity Technical Development Document* [UNEP Global Environment Monitoring System (GEMS) Water Programme, Gatineau, Canada, 2007].
7. E. B. S. Goldfinger *et al.*, *The Ecological Footprint Atlas 2008* (Global Footprint Network, Oakland, CA, 2008).
8. FAO, *Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management* (FAO, Rome, 2006).
9. UNEP-WCMC, *State of the World's Protected Areas: An Annual Review of Global Conservation Progress* (UNEP-WCMC, Cambridge, 2008).
10. S. H. M. Butchart *et al.*, *PLoS One* **2**, e140 (2007).
11. J. Loh *et al.*, *Philos. Trans. R. Soc. London B Biol. Sci.* **360**, 289 (2005).
12. B. Collen *et al.*, *Conserv. Biol.* **23**, 317 (2009).
13. J. E. M. Baillie *et al.*, *Conserv. Lett* **1**, 18 (2008).
14. M. C. Hansen *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 9439 (2008).
15. CBD, *Global Biodiversity Outlook 2* (Secretariat of the CBD, Montreal, 2006).
16. G. M. Mace, J. E. M. Baillie, *Conserv. Biol.* **21**, 1406 (2007).
17. R. J. Scholes *et al.*, *Science* **321**, 1044 (2008).
18. H. M. Pereira, H. D. Cooper, *Trends Ecol. Evol.* **21**, 123 (2006).

Biodiversity indicators

Components of biodiversity

Trends in extent of selected biomes, ecosystems, habitats	
Trends in abundance of selected species	
Coverage of protected areas	
Changes in status of threatened species	
Trends in genetic diversity	

Sustainable use

Area under sustainable management	
Proportion of products from sustainable sources	
Ecological footprint and related concepts	

Threats to biodiversity

Nitrogen deposition	
Trends in invasive alien species	

Ecosystem integrity, goods and services

Marine Trophic Index	
Water quality of freshwater ecosystems	
Trophic integrity of other ecosystems	
Connectivity/fragmentation of ecosystems	
Human-induced ecosystem failure	
Health and well-being of communities	
Biodiversity for food and medicine	

Status of knowledge, innovations, and practices

Linguistic diversity	
Indigenous and traditional knowledge	

Status of access and benefits sharing

Access and benefits sharing	

Status of resource transfers

Official development assistance	
Technology transfer	

Table 1. Current development of the headline biodiversity indicators within the CBD framework. ■ Fully developed with well-established methodologies and global time-series data, ■ under development, and ■ not being developed. Multiple labels indicate multiple measures under each headline. See also SOM and 2010 Biodiversity Indicators Partnership, www.twentyten.net.

Systematics and Biodiversity

Biodiversity and systematics: how have we fared in the International Year of Biodiversity?

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Invited Perspective

Biodiversity and systematics: how have we fared in the International Year of Biodiversity?

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The 2010 target to achieve a significant reduction in the current rate of loss of biodiversity at global, regional and national levels was not met. However, progress was made and the International Year of Biodiversity has kept biodiversity in the spotlight—illuminating our limited successes as well as the failures. Much has been learned from the process and the new generation of 2020 targets, agreed at Nagoya, includes a range of more focused practical goals as well as the longer-term, aspirational changes that need to take place. We recognise that there is a shift in thinking towards increasing the management of all ecosystems – "gardening the planet" – but we are concerned that the science of ecosystem management is insufficiently developed to deliver. In particular, our knowledge of the components of biodiversity of many ecosystems, and of their interactions, is dangerously incomplete and for many natural systems we are ill-informed to make decisions on their management. Taxonomists must help to fill these gaps in the science underpinning the field of biodiversity and ecosystem services. We welcome the proposed Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) as a mechanism for integrating the relevant science, from taxonomy and ecology to earth system modelling. Its work will likely be subject to intense scrutiny, just like the reports of the International Panel on Climate Change, and its focus must similarly always be on the evidence base and on the clarity and transparency of its arguments.

Key words: biodiversity, ecosystem management, targets, taxonomy

Introduction

Activities over the past year have focused minds, and hopefully hearts, on the plight of the rest of life on Earth. The International Year of Biodiversity (IYOB) coincided with the date made explicit in the 2010 target agreed by Heads of State in 2002 to "achieve, by 2010, a significant reduction of the current rate of biodiversity loss at the global, regional and national levels as a contribution to poverty alleviation and to the benefit of all life on Earth." Unfortunately, this target has not been met (Fisher, 2009; Walpole *et al*., 2009; Butchart *et al*., 2010), but considerable progress has been made in some of the more detailed aspects inherent in such a broad ambition. For example, area of land in protected areas has increased, and development assistance related to biodiversity has greatly improved (Secretariat of the Convention on Biological Diversity, 2010). The level of attention being paid to conservation targets has greatly increased; individual regions have set their own targets, both for 2010 (Fontaine *et al*., 2007) and undoubtedly post-

IYOB, beyond. At the CBD Conference of the Parties in Nagoya, Japan, signatories assessed the extent to which the 2010 biodiversity target was met, and set new targets for 2020 as part of a strategic vision to 2050. If we concentrate on the target at the expense of biodiversity itself, we will have missed our big chance, that is, to use this IYOB to generate a truly sustained change of heart towards the rest of life on Earth. Targets, while a feature of 21st century life, are not necessarily meant to be hit at the centre every time; they should be aspirational and challenging, we ought to be celebrating where things have gone right and progress has been made. However, it is right to continue to be concerned about biodiversity; it is central to achieving a range of other societal imperatives (Sachs *et al*., 2009).

The indicators associated with the 2010 target that were considered not developed (i.e., failures) include key pieces of the ecological puzzle such as the trophic integrity of ecosystems (Walpole *et al*., 2009) and decline in extent of habitat (Secretariat of the Convention on Biological Diversity, 2010). Rockström *et al*. (2009) developed a concept of "planetary boundaries" in which they identified

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aspects of Earth's systems whose measurement could identify parameters within which humanity could operate safely – within the boundaries. The three planetary boundaries already transgressed by humanity are those involved with climate change, nitrogen accumulation and biodiversity (Rockström *et al*., 2009). They suggested that biodiversity loss is both the least well-characterized and most likely to have already entered into a zone where undesired system change cannot be excluded, in other words, we may have already passed the tipping point. One reason that biodiversity in their model is so unpredictable is that while the real regulating role of biodiversity has been recognized it has not yet been characterized in a quantitative way. Biodiversity itself, the components which generate all of the services of ecosystems that are essential for continued human well-being (MEA, 2005), is not itself particularly well characterized. It is telling that the indicators associated with the 2010 target all depend upon a few taxa of vertebrates; this is not to say of course that vertebrates are not important components of the diversity of life on Earth, but the use and re-use of these same taxa bring with it some risk. Most of life on Earth is invertebrate or micro-organismal by orders of magnitude; do the patterns of threat, extinction and trajectory match those observed for vertebrates? We just don't know, but indications are that some of the correlates of risk observed in vertebrates do not predict risk of extinction in flowering plants (V. Savolainen, pers. comm., 2010) and in Europe, listed protected species may not be those at most risk of extinction (Fontaine *et al*., 2007). It is clear that we need more data across the Tree of Life with which to assess how best to preserve its evolutionary potential.

Taxonomy and systematics

This is where taxonomy and systematics come into the equation. Understanding of the species or populations with which we share the planet, comes from knowing what they are, where they live and how they vary. With this baseline knowledge we can proceed to study population dynamics, or the effects of climate change. If ecosystem services are a black box out of which flow benefits for humankind, then it is the microbes, plants and animals that are inside the box that generate the services. The sheer magnitude of the diversity of life, especially in invertebrates and micro-organisms, has in the past often caused paralysis and a sense of helplessness in those involved in describing and documenting this diversity, but new generations of tools have provided new analytical approaches to studying functional diversity. The other side of that coin is the feeling that the entire enterprise is merely a listing exercise, tantamount to "fiddling while Rome burns". Accelerating global taxonomy has been a topic of discussion for several years; most reviews have concluded that both speed and scale need radical change, just scaling up what was standard practice is not enough (EDIT,

2008). New technologies such as sequencing, both barcoding (http://www.barcodeoflife.org/) and next-generation high-throughput sequencing, automated digital identification and bioinformatics have all had an effect on taxonomy. But at its core, taxonomy and systematics is partly about recognizing units in nature, what we call species in eukaryotes; other aspects of taxonomy are focused on identification and the investigation of the evolutionary relationships of organisms, phylogeny (Godfray & Knapp, 2004). Overall measures of diversity have long been used to assess the health of ecosystems (Hector & Hooper, 2002); these in general measure things like species richness or abundance without taking into account the identities of individual species. For these indices, taxonomy might not really matter. But the identity of species does matter; Magurran & Henderson (2010) showed that taking into account species identity rather than only species richness provides better early warning of impact over time. They suggest that new models tracking biodiversity change through time need to account for changing species composition (what the species actually are) as well as tracking changes in species abundance (how many species there are). The former is utterly dependent on good taxonomy, whether based on morphology or molecules.

Taxonomy and systematics have themselves been considered under threat in the UK (House of Lords' Select Committee on Science and Technology, 2008), and were identified as one of the critical skills gaps in a review of skills requirements in the environmental sector over the next ten years, undertaken by the UK's Environment Research Funders' Forum (ERFF, 2010). These skills were recognized as crucial for "monitoring and understanding the functionality of the marine environments", and for "recognising the role of biodiversity and ecosystem resilience in a changing climate". The critical shortage of same skills was also apparent in other areas highlighted by the review, including fieldwork – where "survey skills including species identification" was a specific need, and Sustainability Science and Planning – where "environmental impact assessment" was a specific need. It appears that, at the very time when the importance of biodiversity has been realised, our capability of describing and documenting it has been eroded to a crisis point.

The future

So what of the future? We have a new set of twenty key biodiversity targets for 2020 agreed at Nagoya, which include:

- Cutting the rate of loss of natural habitats, such as forest, by at least 50%
- Restoring at least 15% of areas where biodiversity is classified as degraded
- Increasing terrestrial nature reserves from 13% to 17% of the global land area

- Increasing marine and coastal nature reserves from 1% to 10% of the global ocean.
- Preventing the extinction of threatened plant and vertebrate species

If achieved these practical targets should offer greater protection for natural systems, although as Agardy *et al.* (2003) point out, there is a danger that nature reserves (specifically marine protected areas) implemented without a firm understanding of the underlying conservation science can actually threaten *bona fide* progress in conservation. As these targets imply, there is a shift in thinking towards increasing the management of ecosystems – encapsulated in the emergence of the "gardening the planet" concept. Given that all four of the scenarios developed by the Millennium Ecosystem Assessment to explore the possible futures of ecosystems predict loss of biodiversity, it is clear that the science of ecosystem management does need to be developed strongly in order to meet the growing demands for food and energy, and to enhance the ability of ecosystems to deliver multiple benefits (IAP, 2010).

Biodiversity agenda

Improving knowledge of biodiversity will be central to the development of ecosystem management, but we will need to be transparent in acknowledging that there is a duality at the heart of biodiversity research. There has long been a biodiversity conservation agenda, built on moral and ethical arguments, targeting the conservation of species and ecosystems. A second biodiversity agenda has really grown out of the study of ecosystem functioning. As the Millennium Ecosystem Assessment (MEA, 2005) articulated so clearly, continued human well being is dependent upon the provision of ecosystem services across all categories from supporting and regulating services, through cultural services to the more obvious provisioning services. The agenda that has crystallised strongly over the past decade has been that biodiversity must be maintained and responsible stewardship practised because we are dependent on it; i.e., it is in our own direct self interest to maintain biodiversity because it provides ecosystem services. This argument, despite its inherently abstract quality has generated considerable traction with policy makers. But can evolution continue to occur in a totally managed system? It is worth thinking about.

These two approaches to biodiversity are different. They may have overlapping or even shared goals at times, but it is important to maintain clarity and transparency in our articulation of the issues surrounding biodiversity research. The inconvenient fact is that key ecosystem services are often provided by unnoticed, and probably unloved, organisms. Bacteria, for example, effectively run the nitrogen cycle. In the oceans, we now know that bacterial photosynthesis can in certain areas contribute more to primary productivity than typical green alga/chlorophyll based photosynthesis. Using metagenomics methods, Venter *et al.* (2004), for example, recorded hundreds of different bacterial rhodopsin genes in a cubic metre of Sargasso Sea water. These bacteria are undetected by the chlorophyll-attuned remote sensors that measure oceanic primary productivity from satellites. Their abundance illustrates how relatively crude our earth system models still are. Key ecosystem services are often provided by the least charismatic organisms and the argument that functioning ecosystems must be protected can be harder to make than the need to conserve particular species or fragile systems. So there is a tendency to conflate the two core concepts: to conserve biodiversity because it is the right thing (the moral/ethical approach) and to preserve ecosystem functioning because we must (the self interest approach). The planetary boundaries study of Rockström *et al.* (2009) is an example. They identified the rate of biodiversity loss as being beyond a critical threshold, noting that its importance was due to its impact on many other boundaries, such as Carbon storage, freshwater, Nitrogen and Phosphorus cycles and land systems. However, they also added "Massive loss of biodiversity unacceptable for ethical reasons". So, even when focusing on functioning of the earth system and using a semi-quantitative approach, biodiversity loss and its impact are considered using arguments marshalled both from the conservation and ecosystem services agendas.

Conclusions

Science-policy links in biodiversity and ecosystem services need to be strengthened and one mechanism for achieving this is the creation of the proposed Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), modelled along the lines of the Intergovernmental Panel on Climate Change (IPCC). Lessons the IPBES must learn from the often rocky ride experienced by the reports of the IPCC, include the need to be absolutely clear in the presentation of evidence, and to present clear and transparent arguments. The duality at the core of biodiversity science makes this harder to achieve. It is equally important that the role of taxonomy and systematics in delivery of biodiversity research is articulated with clarity and transparency. The legacy of the IYOB must include action in taxonomy: action to accelerate the task of documenting and describing the components of biodiversity. Failure to ensure the conservation of a dynamic planet, with biota that are able to evolve and change, and with ecosystems that have resilience and adaptability, will move us closer to the fictional scenario envisaged by Adams (2010).

References

ADAMS, W.M. 2010. Conservation plc. *Oryx* **44**, 482–484.

AGARDY, T., BRIDGEWATER, P., CROSBY, M.P., DAY, J., DAYTON, P.K., KENCHINGTON, R, LAFFOLEY, D., MCCONNEY, P., MURRAY, P.A., PARKS, J.E. & PEAU, L. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**, 353–367.

BUTCHART, S.H.M., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J.P.W., ALMOND, R.E.A., BAILLIE, J.E.M., BOMHARD, B., BROWN, C., BRUNO, J., CARPENTER, K.E., CARR, G.M., CHANSON, J., CHENERY, A.M., CSIRKE, J., DAVIDSON, N.C., DENTENER, F., FOSTER, M., GALLI, A., GALLOWAY, J.N., GENOVESI, P., GREGORY, R.D., HOCKINGS, M., KAPOS, V., LAMARQUE, J-F., LEVERINGTON, F., LOH, J.,. MCGEOCH, M.SA., MCRAE, L., MINASYAN, A., HERNÁNDEZ MORCILLO, M., OLDFIELD, T.E.F., PAULY, D., QUADER, S., REVENGA, C., SAUER, J.R., SKOLNIK, B., SPEAR, D., STANWELL-SMITH, D., STUART, S.N., SYMES, A., TIERNEY, M., TYRRELL, T.D., VIÉ, J-C., & WATSON, R. 2010. Global Biodiversity: Indicators of Recent Declines (2010). *Science*, **328**, 1164–1168.

EDIT [EUROPEAN DIGITAL INSTITUTE OF TAXONOMY]. 2008. Taxonomy in Europe in the 21st century. Unpublished report to the EDIT 4th BoD meeting, 25 January 2008, http://www.e-taxonomy.eu/files/Taxonomy21report.pdf [accessed 19 November 2010].

ERFF [ENVIRONMENTAL RESEARCH FUNDERS' FORUM]. 2010. *Most Wanted. Skills Needs in the Environmental Sector.* ERFF Report 07. http://www.ukcds.org.uk/_assets/file/publications/ERFF-Most-Wanted-report.pdf [accessed 19 November 2010].

FISHER, M. 2009. 2010 and all that – looking forward to biodiversity conservation in 2010 and beyond. *Oryx* **43**, 449–450.

FONTAINE, B., BOUCHET, P., VAN ACHTERBERG, K., ALONSO-ZARAZAGA, M.A., ARAUJO, R., ASPÖCK, U., AUDISIO, P., AUKEMA, B., BAILLY, N., BALSAMO, M., BANK, R.A., BARNARD, P., BELFIORE, C., BOGDANOWICZ, W., BONGERS, T., BOXSHALL, G.A., BURCKHARDT, D., CAMICAS, J.L., CHYLARECKI, P., CRUCITTI, P., DEHARVENG, L., DUBOIS, A., ENGHOFF, H., FAUBEL, A., FOCHETTI, R., GARGOMINY, O., GIBSON, D.I., GIBSON, R., GÓMEZ LÓPEZ, M.S., GOUJET, D., HARVEY, M.S., HELLER, K.-G., VAN HELSDINGEN, P., HOCH, H., DE JONG, H., DE JONG, Y., KARSHOLT, O., LOS, W., LUNDQVIST, L., MAGOWSKI, W., MANCONI, R., MARTENS, J., MASSARD, J.A., MASSARD-GEIMER, G., MCINNES, S.J., MENDES, L.F., MEY, E., MICHELSEN, V., MINELLI, A., NIELSEN, C., NIETO NAFRÍA, J.M., VAN NIEUKERKEN, E., NOYES, J., PAPE, T., POHL, H., DE PRINS, W., RICCI, C., ROSELAAR, C., ROTA, E., SCHMIDT-RHAESA, A., SEGERS, H., ZUR STRASSEN, R., SZEPTYCKI, A., THIBAUD, J.-M., THOMAS, A., TIMM, T., VAN TOL, J., VERVOORT, W. & WILLMANN, R. 2007. The European Union's 2010 target: Putting rare species in focus. *Biological Conservation* **139**, 167–185.

GODFRAY, H.C.J. & KNAPP, S. 2004. Introduction, Taxonomy for the 21st century. *Philosophical Transactions of the Royal Society*, B, **359**, 559–569.

HECTOR, A. & HOOPER, R. 2002. Darwin and the first ecological experiment. *Science* **295**, 639–640.

HOUSE OF LORDS' SELECT COMMITTEE ON SCIENCE AND TECHNOLOGY. 2008. *Systematics and Taxonomy Followup: Report with Evidence.* 5th report (2007–08) (HL Paper 162). The Stationery Office Limited, London.

IAP [THE INTERACADEMY PANEL ON INTERNATIONAL ISSUES]. 2010. Communiqué of the InterAcademy Panel on Biodiversity Conference 13–14 January 2010. http://royalsociety.org/Communique-of-the-IAP-Biodiversity-Conference/ [accessed 19 November 2010].

MAGURRAN, A. & HENDERSON, P.A. 2010. Temporal turnover and the maintenance of diversity in ecological assemblages. *Philosophical Transactions of the Royal Society*, B **365**, 3611–3620.

MEA [MILLENNIUM ECOSYSTEM ASSESSMENT]. *Biodiversity Synthesis Report*, 2005. http://www.maweb.org/ [accessed 19 November 2010].

ROCKSTRÖM, J., STEFFEN, W., NOONE, K., PERSSON, A., CHAPIN, F.S. III, LAMBIN, E. LENTON, T.M., SCHEFFER, M., FOLKE, C., SCHNELLNHUBER, H.J., NYKVIST, B., de WIT, C.A., HUGHES, T., VAN DER LEEUW, S., RODHE, H., SÖRLIN, S., SYNDER, P.K., COSTANZA, P., SVEDIN, U., FALKENMARK, M., KARLBERG, L., CORELL, R.W., FABRY, V.J., JANSEN, J., WALKER, B., LIVERMAN, D., RICHARDSON, K., CRUTZEN, P. & FOLEY, J. 2009. Planetary boundaries: exploring the safe operating space for humanity. *Ecology and Society* **14**, 32 http://www.ecologyandsociety.org/vol14/iss2/art32/ [accessed 19 November 2010].

SACHS, J.D., BAILLIE, J.E.M., SUTHERLAND, W.J., ARMSWORTH, P.R., ASH, N., BEDDINGTON, J., BLACKBURN, T.M., COLLEN, B., GARDINER, B., GASTON, K.J., GODFRAY, H.C.J., GREEN, R.E., HARVEY, P.H., HOUSE, B., KNAPP, S., KÜMPEL, N.F., MACDONALD, D.W., MACE, G.M., MALLET, J., MATTHEWS, A., MAY, R.M., PETCHEY, O., PURVIS, A., ROE, D., SAFI, K., TURNER, K., WALPOLE, M., WATSON, R. & JONES, K.E. 2009. Biodiversity conservation and the Millennium Development Goals. *Science* **325**, 1502–1503.

SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY. 2010. *Global Biodiversity Outlook 3*. Montreál, Canada.

VENTER, J.C., REMINGTON, K., HEIDELBERG, J.F., HALPERN, A.L., RUSCH, D., EISEN, J.A., WU, D., PAULSEN, I., NELSON, K.E., NELSON, W., FOUTS, D.E., LEVY, S., KNAP, A.H., LOMAS, M.W., NEALSON, K., WHITE, O., PETERSON, J., HOFFMAN, J., PARSONS, R., BADEN-TILLSON, H., PFANNKOCH, C., ROGERS, Y. & SMITH, H.O. 2004. Environmental genome shotgun sequencing of the Sargasso Sea. *Science* **304**, 66–74. doi: 10011226/science.1093857

WALPOLE, M., ALMOND, R.E.A., BESANÇON, C., BUTCHART, S.H.M., CAMPBELL-LENDRUM, D., CARR, G.M., COLLEN, B., COLLETTE, L., DAVIDSON, N.C., DULLOO, E., FAZEL, A.M., GALLOWAY, J.N., GILL, M., GOVERSE, T., HOCKINGS, M., LEAMAN, D.J., MORGAN, D.H.W., REVENGA, C., RICKWOOD, C.J., SCHUTYSER, F., SIMONS, S.,. STATTERSFIELD, A.J., TYRRELL, T.D., VIÉ, J-C., & ZIMSKY, M. 2009. Tracking progress toward the 2010 biodiversity target and beyond. *Science* **325**, 1503–1504.

Why biodiversity is important to the functioning of real-world ecosystems

J Emmett Duffy

Controlled experiments have substantially advanced our understanding of the links between changing biodiversity and ecosystem functioning (BEF) in recent years. However, controversy continues regarding the relevance of BEF experiments to the complex ecosystems and large spatial and temporal scales of interest in conservation and management. Here, I address some of the persistent criticisms regarding experimental BEF research and argue that these have been overstated. Contrary to some suggestions, many putative artifacts attributed to experiments render their conclusions about BEF links stronger, rather than weaker. Like other broad ecological concepts, BEF focuses on general patterns, rather than looking at species-level, applied conservation problems. Nevertheless, insights from BEF experiments conducted to date are likely to underestimate, rather than overestimate, the importance of biodiversity to ecosystem functioning and the provision of ecosystem services in the real world. These experiments suggest that managing ecosystems to promote biodiversity can have important practical benefits.

The mass extinction of species currently underway has generated concern for many reasons, ranging from aesthetic and spiritual to purely commercial. But from the utilitarian perspective that underpins most policy, perhaps the most important concerns involve the potential consequences of species loss for the continued functioning of ecosystems and the services they provide to humanity. This recognition stimulated a rapid growth of research on links between biodiversity and ecosystem functioning (BEF) over the past decade. These studies have generated continuing controversy (eg Huston 1997; Wardle *et al.* 2000; Leps 2004), leading some reviewers to conclude that the results of BEF experiments are too variable to draw general conclusions (Giller *et al.* 2004; Thompson and Starzomski 2007). The latter concern has now been largely resolved by two comprehensive meta-analyses that examined the results of over 100 experiments and >400 measures of biodiversity effects (Balvanera *et al.* 2006; Cardinale *et al.* 2006). These analyses revealed evidence that mixtures of species produce more biomass and use more resources, on average, than do single species. This pattern is surprisingly consistent across taxa, trophic levels, and habitats. Even within more realistic, multilevel food webs, experiments show that biodiversity tends to have predictable effects, with prey diversity generally supporting higher predator growth, but lower predator impact on total prey biomass (Duffy *et al.* 2007).

BEF research has often been justified in the context of understanding the consequences of looming extinction for human welfare. However, in practice, most research has been more narrowly focused, employing small-scale, highly controlled experiments with designs whose relevance to natural ecosystems and realistic extinction scenarios is often unclear. For these reasons, research on BEF links has persistently been criticized, suggesting to some authors that invoking BEF relationships to justify biodiversity conservation may be misleading or counterproductive (Wardle 1999; Srivastava and Vellend 2005; Thompson and Starzomski 2007). In this paper, I argue that many of these criticisms are overstated, and that the experimental evidence for BEF is generally consistent and has important practical implications for conservation and management.

As others have emphasized elsewhere (eg Srivastava and Vellend 2005), discussions of BEF research have sometimes confused scientific concepts (functioning) with value or normative judgments (services). I distinguish an ecosystem *property* as any aggregate structural variable, ie a measure of the current state of the system,

In a nutshell:

- The dominant influence of individual species (compared with diverse communities) on ecosystem functioning in experimental settings is largely an artifact of their simplified environments and the single response variables considered
- As a result, experiments have probably underestimated the importance of biodiversity to real-world ecosystem functioning
- Suggested discrepancies between diversity–productivity relationships in nature versus those in experiments are largely illusory, and stem from the bidirectional influence between productivity (potential or realized) and diversity
- Several lines of evidence indicate that maintaining multiple ecosystem services over time in a changing world is enhanced by high local and regional diversity

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such as biomass or soil nitrogen content, and an ecosystem *function* as any aggregate process, such as production, respiration, or grazing rate. The sign, whether positive or negative, and the magnitude of these variables are neither "good" nor "bad". In contrast, an ecosystem *service* is a process considered to have some, necessarily subjective, value to humanity. Thus, a diversity-mediated increase in the ecosystem function of primary production can be considered either a service (eg a crop, or the foundation species of a valued ecosystem) or a disservice (eg a eutrophic water body). For the sake of clarity, I refer to changes in any of these aggregate ecosystem variables as ecosystem responses. Most BEF experiments and theory have focused on species richness as the metric of biodiversity, so I follow that usage here, although a growing body of evidence suggests that the influence of biodiversity on ecosystem functioning is broadly similar across levels of organization.

■ Responses to some criticisms of BEF research

Criticism 1: Most BEF relationships result from statistical sampling effects, rather than from "true" effects of diversity

In experiments, diverse mixtures of species can show higher productivity than the average single-species plot, simply because they are more likely to contain the one species that grows best under local conditions, if that species then comes to dominate the plot. This statistical phenomenon has been termed the "sampling effect" (Huston 1997; Tilman *et al.* 1997). Since, under this hypothesis, functioning is dominated by a single species, it has been considered an artifact, rather than a "true" effect of diversity (Huston 1997; Wardle 1999). From a conservation perspective, even BEF relationships that can be explained by this sampling mechanism are important in showing that species loss can substantially change normal ecosystem functioning (Srivastava 2002). But the question remains: is the sampling effect in fact common and important? Meta-analysis of 111 experiments confirmed that diverse mixtures of species rarely produced more biomass than the most productive single species (Cardinale *et al.* 2006), a result superficially consistent with the sampling effect.

However, three points caution against accepting this interpretation at face value. First, the failure of polycultures to outperform the best monoculture can result not only from the sampling effect, but also from a combination of positive complementarity (ie resource partitioning or facilitation) and negative selection effects (ie dominance by a poor performer; Loreau and Hector 2001). In fact, experiments with both terrestrial (Hector *et al.* 2002; Hooper and Dukes 2004) and marine (Bruno *et al.* 2005) plants found that the failure of diverse assemblages to outperform the best monoculture was indeed due to a combination of negative selection and complementarity,

not to the sampling effect. Although this may seem an arcane distinction, it is fundamentally important because this interaction of selection and complementarity allows multiple species to coexist in the community, whereas in the classical sampling effect model (Huston 1997; Tilman *et al.* 1997), the single best-performing species outcompetes the others, which eventually results in a monoculture. The second point is that the complementary resource use that underlies BEF relationships is predicted to emerge over time (Pacala and Tilman 2002), yet many experiments have not run for long enough to see complementarity become important. Those that have done so (Tilman *et al.* 2001; Hooper and Dukes 2004; Stachowicz *et al.* 2008) found that, over time, the BEF relationship and the importance of complementarity become stronger, and that the number of species required to maximize function increases. These general patterns are confirmed by a recent meta-analysis of 44 experiments (Cardinale *et al.* 2007; Figure 1). Third, and finally, the sampling effect implicitly focuses on a single response variable, typically plant biomass accumulation. In the context of management and conservation, we are interested in ecosystems that perform multiple functions and services. Even in cases where a single species dominates a given ecosystem process, it is unlikely to dominate all of the processes of interest. Indeed, simulations of empirical data show that, as the number of ecosystem processes we consider increases, redundancy among species decreases and the relationship between species richness and (multivariate) ecosystem functioning grows stronger (Petchey and Gaston 2002b). Recent BEF experiments support this prediction, showing that, even where particular species monocultures can match diverse mixtures for individual ecosystem processes, different species maximize different ecosystem properties. The result is that only the diverse mixture maximizes multiple properties simultaneously, a phenomenon termed "multivariate complementarity" (Duffy *et al.* 2003; Bracken and Stachowicz 2006; Hector and Bagchi 2007; Gamfeldt *et al.* 2008; Figure 2). These considerations show that, from the perspective of maintaining integrity of multifunctional ecosystems, the classical argument about the sampling effect in BEF experiments is a red herring, arising from a narrow focus on single response variables and short-term experiments. Maintenance of the multiple functions provided by real, complex ecosystems requires multiple species.

Criticism 2: BEF relationships usually reach an asymptote at very low species richness

Arguments for the functional importance of biodiversity seem incompatible with the common finding that, in experiments, ecosystem function typically saturates at a species richness much lower than that found in nature (Schwartz *et al.* 2000). The probable reason for this is that ecosystem processes tend to be most strongly influenced by dominant species (Grime 1998; Polley *et al.*

2007). An obvious conclusion would be that very few species are needed to maintain normal ecosystem functioning, but recent research shows that this conclusion is unjustified for several reasons. First, as the previous section showed, the short durations of many previous experiments probably precluded expression of diversity effects. Second, and perhaps more importantly, nearly all BEF experiments to date have focused on a single response variable at a time. But, as discussed above, even where sampling might explain individual ecosystem responses, different species can dominate different ecosystem response variables, so maintaining multiple functions requires more species (Figure 2). Third, most experiments have been conducted in small plots, under highly controlled, homogenized conditions, yet theory predicts that the influence of diversity increases in heterogeneous environments or landscapes (Tilman *et al.* 1997; Cardinale *et al.* 2000; Loreau *et al.* 2003). Recent evidence from several wild, non-experimental systems supports this prediction (Tylianakis *et al.* 2008; Figures 3, 4). More generally, there is considerable evidence that rare species can make important contributions to ecosystem processes under changing conditions (Lyons *et al.* 2005). Finally, because of the well-documented relationship between species richness and area, maintenance of a given level of diversity at the local (plot) level depends on a considerably higher regional diversity. Thus, maintaining a given level of local species richness requires conserving a larger number of species at the regional scale. All of these considerations suggest that the apparent saturation of ecosystem function at low species richness is largely an artifact of the homogeneous conditions, short time scales, small plot sizes, and narrow focus of experiments conducted to date. Again, the conclusion is that experiments have underestimated, not overestimated, the importance of biodiversity to the functioning of real, complex ecosystems.

Figure 1. The importance of biodiversity and complementary resource use to plant productivity increases with time. (a) In a grassland experiment, both the magnitude of the diversity effect on primary production (upper panel) and the relative importance of complementarity (lower panel) increased through time; colored lines and numbers indicate the number of years after beginning of the experiment (± SE; after Tilman et al. 2001). (b) Similarly, in a marine intertidal experiment, enhancement of biomass accumulation by seaweed diversity increased as the experiment matured from 3 months to 3 years (± SE; Stachowicz et al. 2008). (c) Quantitative meta-analysis confirms that these examples are not atypical. Among 44 experiments, both the net effect of species richness on production (upper panel) and the magnitude of the diversity effect relative to the most productive monoculture (lower panel) increased with time (adapted from Cardinale et al. 2007).

Criticism 3: Experimental diversity gradients bear no resemblance to real-world extinction scenarios

The artificiality of random assembly in BEF experiments has been noted repeatedly (eg Huston 1997; Srivastava 2002; Giller *et al.* 2004; Leps 2004). Random assembly designs were used in many early BEF experiments, because they avoid confounding the effects of species richness – the object of most such experiments – with the effects of species composition. Although the first genera-
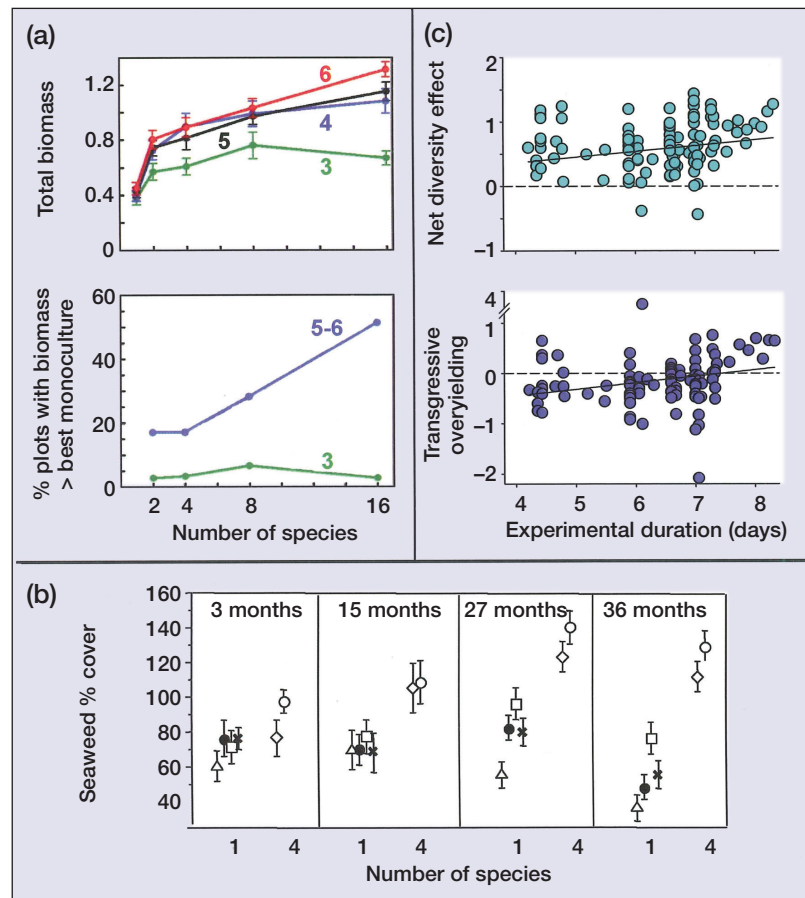
tion of BEF experiments required these designs to separate richness and complementarity effects (Huston 1997), it has long been recognized that random assembly trades off realism for this precision in interpretation. To remedy this, researchers have used theory (Gross and Cardinale 2005), simulations (Petchey and Gaston 2002a; Ostfeld and LoGiudice 2003; Solan *et al.* 2004), and experiments (Jonsson *et al.* 2002; Zavaleta and Hulvey 2004) to explore effects of non-random loss scenarios. These studies confirm the intuitive expectation that order of loss affects ecosystem responses, and most show more specifically that realistic extinction orders have larger effects on ecosystem responses than do random loss sequences. Thus, if existing experimental results can be generalized, they suggest that random loss designs underestimate the ecosystem consequences of diversity loss. Again, conclu-
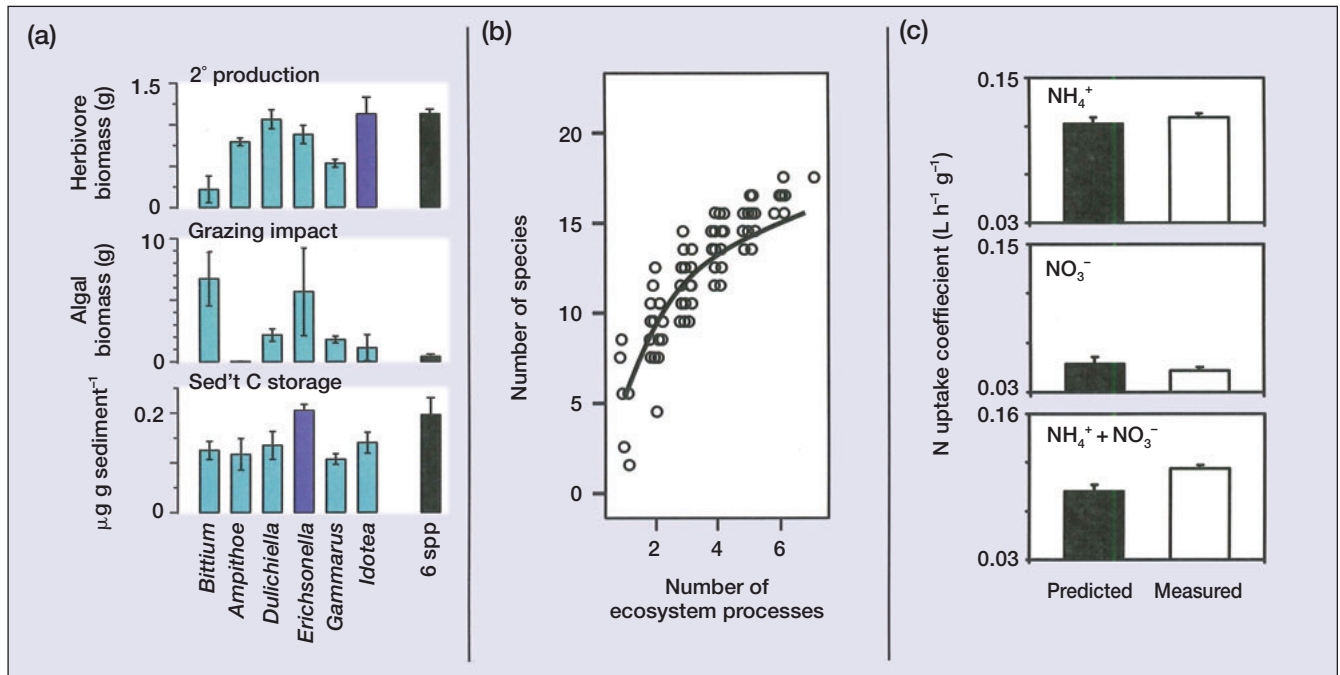
Figure 2. *Multifunctional ecosystems require many species. (a) In experimental seagrass systems, different herbivore species maximized different ecosystem properties, but only the diverse assemblage containing all species (black) maximized all simultaneously (± SE; data from Duffy* et al. *2003). (b) In grassland experiments, the number of species required to maximize ecosystem functioning increased with the number of ecosystem processes considered (modified from Hector and Bagchi 2007). (c) Similarly, in a seaweed assemblage, uptake of individual nutrients was predictable by summing contributions of individual species (predicted = measured), whereas total nitrogen uptake ($NH_4^+ + NO_3^-$) was greater than predicted from individual species contributions (± SE; modified from Bracken and Stachowicz 2006).*

sions about the functional consequences of diversity loss from random assembly experiments appear conservative.

Criticism 4: Diversity may enhance productivity in experiments, but the opposite pattern is found in nature

It has been suggested by some authors that the frequently negative relationship between resource availability ("productivity") and plant diversity in nature contradicts the results of BEF experiments (Huston 1997; Wardle *et al.* 2000). However, others have shown that this contradiction is illusory, stemming from conflation of two distinct phenomena that are both referred to as "productivity". The apparent discrepancy can be explained by the fact that relationships between species diversity and "productivity" are bidirectional (Loreau *et al.* 2001). Within-habitat diversity generally increases as resource availability (productivity potential) rises from low to moderate levels, because the more favorable environment allows species to persist that could not do so with less abundant resources. However, as resources increase in abundance, intensifying competition reduces diversity, illustrating the "paradox of enrichment". Thus, cross-site comparisons over the higher end of this resource availability range often show negative relationships between environmental "productivity" (eg nutrient supply) and plant diversity (reviewed by Huston 1997). Such comparisons

consider a gradient in the abiotic environment and assume implicitly that a large regional pool of species is available to colonize all sites. In this situation, one expects a negative correlation between aggregate biomass, which reflects carrying capacity and local diversity. However, this relationship occurs because variance in resource availability (environmental "productivity") is determining diversity, rather than vice versa.

In contrast, BEF experiments seek implicitly to address the opposite phenomenon, the consequences of global or regional species loss from a system in which resources and the abiotic environment are held constant. Thus, surveys and experiments test different causal directions of the biodiversity–productivity relationship. Surveys of unmanipulated systems test how local diversity responds to changing resource availability ("productivity"), whereas experiments test how productivity (biomass production per unit time) responds to changing species diversity. Importantly, the two phenomena are not mutually exclusive: at any given site along a resource gradient, resource availability will determine which, and how many, species from the available pool persist in the community (ie diversity). However, as theory and experiments show, the actual production of plant biomass at that site is likely to be lower when the pool of species available to colonize it is reduced (Loreau *et al.* 2001). Thus, the patterns in nature and in experiments are not contradictory. Moreover, the apparent discrepancy between experi-

ments and field patterns for land plants is not seen in some marine benthic systems, where the greater impacts of diverse assemblages on invaders and on prey are consistent with patterns in the field (Stachowicz *et al.* 2002; Byrnes *et al.* 2006; see also Figure 3).

Criticism 5: Biodiversity effects, when present, are probably minor as compared with resource supply and other drivers of ecosystem processes

At regional or continental scales, plant production is closely correlated with resource availability. How much extra variance, if any, is explained by plant diversity? Few experiments have explicitly compared the quantitative importance of changing diversity within trophic levels to that of nutrient loading, cascading predator effects, and other factors. The few that have done so suggest that changing biodiversity within trophic levels can be of comparable importance to realistic ranges of bottom-up and top-down forcing. In the most comprehensive example, changing species richness of herbivorous pond snails had comparable or greater effects on a range of ecosystem processes than did a fourfold change in nutrient supply or exclusion of predators (Wojdak 2005). Experiments in seagrass ecosystems showed similar results; effects of changing herbivore diversity were comparable in magnitude to those of cascading predator effects (Duffy *et al.* 2005) and often greater than those of changing light availability or seasonal forcing (Spivak *et al.* 2007; Duffy *et al.* unpublished data). Earlier experiments that manipulated both nutrients and plant diversity (Fridley 2002) concluded that nutrient effects overwhelmed diversity effects, but used large ranges in nutrient supply and relatively modest ranges in diversity. Again, cases where field patterns and experimental results are concordant (Stachowicz *et al.* 2002; Byrnes *et al.* 2006) further support the importance of diversity in some real ecosystems. Thus, the few available experimental data suggest that changing diversity within trophic levels has non-trivial consequences, even within the context of dynamic ecosystems impacted by other factors.

Criticism 6: Effects of declining biodiversity on ecosystem functioning are indirect and weaker than direct impacts of habitat destruction

This is a compelling argument for terrestrial systems, where habitat destruction is the major threat to ecosystems (Srivastava 2002; Srivastava and Vellend 2005). It arguably carries less weight in the oceans, where the greatest threat to biodiversity is direct overharvesting (Figure 5). Even on land, this argument applies more to short-term than to long-term effects of biodiversity loss. Clearly, habitat destruction, which involves both biodiversity loss and abiotic habitat alteration, will usually have stronger impacts on ecological processes than will species loss alone. And, in practice, focusing conserva-
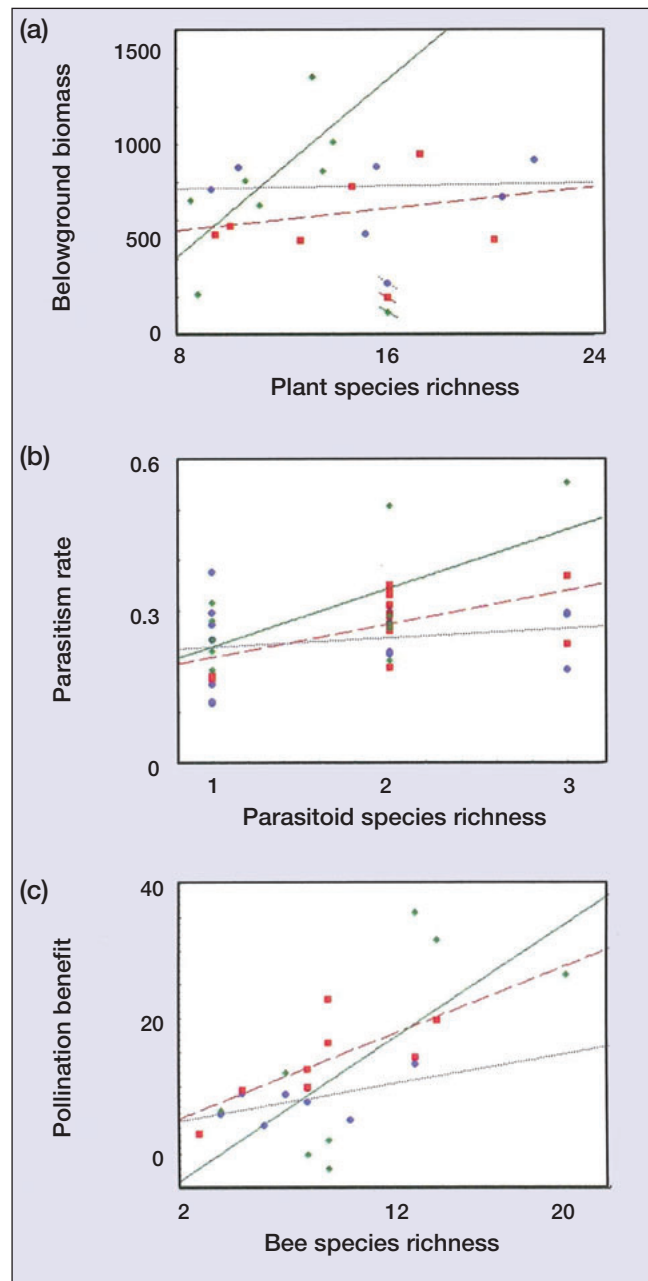

Figure 3. The influence of biodiversity on ecosystem processes increases with environmental heterogeneity in wild, non-experimental systems. More spatially heterogeneous environments exhibit stronger relationships between (a) plant richness and plant biomass production in a European grassland; (b) natural enemy richness and rates of parasitism on wasps in coastal Ecuador; and (c) wild bee richness and pollination effectiveness on coffee plantations in Indonesia. In each panel, data are divided into three classes of environmental heterogeneity: low (blue symbols, dotted line), medium (red symbols, dashed line), and high (green symbols, solid line). After Tylianakis et al. (2008).

tion effort on protecting habitat is likely to conserve both biodiversity per se and the abiotic and structural components necessary to sustain it. Nevertheless, biodiversity loss remains uniquely important because, within limits,
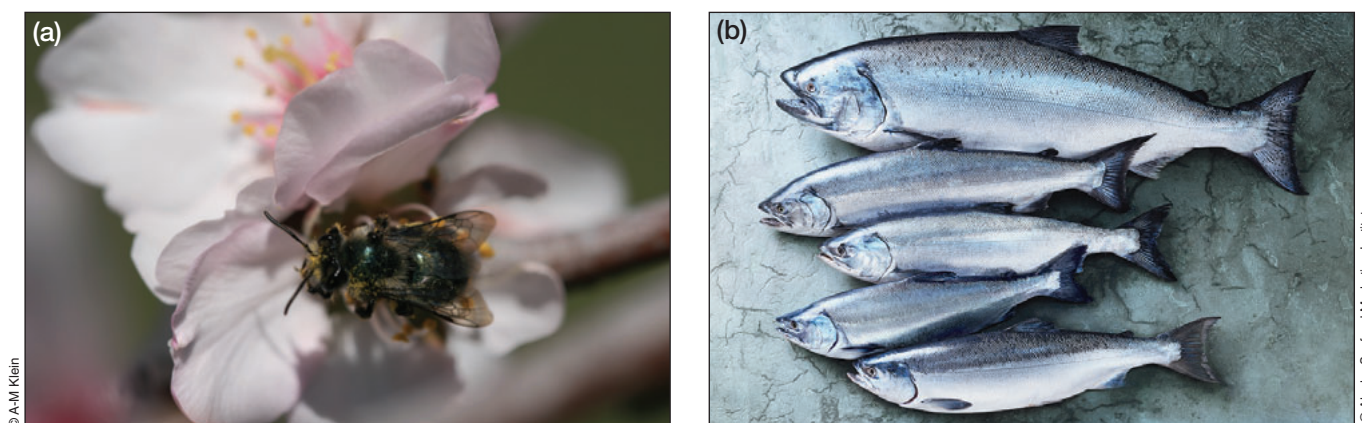
Figure 4. *Examples in which species or genetic diversity have been shown to enhance important ecosystem services in the real world. (a) Crop pollination is often more effective in areas with higher native bee diversity (Klein et al. 2003). The picture shows the native bee* Andrena cerasifolii *visiting an almond flower in California. (b) Harvest of salmon in Alaska has been relatively stable over recent decades, despite strong fluctuations in individual stocks, because ecologically differentiated stocks respond differently to climate change and other environmental variation (Hilborn et al. 2003).*

degraded habitats can potentially be restored, whereas extinction of species is permanent. In Costa Rica, for example, forest cover had declined by 80% before reclamation and tree planting brought it back above 50%. Yet, any species lost to extinction during that deforestation cannot be reclaimed. Thus, over the long term and across systems, conserving species is probably as important as preventing habitat loss.

■ **Conclusions**

Experimental BEF research has now matured sufficiently to allow us to conclude with some confidence that, on average, higher species richness increases biomass accu-

mulation and resource use within trophic levels, and decreases variance in those responses through time. In many cases, these effects on structure and functioning also have implications for ecosystem services of value to humanity. Although the real-world implications of this BEF research have often been questioned, the issues considered here suggest that experimental results generally underestimate the influence of biodiversity on functioning of complex ecosystems and, thus, are conservative. Maintenance of the multiple ecosystem services that support society over extended time scales in a changing world will probably require a much greater number of species than are typically used in BEF experiments. Thus, management to conserve biodiversity should often pro-

Figure 5. *Drivers of environmental change differ among systems, with implications for how biodiversity affects ecosystem processes. (a) In terrestrial systems, such as Southeast Asian rainforests, habitat loss and degradation drive changes in ecosystem processes both directly and indirectly, through their impacts on biodiversity. (b) In the ocean, overharvesting is a pervasive human impact and is likely to influence ecosystem functioning indirectly, through the changing interactions that stem from loss or ecological extinction of species.*

vide utilitarian benefits, which serve as one among the several rationales for conservation. Palumbi *et al.* (2009) have made essentially the same case in the context of implementing ecosystem-based management (EBM) of marine fisheries. EBM has been federally mandated, in part because of frequent failure of, and conflict involved in, management efforts focusing on single fishery species. Palumbi *et al.* argue that ecosystems are so complex that we will rarely understand their workings mechanistically, so that maintenance of biodiversity may serve as a useful proxy for a system state that supplies the multiple ecosystem services of interest. Thus, managing to maximize biological diversity (however defined) may be a workable way to ensure long-term maintenance of an acceptable balance among the sometimes competing demands for various ecosystem services. This is an example where a broad-brush approach, informed by BEF research, may actually prove more effective in conservation than one based on the biology of individual species. Clearly, managing for biodiversity is not a substitute for identifying key ecosystem service providers, community interactions, and environmental drivers within particular systems (Kremen 2005). However, by providing a conceptual framework based on general principles, it can provide a complementary approach.

Previous research and controversies offer several points of guidance for future work and application. One way to make BEF research more realistic and applicable is to focus on key traits of organisms – specifically, the covariance between traits that predispose species to extinction and traits that influence ecosystem properties (Gross and Cardinale 2005). There is a growing body of empirical data on extinction sequences and extinction traits (eg Purvis *et al.* 2000; Dulvy *et al.* 2004) and a growing interest in how traits influence vital ecosystem processes. An important step involves uniting these bodies of knowledge with community ecological theory to build predictive models of how realistic extinction scenarios will influence ecosystem processes and services (Srivastava 2002; Kremen 2005). Since one of the most consistent extinction predictors is high trophic level, practical application of BEF research will also require a more intensive focus on effects of changing diversity in multitrophic systems (Duffy *et al.* 2007). In the meantime, we have learned enough from theory and experiments about how biodiversity affects ecosystem functioning to justify a general goal of conserving biodiversity for utilitarian as well as other reasons.

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■ References

Balvanera P, Pfisterer AB, Buchmann N, *et al.* 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* **9**: 1146–56.

Bracken MES and Stachowicz JJ. 2006. Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology* **87**: 2397–2403.

Bruno JF, Boyer KE, Duffy JE, *et al.* 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol Lett* **8**: 1165–74.

Byrnes J, Stachowicz JJ, Hultgren KM, *et al.* 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecol Lett* **9**: 61–71.

Cardinale BJ, Nelson K, and Palmer MA. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* **91**: 175–83.

Cardinale BJ, Srivastava DS, Duffy JE, *et al.* 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–92.

Cardinale BJ, Wright JP, Cadotte MW, *et al.* 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *P Natl Acad Sci USA* **104**: 18123–28.

Duffy JE, Cardinale BJ, France KE, *et al.* 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol Lett* **10**: 522–38.

Duffy JE, Richardson JP, and Canuel EA. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol Lett* **6**: 637–45.

Duffy JE, Richardson JP, and France KE. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol Lett* **8**: 301–09.

Dulvy NK, Ellis JR, Goodwin NB, *et al.* 2004. Methods of assessing extinction risk in marine fishes. *Fish Fisher* **5**: 255–76.

Fridley JD. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia* **132**: 271–77.

Gamfeldt L, Hillebrand H, and Jonsson PR. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**: 1223–31.

Giller PS, Hillebrand H, Berninger UG, *et al.* 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* **104**: 423–36.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* **86**: 902–10.

Gross K and Cardinale BJ. 2005. The functional consequences of random vs ordered species extinctions. *Ecol Lett* **8**: 409–18.

Hector A and Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* **448**: 188–96.

Hector A, Bazeley-White E, Loreau M, *et al.* 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol Lett* **5**: 502–11.

Hilborn R, Quinn TP, Schindler DE, and Rogers DE. 2003. Biocomplexity and fisheries sustainability. *P Natl Acad Sci USA* **100**: 6564–68.

Hooper DU and Dukes JS. 2004. Overyielding among plant functional groups in a long-term experiment. *Ecol Lett* **7**: 95–105.

Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449–60.

Jonsson M, Dangles O, Malmqvist B, and Guerold F. 2002. Simulating species loss following perturbation: assessing the effects on process rates. *P Roy Soc Lond B Bio* **269**: 1047–52.

Klein AM, Steffan-Dewenter I, and Tscharntke T. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *P Roy Soc Lond B Bio* **270**: 955–61.

Kremen C. 2005. Managing ecosystem services: what do we need to

know about their ecology? *Ecol Lett* **8**: 468–79.

Leps J. 2004. What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic Appl Ecol* **5**: 529–34.

Loreau M and Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**: 72–76.

Loreau M, Mouquet N, and Gonzalez A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *P Natl Acad Sci USA* **100**: 12765–70.

Loreau M, Naeem S, Inchausti P, *et al*. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**: 804–08.

Lyons KG, Brigham CA, Traut BH, and Schwartz MW. 2005. Rare species and ecosystem functioning. *Conserv Biol* **19**: 1019–24.

Ostfeld RS and LoGiudice K. 2003. Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* **84**: 1421–27.

Pacala S and Tilman D. 2002. The transition from sampling to complementarity. In: Kinzig AP, Pacala SW, and Tilman D (Eds). The functional consequences of biodiversity. Empirical progress and theoretical extensions. Princeton, NJ: Princeton University Press.

Palumbi SR, Sandifer PA, Allan JD, *et al*. 2009. Managing for ocean biodiversity: creating a national biodiversity conservation agenda to sustain marine ecosystem services. *Front Ecol Environ* **7**: 204–11.

Petchey OL and Gaston KJ. 2002a. Extinction and the loss of functional diversity. *P Roy Soc Lond B Bio* **269**: 1721–27.

Petchey OL and Gaston KJ. 2002b. Functional diversity (FD), species richness and community composition. *Ecol Lett* **5**: 402–11.

Polley HW, Wilsey BJ, and Derner JD. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* **116**: 2044–52.

Purvis A, Gittleman JL, Cowlishaw G, and Mace GM. 2000. Predicting extinction risk in declining species. *P Roy Soc Lond B Bio* **267**: 1947–52.

Schwartz MW, Brigham CA, Hoeksema JD, *et al*. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**: 297–305.

Solan M, Cardinale BJ, Downing AL, *et al*. 2004. Extinction and ecosystem function in the marine benthos. *Science* **306**: 1177–80.

Spivak AC, Canuel EA, Duffy JE, and Richardson JP. 2007. Top-down and bottom-up controls on sediment organic matter composition in an experimental seagrass ecosystem. *Limnol Oceanogr* **52**: 2595–2607.

Srivastava DS. 2002. The role of conservation in expanding biodiversity research. *Oikos* **98**: 351–60.

Srivastava DS and Vellend M. 2005. Biodiversity–ecosystem function research: is it relevant to conservation? *Annu Rev Ecol Evol Syst* **36**: 267–94.

Stachowicz JJ, Fried H, Osman RW, and Whitlatch RB. 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* **83**: 2575–90.

Stachowicz JJ, Graham M, Bracken MES, *et al*. 2008. Diversity enhances cover and stability of seaweed assemblages: the role of heterogeneity and time. *Ecology* **89**: 3008–19.

Thompson R and Starzomski BM. 2007. What does biodiversity actually do? A review for managers and policy makers. *Biodivers Conserv* **16**: 1359–78.

Tilman D, Lehman CL, and Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *P Natl Acad Sci USA* **94**: 1857–61.

Tilman D, Reich PB, Knops J, *et al*. 2001. Diversity and productivity in a long-term grassland experiment. *Science* **294**: 843–45.

Tylianakis JM, Rand TA, Kahmen A, *et al*. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol* **6**: 947–56.

Wardle DA. 1999. Is "sampling effect" a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* **87**: 403–07.

Wardle DA, Huston MA, Grime JP, *et al*. 2000. Biodiversity and ecosystem function: an issue in ecology. *B Ecol Soc Am* **81**: 235–39.

Wojdak JM. 2005. Relative strength of top-down, bottom-up, and consumer species richness effects on pond ecosystems. *Ecol Monogr* **75**: 489–504.

Zavaleta ES and Hulvey KB. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* **306**: 1175–77.