

# 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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Sandra Díaz is principal researcher and associate professor of ecology and biogeography at Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEfYN, Universidad Nacional de Córdoba, Argentina. Joseph Fargione is research assistant faculty at the Department of Biology, University of New Mexico, Albuquerque, New Mexico, United States of America. F. Stuart Chapin III is professor of ecology at the Institute of Arctic Biology, University of Alaska at Fairbanks, Fairbanks, Alaska, United States of America. David Tilman is the McKnight Presidential Chair in Ecology at the Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota, United States of America.

\* To whom correspondence should be addressed. E-mail: sdiaz@com.uncor.edu

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).

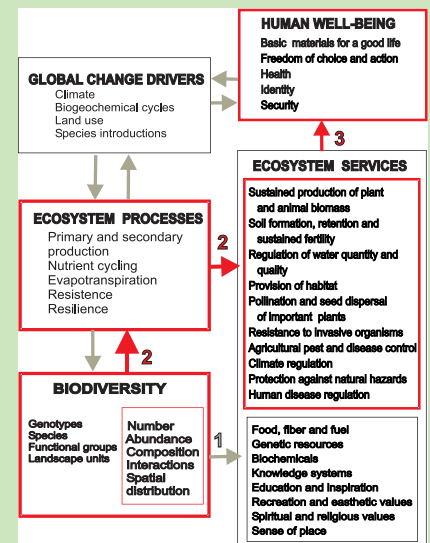
**Ecosystem services** are the benefits provided by ecosystems that contribute to making human life both possible and worth living. Ecosystem services are context-dependent; that is, the same ecosystem process can produce an ecosystem service that is highly valued by one society or stakeholder group 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].

**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).

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



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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].

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.

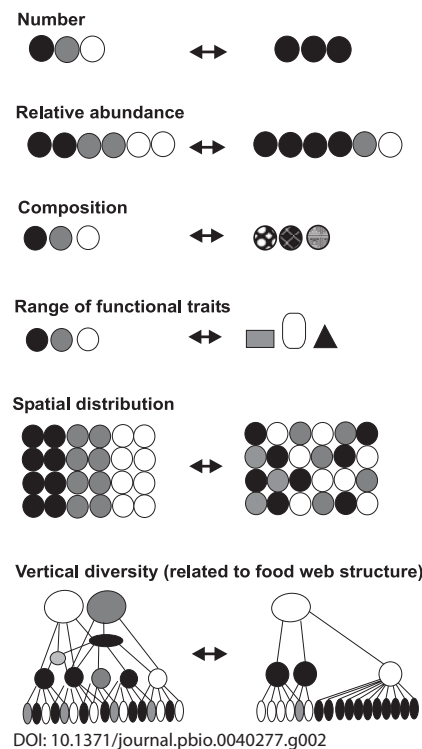
Most of the links between biodiversity and ecosystem services summarized in Table 1 emerged from theory and manipulative experiments, involved biodiversity within a single trophic level (usually plants), and operated mostly at the level of local communities. However, the most dramatic examples of effects 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

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



**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.

**Table 1. Biodiversity Components Affect Ecosystem Services in Multiple and Complex Ways**

<b>Ecosystem Services</b>	<b>Main Components of Diversity Involved and Mechanisms That Produce the Effect</b>
Amount of biomass produced by plants considered important by humans	<p>*** 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.</p> <p>** 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.</p>
Stability of biomass production by plants considered important by humans	<p>*** Genetic diversity—Large genetic variability within a crop species buffers production against losses due to diseases and environmental change.</p> <p>*** Number of species—Cultivation of more than one species in the same plot or landscape maintains production over a broader range of conditions.</p> <p>*** 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.</p>
Preservation of the fertility of soils that sustain the production of plants and animals considered important by humans	<p>*** Functional composition—Fast-growing, nutrient-rich plants enhance soil fertility; dense root systems prevent soil erosion.</p>
Regulation of quantity and quality of water available to humans, domestic animals, and crops	<p>*** Arrangement and size of landscape units—Intact riparian corridors and extensive areas with dense vegetation cover reduce erosion and improve water quality.</p> <p>*** Functional composition—Vegetation dominated by large, fast-growing, big-leafed, deep-rooted plants has high transpiration rate, reducing stream flow.</p>
Pollination essential for the immediate production of fruits by, and the perpetuation of, important plant species	<p>*** Functional composition of pollinator assemblage—Loss of specialized pollinators leads to genetic impoverishment and lower number and quality of fruits.</p> <p>** Number of species of pollinator assemblage—Lower number of pollinator species leads to genetic impoverishment of plant species.</p> <p>** 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.</p>
Resistance to invasive organisms that have negative ecological, economic, and/or cultural impacts	<p>*** Functional composition—Some key native species are very competitive or can act as biological controls to the spread of aliens.</p> <p>*** 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.</p> <p>** 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.</p>
Pest and disease control in agricultural systems	<p>*** Genetic diversity of crops—High intraspecific genetic diversity reduces density of hosts for specialist pests and, thus, their ability to spread.</p> <p>** 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.</p> <p>** Spatial distribution of landscape units—Natural vegetation patches intermingled with crops provide habitat for natural enemies of insect pests.</p>
Regulation through biophysical feedbacks of climatic conditions suitable to humans and the animals and plants they consider important	<p>*** 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.</p> <p>** Functional composition—Height, structural diversity, architecture, and phenology modify albedo, heat absorption, and mechanical turbulence, thus changing local air temperature and circulation patterns.</p>
Regulation through carbon sequestration in the biosphere of climatic conditions suitable to humans and the animals and plants they consider important	<p>*** 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.</p> <p>** 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.</p> <p>* 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.</p>
Protection against natural hazards (storms, floods, hurricanes, fires) that cause damage to humans and the animal production systems that they depend on	<p>*** 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.</p> <p>*** 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.</p>

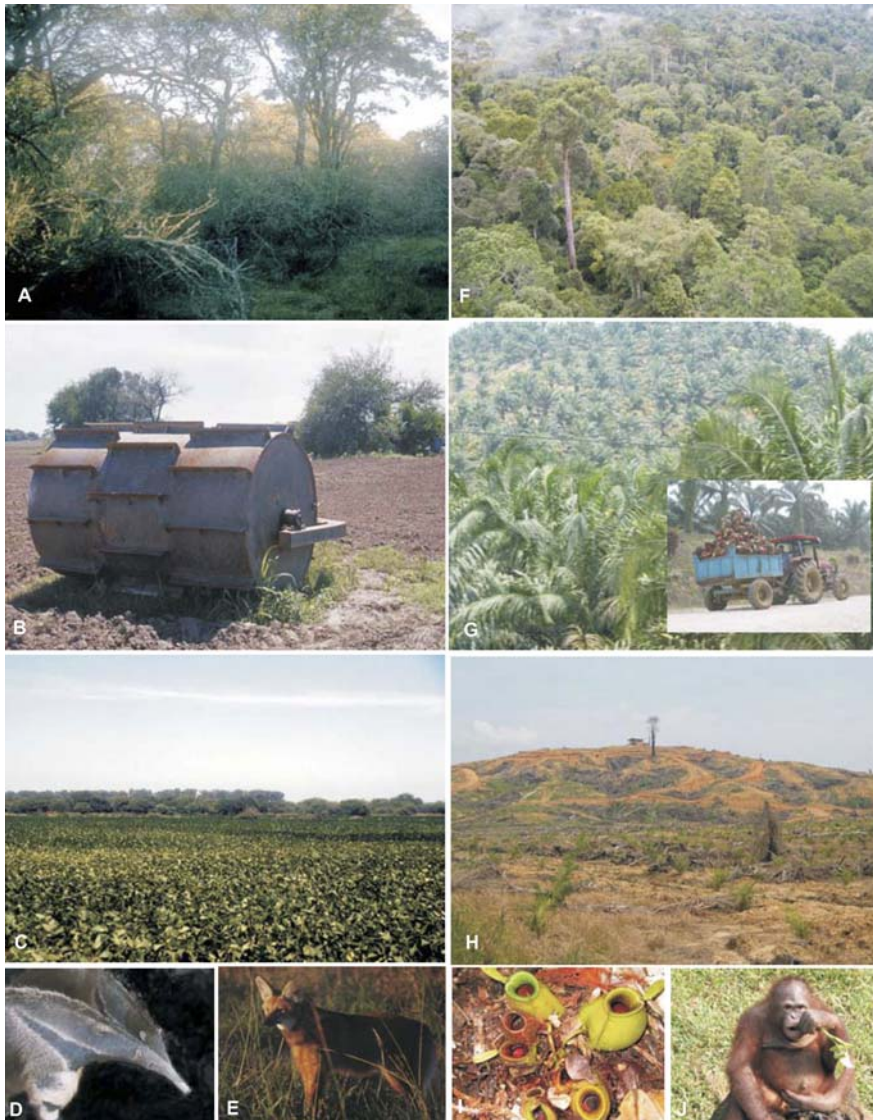
Asterisks indicate importance and/or degree or certainty (\*\*\*) > \*\* > \*) of the link between the ecosystem service in question and different components of biodiversity. Biodiversity components refer to plant assemblages unless otherwise specified. The putative mechanisms have been empirically tested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

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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.



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### 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 Dipterocarp 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

- Baillie JEM, Hilton-Taylor C, Stuart SN (2004) IUCN Red List of Threatened Species: A Global Species Assessment. Gland (Switzerland): IUCN.
- 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.
- 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.
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: Biodiversity synthesis. Washington (D. C.): World Resources Institute. 86 p.
- Stokstad E (2005) Ecology: Taking the pulse of earth's life-support systems. *Science* 308: 41–43.
- Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? *Ecol Lett* 8: 468–479.
- 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.
- McKinney M, Lockwood J (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14: 450–453.
- Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. Chichester (United Kingdom); New York: John Wiley & Sons. 417 p.
- 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.
- 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.
- 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.
- 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.
- Tilman D (1999) Diversity and production in European grasslands. *Science* 286: 1099–1100.
- 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.
- 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.
- Trenbath B (1999) Multispecies cropping systems in India: Predictions of their productivity, stability, resilience and ecological sustainability. *Agroforestry Systems* 45: 81–107.
- Altieri M (2004) Linking ecologists and traditional farmers in the search for sustainable agriculture. *Frontiers in Ecology and the Environment* 2: 35–42.
- Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.
- 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.
- 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.
- 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.
- 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.
- Naylor RL, Goldberg RJ, Primavera JH, Kautsky N, Beveridge MCM, et al. (2000) Effect of aquaculture on world fish supplies. *Nature* 405: 1017–1024.
- 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.
- 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.
- Díaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. *Trends Ecol Evol* 18: 140–146.
- 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.
- 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.
- Boyd J, Banzhaf S (2006) What are ecosystem services? The need for standardized environmental accounting units. Washington (D. C.): Resources for the Future.