The Functions of Biological Diversity in an Age of Extinction

Article *in* Science · June 2012

DOI: 10.1126/science.1215855 · Source: PubMed

Shahid Naeem
Columbia University

J. Emmett Duffy
Smithsonian Institution

The Functions of Biological Diversity in an Age of Extinction

Shahid Naeem,[1]* J. Emmett Duffy,[2] Erika Zavaleta[3]

Ecosystems worldwide are rapidly losing taxonomic, phylogenetic, genetic, and functional diversity as a result of human appropriation of natural resources, modification of habitats and climate, and the spread of pathogenic, exotic, and domestic plants and animals. Twenty years of intense theoretical and empirical research have shown that such biotic impoverishment can markedly alter the biogeochemical and dynamic properties of ecosystems, but frontiers remain in linking this research to the complexity of wild nature, and in applying it to pressing environmental issues such as food, water, energy, and biosecurity. The question before us is whether these advances can take us beyond merely invoking the precautionary principle of conserving biodiversity to a predictive science that informs practical and specific solutions to mitigate and adapt to its loss.

The biological organisms that are the engines of Earth's biogeochemistry, which strongly influences environmental conditions from local to global scales, also provide our food, biomaterials, biofuels, pollination, biocontrol, genetic resources, cultural values, and many other benefits. At a basic level, it is the cumulative mass of these organisms and their collective biological processes that fundamentally govern an ecosystem's biogeochemistry, but this mass often comprises a staggering diversity of organisms. Whereas the biological processes underlying biogeochemistry are generally well characterized, understanding the relationship of life's extraordinary diversity to biogeochemical or ecosystem functioning poses a fundamental challenge of modern science: Is biodiversity necessary to the functioning of ecosystems, or is it essentially an epiphenomenon of long- and short-term evolutionary and ecological processes?

The question of biodiversity's role in the functioning of ecosystems has been under intense investigation for two decades. Three volumes, one documenting the beginning, another the maturation, and the most recent the current state of the discipline, have been published; two consensus papers have addressed debates that dogged its early years; and numerous meta-analyses have quantitatively assessed central findings (*1*). From this rapidly expanding literature, we review three scientific frontiers that shape current research. Here, we focus primarily on the science, but given that we are living in an age of extinction (*2*) due to multiple anthropic drivers of biodiversity loss (Fig. 1)—with potentially profound implications for our future—we also touch on environmental insights gained from these two decades of research.

The Frontier of Integrative Biodiversity

The first generation of studies on biodiversity's influence over ecosystem functioning asked simply whether the production of biomass (a commonly studied ecosystem function) varies predictably with species richness. Biodiversity, however, has many dimensions, species richness being only a measure of the taxonomic dimension (Box 1). Functional diversity, assessed as the number of functional groups, was recognized early on as a dimension that was a better predictor of ecosystem functioning; a proliferation of more objective trait-based measures of functional diversity followed (*3*). Working with multiple rather than single dimensions of biodiversity, of course, increases the complexity of current research. For example, Mouillot *et al*. (*4*) explored two measures of taxonomic diversity and six measures of functional diversity (based on five plant traits) to explain four independent ecosystem functions in an experimental manipulation of plant species richness in Germany—a far cry from simply comparing species richness to biomass production.

Adding functional diversity to taxonomic diversity in single studies was just a first step. Among several additional components of biodiversity, phylogenetic diversity has emerged as the best predictor of ecosystem functioning in several systems (*5*–*7*). Within species, genetic or genomic diversity is also proving to be an important dimension of biodiversity in governing ecosystem function (*8*–*11*). In experimental grassland plots, for example, increasing genetic diversity (one to eight genotypes) of a single species of primrose (*Oenothera biennis*) had the same positive effect on production as increasing taxonomic diversity from one to eight plant species, excluding primrose (*9*). Going further still, taxonomic diversity has been linked to interaction diversity, the complex web of interactions among species in a system. For example, in a grassland experiment, low-diversity plots (four plant species) produced lower interaction diversity among the 427 resident arthropod species than did high-diversity plots (16 plant species) (*12*). Taken to the extreme, the next step might seem to require conducting an experiment that examines the effects of taxonomic, functional, phylogenetic, genetic, spatial, temporal, landscape, and interaction diversity (all the dimensions we list in Box 1) to explain multiple ecosystem functions.

But such an additive progression—in which biodiversity and ecosystem function research steadily increases the number of dimensions of biodiversity it investigates—is not integrative nor likely tractable. Additive approaches primarily pit different dimensions of biodiversity against one another to identify the best predictor. In contrast, an integrative approach would seek the mechanistic underpinnings of ecosystem responses to biodiversity loss by focusing on the relationships among genes, traits, phylogeny, the biotic and abiotic factors that affect these relationships, and how all these ultimately explain ecosystem functioning.

The data requirements and statistical complexity involved in such an approach are daunting, but new technologies offer means by which they might be addressed. One promising example examined the functional genetics of how below-ground microbial diversity mediated ecosystem responses to elevated CO_2 by using 454 pyrosequencing of polymerase chain reaction amplicons and the GeoChip functional gene array containing more than 27,000 probes of more than 57,000 gene sequences in more than 250 gene families (*13*). This tool was used to quantify CO_2-induced changes in the composition of microbial functional genes associated with metabolic pathways in C, N, P, and S cycling, and related these responses to ecosystem functions such as soil C, soil N, and aboveground biomass production. This study illustrates our developing ability to integrate across relatively unexplored dimensions of biodiversity, such as microbial genetic and functional diversity, to explain ecosystem responses to key global change factors including biodiversity loss.

New technologies and newly accessible dimensions of biodiversity are currently shifting the field's goals. Once focused on simply examining which dimension of biodiversity was the better predictor of ecosystem functioning, the goals are now to better understand why and how multiple dimensions of biodiversity simultaneously influence ecosystem functioning.

Ecological Structure

Ecosystems are not random assemblages of species engaged in a hodgepodge of biogeochemical

---

[1]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY 10027, USA. [2]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, USA. [3]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA.

*To whom correspondence should be addressed. E-mail: sn2121@columbia.edu

processes. Rather, they are highly structured around two related elements. First, communities are structured by networks of interactions, in which species are the nodes and biotic interactions are the links (Fig. 2, lower panel). These links reflect exchanges or transfers of energy (in the form of organic compounds) and material (nutrients, water, biochemicals, and their elemental constituents) among interacting organisms. Second, ecosystems are structured by a network of biogeochemical pathways (Fig. 2, upper panel). Neither interaction networks nor biogeochemical pathways exist independently of the other: Organisms are pools of elements in biogeochemical pathways. This is a core idea in biodiversity and ecosystem functioning research, and is the basis of the unified theoretical framework recently developed by Loureau (*14*).

A growing body of work illustrates the key importance of this ecological structure to ecosystem functioning, operating through a multiplicity of effects of biodiversity change. Zavaleta *et al.* (*15*), for example, found that changes in plant species diversity in experimental grassland plots more strongly affected ecosystem functions and properties as more functions were considered together. Other experiments similarly highlight how ecological structure mediates complex effects on functioning, showing that loss of plant diversity cascades "upward" to trophic levels above ground and in the soil (*16*), that changes in plant diversity influence the stability of multiple insect trophic levels (*17*), that manipulations of arthropod trophic structure cascade "downward" to plants and ecosystem functions (*18*), and that manipulating fish biodiversity in freshwater systems influences ecosystem properties (*19*).

The influence of ecological structure on different dimensions of stability has been a mainstay of community ecological research since the late 1950s, but biodiversity and ecosystem functioning research has brought functional stability into sharper focus. Of particular note is that populations of individual species in diverse communities often fluctuate more in the face of environmental heterogeneity than ecosystem functions that are generally aggregate properties of all populations, although the particular outcome is dependent on the degree of interspecific interactions and demographic synchrony (*20*) among species. For example, the relative abundance of grassland species in Inner Mongolia fluctuates with precipitation over time, yet overall primary production of the system is less variable where diversity is high (*21*). Similarly, wild salmon populations in individual tributaries at Bristol Bay, Alaska, fluctuate considerably, but total production of salmon biomass through the whole system is much more constant (*22*). In these and other studies, it is the complementarity of species' responses to environmental heterogeneity that allows increased functional stability. Greater biodiversity can also allow for greater species turnover and compensatory growth as environments change, lowering system variability (*23*–*25*). These effects are variously known as statistical averaging, biological insurance, or the portfolio effect [see (*26*) for a review].

The impacts of biodiversity change on ecosystem function are clearly far richer than our historical focus on predominantly monotrophic,

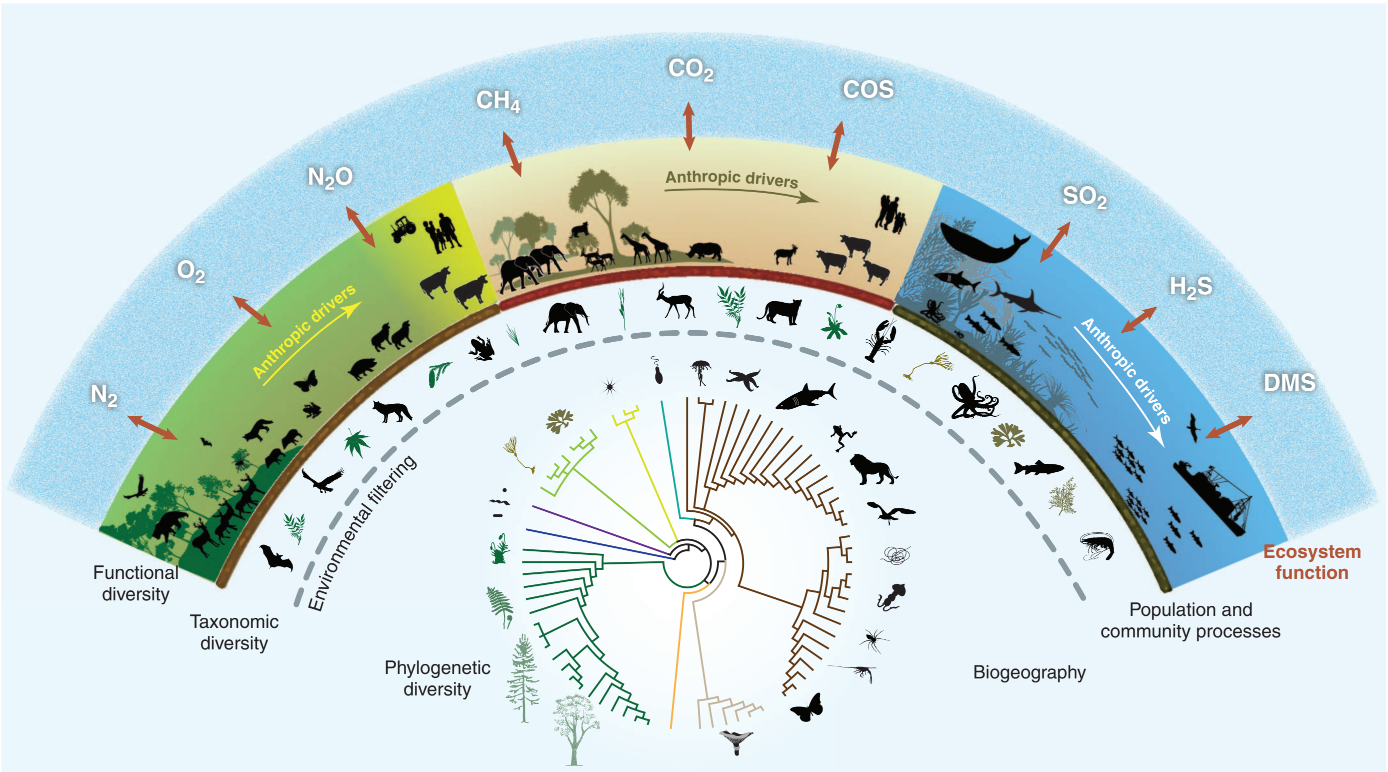

Fig. 1. Biodiversity and ecosystem functioning in an age of extinction. The phylogenetic tree of life, currently populated by about 10 million species, ranges from microscopic to enormous multicellular organisms, of which only a few representative phyla and divisions are shown as icons at the tips of the branches. Where species from the global phylogenetic pool are found is largely determined by environmental filters, represented here as a barrier with pores (dashed arch). Here we show only phylogenetic and taxonomic diversity, but biogeography, population processes, biotic interactions, metagenomic and intragenomic variation, and functional traits contribute to different dimensions of biodiversity (Box 1) that characterize the biota of each ecosystem. Three representative ecosystems are illustrated: a forested ecosystem (left arch), savanna ecosystem (center arch), and marine ecosystem (right arch). Microorganisms are represented by soils and sediments, illustrated as a dark band at the base of each arch. Each ecosystem contributes to ecosystem functioning, shown here primarily as biogeochemical processes (chemical exchanges between the atmosphere and biosphere shown in the outermost arch). Widespread extinction attributable to anthropic drivers (human transformations of ecosystems going from left to right in each arch) lead to biotic impoverishment (reductions in local biodiversity) and biotic homogenization (increasing dominance by domestic species). For clarity, the complexity of biogeochemical pathways and interaction networks (Figs. 2 and 3) is not shown.

Box 1. Dimensions of Biodiversity

Since 1988, when the term biodiversity was first published, its use has risen exponentially. Currently, as indexed by *Biological Abstracts*, more than 66,300 journal articles have used the term. Definitions, however, vary widely from the all-encompassing "diversity of life on Earth" to the enigmatic definition adopted by the UN Convention on Biological Diversity, "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."

Connecting biodiversity to ecosystem functioning entails locating ecosystems in a multivariate space defined by dimensions that describe different ways of relating organisms to one another. Examples of these dimensions include:

- Taxonomic diversity: the number and relative abundance of taxa (e.g., species, genera, families, and onward) defined by a hierarchical, evolutionary classification
- Phylogenetic diversity: relationships among taxa based on elapsed time since divergence (e.g., sum of the branch lengths linking species in a phylogeny)
- Genetic diversity: nucleotide, allelic, chromosomal, genotypic, or other aspects of genomic variability
- Functional diversity: variation in the degree of expression of multiple functional traits
- Spatial or temporal diversity: rates of turnover of species through space or time
- Interaction diversity: characteristics of the network of linkages defined by biotic interactions, such as competition, predation, parasitism, or facilitation, with other species (food web and trophic networks are subsets of biotic networks)
- Landscape diversity: number, relative abundance, and distribution of different habitat types within a landscape

By these definitions, one community may be called more diverse than another if it has any combination of more species (taxonomic diversity), greater cumulative phylogenetic distance among its species (phylogenetic diversity), greater genotypic diversity within species (genetic diversity), greater distance among species in multivariate functional trait space (functional diversity), higher species turnover across a unit of space (spatial diversity), greater numbers of links per species in the interaction network (network diversity), and more habitat types within the landscape (landscape diversity). In practice, because the necessary data are often lacking, such a comprehensive assessment is untenable. Assessments are further complicated by the fact that the dimensions are not orthogonal (e.g., taxonomic, phylogenetic, and functional diversity correlate with one another) and may need to be differently weighted for particular applications (e.g., network diversity may be more important than taxonomic diversity when assessing biodiversity's influence over system stability).

monofunctional, monodimensional biodiversity studies has revealed. Such studies generally lacked the ecological structure inherent to ecosystems, which we increasingly realize is key to their functioning. The emphasis now is on discovering why increased biodiversity has mixed effects on stability and how to scale findings up to larger levels such as those of the Inner Mongolia and Alaska studies.

External Validity

In much of experimental ecological research, nature is seen as the complex, species-rich reference against which treatment effects are measured. In contrast, biodiversity and ecosystem functioning experiments often simply compare replicate ecosystems that differ in biodiversity, without any replicate serving as a reference to nature. Consequently, it has often been difficult to evaluate the external validity of biodiversity and ecosystem functioning research, or how its findings map onto the "real" worlds of conservation and decision making. Put another way, what light can be shed on the stewardship of nature by microbial microcosms that have no analogs in nature, or by experimental grassland studies in which some plots have, by design, no grass species?

The quest for external validation or generalizability has resulted in a steady increase in the diversity of taxa, ecosystems, and ecosystem functions and properties investigated. Such studies have dealt with bacteria [e.g., (*27*)], phytoplankton [e.g., (*28*)], marine angiosperms (*29*), trees [e.g., (*30*)], birds (*31*), and more. The generally positive influence of biodiversity on production and resource use efficiency has proven robust in studies that go beyond the traditional monotrophic approach [e.g., (*32*)] and that articulate with other ecological processes such as succession (*33*), metacommunity interactions (*34*), emigration and immigration (*35*), and assembly (*36*) and disassembly (*37*). Finally, longer-term studies that use higher levels of diversity, measure simultaneous effects on multiple functions (*15*, *38*), and measure emergent functions such as reliability (*24*) all suggest that the importance of biodiversity increases as research incorporates increasing complexity to better approximate nature.

Spatial scale is central in assessing the external validity of biodiversity and ecosystem functioning research because, relative to nature, typical experiments have less biodiversity and are smaller in size, shorter in duration, and much simpler in ecological structure. At large scales, in the absence of experimental manipulation, it can be difficult to determine the relationship between biodiversity and ecosystem functioning. The relationship between primary production and plant species richness is a classic example that has not yet been resolved despite more than 30 years of research (*39*). Observational studies can solve some of these problems by using statistical methods to partition the effects of biodiversity from other factors in large ecosystems subject to complex environmental forcing. For example, Maestre *et al*. (*40*) examined the influence of plant species richness—relative to climatic, geopositional, and edaphic factors—on ecosystem multifunctionality (a measure incorporating 14 ecosystem functions) across 224 dryland ecosystems. They found that plant species richness was positively associated with ecosystem multifunctionality, although it explained less than 3% of the variation. Other observational studies that used structural equations modeling to partition covariation among variables in complex causal models have found that biodiversity's effects vary but can be quite strong relative to other environmental drivers [e.g., compare (*30*, *41*)].

Another challenge to evaluating external validity is that theoretical, simulation, observational, and experimental studies often provide seemingly different answers to the same question, making it difficult to identify generalities and achieve consensus. Meta-analyses and integrative studies can help to address this issue. Meta-analyses have identified central tendencies in biodiversity and ecosystem functioning's diverse arrays of studies [e.g., (*42*–*46*)].

An emerging approach of much promise is to manipulate or simulate more realistic scenarios of biodiversity loss, rather than the randomized loss typical of past studies (*47*–*51*); these scenario-based approaches often find quite different impacts on ecosystem functioning than random losses, emphasizing the sensitivity of ecosystem functioning to specific stressors, such as pollution or overharvesting, or perturbations, such as fire or drought. For example, McIntyre *et al*. (*50*) found that simulated random extinctions (typical of traditional approaches in biodiversity and ecosystem functioning research) of freshwater fish species in Rio Las Marias, Venezuela, resulted in linear declines of N cycling rates, but if rare species had a higher probability of extinction due to greater sensitivity to fishing pressures (a more realistic scenario for species loss), then declines were asymptotic.

Although it is not easy to gauge when an ecological discipline has validated itself by showing

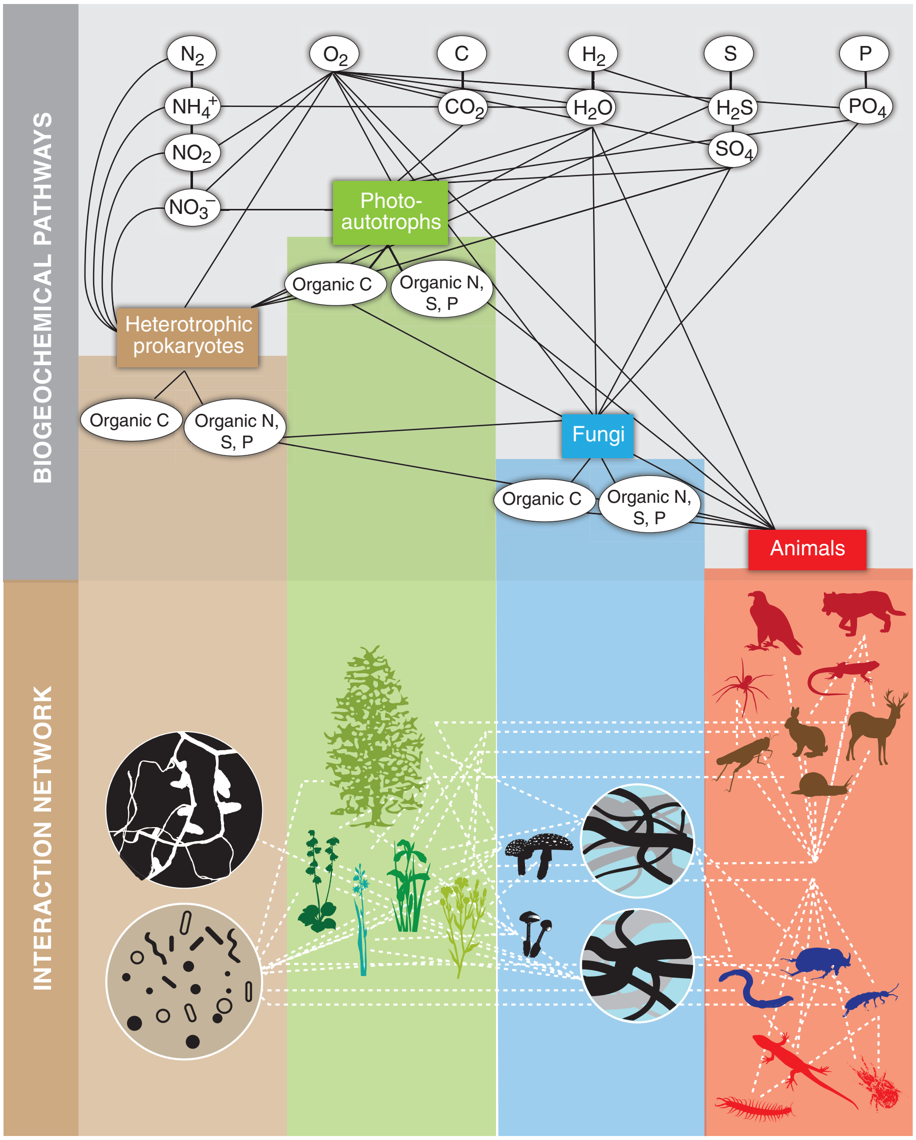

Fig. 2. Ecological structure in terrestrial systems. Biodiversity and ecosystem functioning research couples biogeochemical pathways (upper panel) with interaction networks (lower panel). Biogeochemical pathways, or elemental and material fluxes, are illustrated for C, H, N, O, P, and S. Biological contributions are collected into four groups defined by major taxa: heterotrophic prokaryotes, photoautotrophs (plants), fungi, and animals. Interaction networks are illustrated for each group, with animals organized from top to bottom (by color) as carnivores, herbivores, microbivores and detritivores, and detrital carnivores. We show only two fungal and two heterotrophic prokaryote trophic groups: decomposers and plant uptake facilitators such as rhizobia bacteria living in the nodulated roots of legumes (upper circle of heterotrophic prokaryotes), or fungal mycorrhizal associates (hyphal masses in upper circle and mushrooms in fungi). Colored vertical bars link sources of mass for each species in the lower panel to the biogeochemical group where the mass is produced. The figure shows all organisms, whether above or below ground, as pools of elements and all interactions as pathways of energy and material transfer among organisms.

one-to-one correspondence with all the complexity inherent in nature, hundreds of studies over the past two decades have examined many individual facets of nature's complexity. Collectively, the emerging picture is compelling. Few ecological disciplines have been as thoroughly scrutinized as biodiversity and ecosystem functioning, but there are still many issues to be addressed and gaps to fill. To illustrate, Fig. 3 shows a landscape consisting of a freshwater ecosystem (such as a lake) located within a forested ecosystem, with the many elements of biodiversity and ecosystem function that characterize such an idealized landscape. Most of the elements shown in Fig. 3 have been explored by biodiversity and ecosystem functioning research, although some of these themes would benefit from closer study, such as (i) how the effects of apex species loss ripple through biotic networks and biogeochemical pathways, (ii) how changes in genetic and interaction diversity influence ecosystem functioning, and (iii) how landscape connections are affected by changes in biodiversity.

Although some disagreement remains, the collective results of biodiversity and ecosystem functioning studies offer growing confidence that the general findings of early biodiversity and ecosystem functioning studies are robust and may even underestimate diversity's role in nature (*52*). The frontier now consists of exploring the impacts of realistic loss of multiple biodiversity components on ecological structure and how this affects the dynamics of ecosystem functioning, rather than repeating existing studies with different species in different ecosystems.

Current Challenges

Twenty years of research has answered the initial confirmatory questions in biodiversity and ecosystem functioning research, yielding a field today that is complex, broad in scope, and able to provide important insights into the ecosystem consequences of biodiversity change. The field now grapples with four specific challenges:

1. In order for biodiversity and ecosystem functioning to become a strongly predictive science, it needs efficient ways to extrapolate information about key functional traits of known species to estimate the traits of poorly known species, which number in the millions, especially microbial species.

2. Biodiversity and ecosystem functioning research needs to embrace the challenge of extracting order from complexity. The greater the focus on the multifunctionality and multiple integrated dimensions of biodiversity characteristic of wild nature, the more useful the conclusions that can be drawn concerning how ecological structure shapes the influence of biodiversity changes on the functioning of real ecosystems. Meeting this challenge is particularly important in light of increasing concerns over environmental tipping points and safe planetary boundaries.

3. Ecological research needs to better integrate advanced technologies. The use of such technologies as pyrosequencing and remote sensing will better enable measurement of the impact of changes in functional diversity (at the level of genes and traits of individual organisms) on ecosystem functions at local and global levels.

4. Similarly, research on biodiversity and ecosystem functioning must take advantage of increasingly powerful statistical methodologies and observatory systems such as the recently commissioned National Ecological Observatory Network (NEON), the Global Biodiversity Information Facility (GBIF), and the Global Earth Observation System of Systems (GEOSS). These facilities offer both promise and challenges for more accurately parsing the effects

of biodiversity and biodiversity change from other factors controlling ecosystem functions at larger scales.

The Environmental Implications of Biodiversity and Ecosystem Functioning Research

The chief contribution of research on biodiversity and ecosystem functioning has been to articulate, and provide compelling scientific support for, the idea that maintaining a high proportion of biological diversity leads to efficient and stable levels of ecosystem functioning. Although this review's focus has been on scientific issues, biodiversity and ecosystem functioning research has also contributed to environmental science by linking biodiversity to ecosystem services that benefit humans. This construct formed the foundation of the Millennium Ecosystem Assessment's framework (*53*), is central to the 2020 targets of the Convention on Biological Diversity (*54*), and is also the foundation for the new United Nations Intergovernmental Platform on Biodiversity and Ecosystem Services, signed by 90 member states on 23 April 2012.

The straightforward environmental message of biodiversity and ecosystem functioning is essentially a statement of the precautionary principle: that biodiversity conservation ensures ecosystem functions that in turn ensure ecosystem services benefiting humanity. A number of studies have examined the connections between biodiversity and ecosystem services in the form of food provision, disease resistance, and economic benefits. For example, a detailed survey showed that greater diversity of bird hosts in the eastern United States is associated with lower incidence of West Nile virus in humans (*31*). Higher diversity of wildlife has also been shown to increase economic benefits to human communities in Namibia (*55*). Planting more diverse varieties of rice in Yunnan Province in China improved resistance to fungal pathogens so strongly that fungicides were

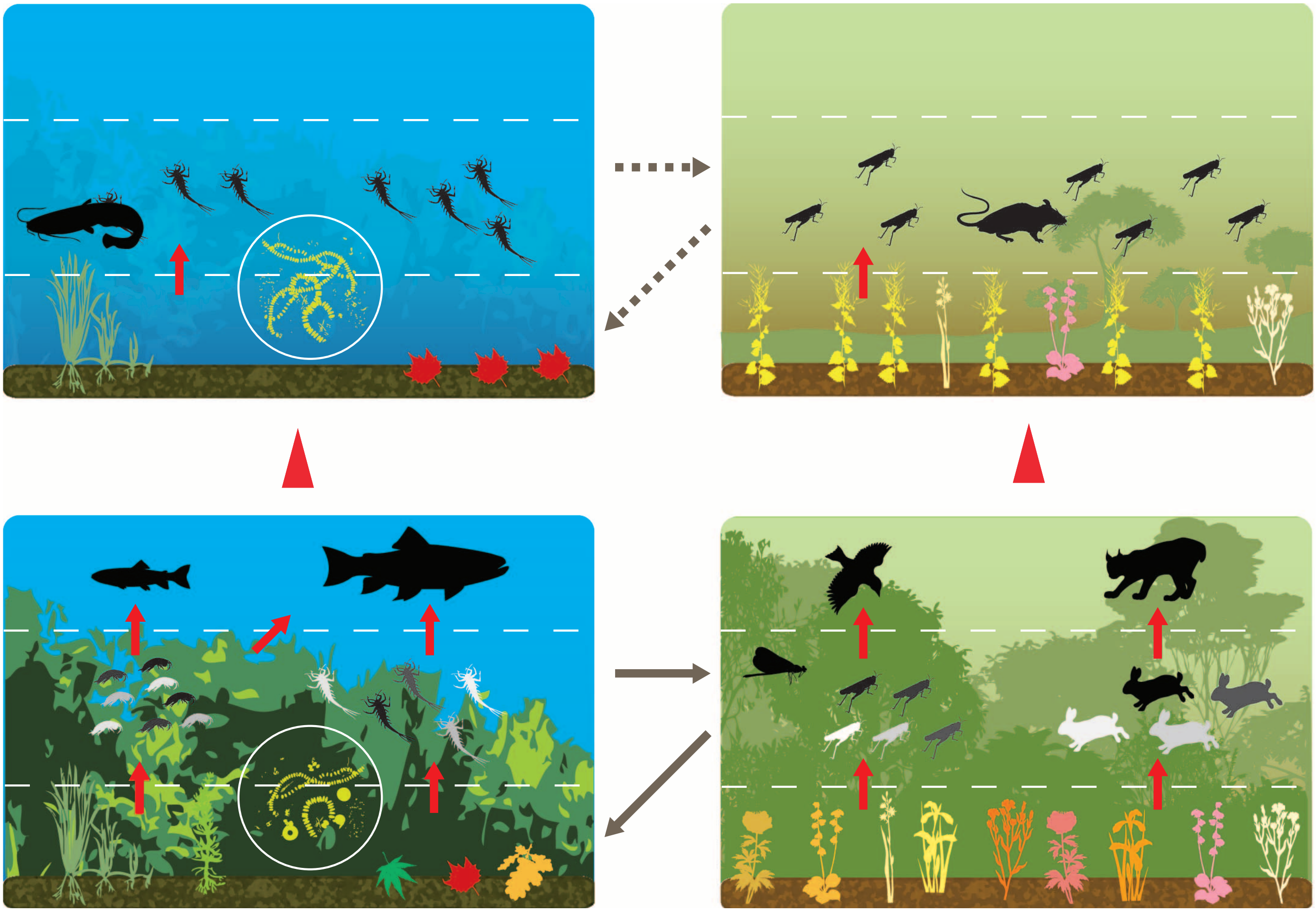

Fig. 3. External validation. Ecosystems are characterized by a complex set of organisms, biogeochemical pathways, energy and nutrient fluxes, and many other elements of ecological structure (Fig. 2), but most biodiversity and ecosystem functioning studies examine only one or a few of these elements, making it difficult to know whether their findings are valid. This figure illustrates several of these elements for a landscape comprising a freshwater aquatic ecosystem within a forested terrestrial ecosystem. Interaction diversity is shown as a three-level trophic network in which species in one level feed on species below them. Taxonomic and functional diversity are shown as different colors and forms within levels. Genetic diversity is shown as different shades of gray among the amphipods and mayfly larvae in the middle level of the freshwater system and for the grasshoppers and rabbits in the terrestrial system. Red arrows within panels indicate the transfer of nutrients and energy between organisms among levels. Gray arrows between lower panels represent how habitat diversity influences nutrient and energy flow within a landscape: The freshwater system receives terrestrial inputs (shown as different tree leaves on the sediment surface) and the terrestrial system receives inputs from the freshwater system (shown as a mayfly entering the terrestrial system). Human impacts on biodiversity are illustrated by the change in each of these elements from the bottom panels to the top panels. Both systems have lost apex predators and their top trophic level is empty, representing a decline in "vertical diversity." Human-mediated gain in biodiversity is shown as an exotic catfish having entered the freshwater system and an exotic rat and plant having entered the terrestrial system. Microorganisms are represented by the brown bands at the base of each panel and also as plankton (in the white circle in the water) in the freshwater system.

not needed in the intercropped system (*56*). A promising frontier in this arena is quantifying the influence of biodiversity on multiple services, to reduce the tendency for single-service analyses to miss important trade-offs (*57*).

After two decades of research, we now appreciate more keenly that biodiversity is one of multiple factors that govern ecosystem properties, and that changes in both the number and identity of species, genes, and functional types imposed by human actions can yield ecosystem effects that vary from small to far-reaching and cascading. The theoretical emphasis of inquiry into biodiversity and ecosystem functioning has also helped to build first principles and new theory for understanding how the natural world works at fundamental levels. That is, we have mechanistic theories, refined through substantial empirical testing across taxa and systems, that we can now carry forward and apply to other systems, including the human-dominated, domesticated ecosystems that already dominate much of the world (*58*).

The Future in an Age of Extinction

The frontiers of biodiversity and ecosystem functioning research are rapidly expanding as new approaches and technologies, and a rapidly growing database, allow researchers to address questions at levels of precision and scale not possible in 1992 when the field formally began. There is no question that we need new data, tools, and approaches to understand how growing biotic impoverishment and biotic homogenization will influence ecosystem functioning and the environmental and economic fates of nations. The Millennium Ecosystem Assessment (*59*), guided in part by advances in biodiversity and ecosystem functioning research, moved us beyond the state of affairs in 1992, when the precautionary principle was the chief message that helped to shape biodiversity policy, by linking biodiversity to human well-being in a range of systems around the world. What biodiversity and ecosystem functioning can continue to contribute includes theory, understanding, and practical tools to tell us when, where, and what kinds of biodiversity changes are likely to have far-reaching and cascading effects on ecosystem properties. An increasingly robust implication of this research for a wide array of ecologically dependent practices and businesses—such as habitat restoration, conservation, public health management, biosecurity, agriculture, agroforestry, aquaculture, and environmental monitoring—is that their short- and long-term goals are often better met by increasing biodiversity and focusing on multiple rather than single functions. But time is short; the next decade will be an important period for testing these implications in the real world, outside the domain of theoretical, laboratory, and field-based experimental studies that dominate present research.

The central environmental message of biodiversity and ecosystem functioning research, to conserve biodiversity to improve human well-being, has historically been essentially utilitarian in its reasoning. This focus is sometimes understandably seen as contrary to widespread and urgent conservation efforts to save species and ecosystems from extinction for non-utilitarian, cultural reasons (*60*). Indeed, species targeted for conservation, reserves, and protected areas represent a tiny fraction of the biosphere and are therefore not likely to strongly influence biogeochemically derived ecosystem services such as carbon sequestration and food production. Yet the cultural values of biological diversity can themselves be construed as ecosystem services, and their preservation is fully coherent with non-utilitarian conservation efforts and arguably no less important. Nothing in biodiversity and ecosystem functioning research should dissuade conservation from its efforts to bring our age of extinction to a halt.

Biodiversity and ecosystem functioning research is now maturing; it has advanced sufficiently to move beyond simply invoking the precautionary principle as it has done throughout its history. This research has helped to clarify why protecting biodiversity is a goal of fundamental importance and can support efforts to safeguard the intrinsic capacity of ecosystems for self-renewal, adaptive dynamics, and supporting humanity now and for generations to come.

References and Notes

1. S. Naeem, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, Eds., *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (Oxford Univ. Press, Oxford, 2009).
2. A. D. Barnosky *et al.*, *Nature* **471**, 51 (2011).
3. D. Schleuter, M. Daufresne, F. Massol, C. Argillier, *Ecol. Monogr.* **80**, 469 (2010).
4. D. Mouillot, S. Villéger, M. Scherer-Lorenzen, N. W. H. Mason, *PLoS ONE* **6**, e17476 (2011).
5. D. F. B. Flynn, N. Mirotchnick, M. Jain, M. I. Palmer, S. Naeem, *Ecology* **92**, 1573 (2011).
6. M. W. Cadotte, J. Cavender-Bares, D. Tilman, T. H. Oakley, *PLoS ONE* **4**, e5695 (2009).
7. J. Connolly *et al.*, *Ecology* **92**, 1385 (2011).
8. L. Latta *et al.*, *Evol. Ecol.* **25**, 1107 (2011).
9. S. C. Cook-Patton, S. H. McArt, A. L. Parachnowitsch, J. S. Thaler, A. A. Agrawal, *Ecology* **92**, 915 (2011).
10. M. W. Cadotte, K. Carscadden, N. Mirotchnick, *J. Appl. Ecol.* **48**, 1079 (2011).
11. C. W. Hargrave, K. D. Hambright, L. J. Weider, *Ecology* **92**, 1226 (2011).
12. M. Rzanny, W. Voigt, *J. Anim. Ecol.* (2012).
13. Z. He *et al.*, *Ecol. Lett.* **13**, 564 (2010).
14. M. Loureau, *From Populations to Ecosytems: Theoertical Foundations for a New Ecological Synthesis* (Princeton Univ. Press, Princeton, NJ, 2010).
15. E. S. Zavaleta, J. R. Pasari, K. B. Hulvey, G. D. Tilman, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1443 (2010).
16. C. Scherber *et al.*, *Nature* **468**, 553 (2010).
17. N. M. Haddad, G. M. Crutsinger, K. Gross, J. Haarstad, D. Tilman, *Ecol. Lett.* **14**, 42 (2011).
18. O. J. Schmitz, *Ecology* **90**, 2339 (2009).
19. M. P. Carey, D. H. Wahl, *Oikos* **120**, 84 (2011).
20. M. Loreau, C. de Mazancourt, *Am. Nat.* **172**, E48 (2008).
21. Y. Bai, X. Han, J. Wu, Z. Chen, L. Li, *Nature* **431**, 181 (2004).
22. D. E. Schindler *et al.*, *Nature* **465**, 609 (2010).
23. E. Allan *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17034 (2011).
24. A. Hector *et al.*, *Ecology* **91**, 2213 (2010).
25. N. R. Franssen, M. Tobler, K. B. Gido, *Oikos* **120**, 582 (2011).
26. J. N. Griffin *et al.*, in *Biodiversity, Ecosystem Functioning, and Human Wellbeing*, S. Naeem, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 78–93.
27. T. Bell, J. A. Newman, B. W. Silverman, S. L. Turner, A. K. Lilley, *Nature* **436**, 1157 (2005).
28. M. Striebel, S. Behl, S. Diehl, H. Stibor, *Am. Nat.* **174**, 141 (2009).
29. C. Gustafsson, C. Boström, *Oikos* **120**, 1037 (2011).
30. A. Paquette, C. Messier, *Glob. Ecol. Biogeogr.* **20**, 170 (2011).
31. J. P. Swaddle, S. E. Calos, *PLoS ONE* **3**, e2488 (2008).
32. J. E. Duffy, J. P. Richardson, K. E. France, *Ecol. Lett.* **8**, 301 (2005).
33. E. Maggi, I. Bertocci, S. Vaselli, L. Benedetti-Cecchi, *Ecology* **92**, 1399 (2011).
34. M. Loreau, N. Mouquet, A. Gonzalez, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 12765 (2003).
35. K. E. France, J. E. Duffy, *Nature* **441**, 1139 (2006).
36. T. Fukami *et al.*, *Ecol. Lett.* **13**, 675 (2010).
37. E. Zavaleta *et al.*, *Ann. N.Y. Acad. Sci.* **1162**, 311 (2009).
38. F. Isbell *et al.*, *Nature* **477**, 199 (2011).
39. P. B. Adler *et al.*, *Science* **333**, 1750 (2011).
40. F. T. Maestre *et al.*, *Science* **335**, 214 (2012).
41. E. Weiher, S. Forbes, T. Schauwecker, J. B. Grace, *Oikos* **106**, 151 (2004).
42. B. J. Cardinale *et al.*, *Nature* **443**, 989 (2006).
43. B. Worm *et al.*, *Science* **314**, 787 (2006).
44. B. Schmid *et al.*, in *Biodiversity, Ecosystem Functioning, and Human Wellbeing*, S. Naeem, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 14–29.
45. D. K. Letourneau, J. A. Jedlicka, S. G. Bothwell, C. R. Moreno, *Annu. Rev. Ecol. Evol. Syst.* **40**, 573 (2009).
46. B. J. Cardinale *et al.*, *Am. J. Bot.* **98**, 572 (2011).
47. F. I. Isbell, D. A. Losure, K. A. Yurkonis, B. J. Wilsey, *Oikos* **117**, 996 (2008).
48. M. E. Bracken, S. E. Friberg, C. A. Gonzalez-Dorantes, S. L. Williams, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 924 (2008).
49. P. C. Selmants, E. S. Zavaleta, J. R. Pasari, D. L. Hernandez, *J. Ecol.* **100**, 723 (2012).
50. P. B. McIntyre, L. E. Jones, A. S. Flecker, M. J. Vanni, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 4461 (2007).
51. S. Naeem, *Trends Ecol. Evol.* **23**, 414 (2008).
52. J. E. Duffy, *Front. Ecol. Environ* **7**, 437 (2009).
53. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: A Framework for Assessment* (Island, Washington, DC, 2003); pdf.wri.org/ecosystems_human_wellbeing.pdf.
54. C. Perrings *et al.*, *Front. Ecol. Environ* **9**, 512 (2011).
55. R. Naidoo, L. C. Weaver, G. Stuart-Hill, J. Tagg, *J. Appl. Ecol.* **48**, 310 (2011).
56. Y. Zhu *et al.*, *Nature* **406**, 718 (2000).
57. I. A. Dickie *et al.*, *J. Appl. Ecol.* **48**, 926 (2011).
58. P. Kareiva, S. Watts, R. McDonald, T. Boucher, *Science* **316**, 1866 (2007).
59. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Synthesis* (Island, Washington, DC, 2005); www.millenniumassessment.org/documents/document.356.aspx.pdf.
60. D. S. Srivastava, M. Vellend, *Annu. Rev. Ecol. Evol. Syst.* **36**, 267 (2005).

Acknowledgments: We thank two anonymous reviewers for their comments and suggestions. Supported by NSF grants OCE-1031061 (J.E.D.), DEB-0639161 (S.N.), and DEB-0918715 (E.Z.).

10.1126/science.1215855