



# Expanding scales in biodiversity-based research: challenges and solutions for marine systems

Shahid Naeem\*

Department of Ecology, Evolution, and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, New York 10027, USA

**ABSTRACT:** As in terrestrial biodiversity, human influences over marine biodiversity will alter the way ecosystems contribute to biogeochemical or ecosystem processes. While many studies have documented how alterations of terrestrial biology affect ecosystem functioning, few studies have examined marine systems. The main challenge faced by biodiversity and ecosystem functioning (BEF) research in marine ecology is dealing with the large scales of marine systems and the logistical difficulties of attempting to conduct the kinds of complex, combinatorial experiments that have been done in terrestrial ecology. BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment) has developed a framework for relating biodiversity, via biomass, to ecosystem functioning and for employing extinction scenarios to explore the realm of possible changes in ecosystem functioning that biodiversity loss could create. This approach may find much utility in marine BEF research because it obviates the need for complex experiments. I provide an overview of the issues, the framework, and some directions marine ecology could take to further our understanding of the ecosystem consequences of marine biodiversity loss.

**KEY WORDS:** Biodiversity · Ecosystem function · Marine · Extinction · Biogeochemistry

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

At one extreme, in the absence of a biota, Earth's biogeochemical processes by definition become geochemical processes that yield an uninhabitable planet, with conditions something between those of Venus and Mars. At the other extreme, today's biota regulate biogeochemical processes that annually move gigatons ( $10^{15}$  g) of materials among the hydro-, litho-, and atmosphere, yielding an environment conducive to life and defining its surface for the last 1.5 billion yr (Love-lock 1979, Schlesinger 1997a, Ernst 2000, Kasting & Siefert 2002, Mathez & Webster 2004).

Earth systems (e.g. global biogeochemical systems) and ecosystems (e.g. local biogeochemical systems) in general are moving to a point somewhere between these extremes in the sense that the role the biota plays in regulating geochemical processes is changing dramatically in the face of human domination of ecosystems (Vitousek et al. 1997, Hollowell 2001, Duraiappah

& Naeem 2005). There are 2 components to this change. The first concerns change in the biologically active mass of the Earth's biota (henceforth, biomass), which can be visualized as a sort of diffuse green or brown slime coating the Earth's surface. Biomass is variously defined, often simply referring to the mass of biogenic organic material, living or dead. Here, I use biomass to refer only to metabolically active or living biomass, which includes standing (static) as well as growing components of organisms.

The second concerns change in the structure of this living mass. Though often modeled as a homogeneous slime in ecosystem, climate, or biogeochemical models, biomass is, of course, actually made up of organisms structured by taxonomy, biotic interactions, functional differences, genetic differences, and differences in distribution over space and time (henceforth, biodiversity). Part of the structure of this biomass stems from inter-specific differences in apportionment of biomass to the standing crop or productivity, inter-specific

\*Email: sn2121@columbia.edu

differences in impacts on elemental cycles, and intra- and inter-specific interactions, especially trophic interactions, which can dramatically affect ecosystem functioning. Clearly, changes in biodiversity mean changes in the structure of biomass which, in turn, means changes in the ways biomass influences ecosystem functioning. For example, it is possible that fluctuations in atmospheric CO<sub>2</sub> may have been driven almost entirely by the biosphere over the last 370 million yr (Rothman 2001). This implies that human dominance over the biosphere, either directly by changes in the mass of living organisms or indirectly by changes in biodiversity, leaves the carbon cycle (and by extension, all other biogeochemical cycles) increasingly in the hands of humans.

Tremendous uncertainty surrounds estimates of how much biomass or biodiversity there is at most scales, let alone how much they have changed or will change under scenarios of continuing human growth and development. Some back-of-the-envelope calculations are, however, instructive. If we consider that estimates of the global biomass of plants range from 501 to 829 Gt C, and estimates of heterotrophic biomass range from 353 to 565 Gt, this gives us roughly a biosphere made up of about 1000 Gt C (summed from Appendix F in Smil 2002). This biomass moves about 110.2 Gt C among the spheres annually (assuming all the carbon taken up by the biosphere in a year is released in the same year) (Schlesinger 1997b). If we consider that the total amount of carbon in the atmosphere is about 750 Gt, the biosphere moves that much in about 7 yr. Of the active carbon in soils, the biosphere moves an equivalent amount in about 15 yr. To move an amount of active carbon equivalent to what is present in the oceans, however, would take 40 yr.

Continuing with this simplistic exercise, given Balmford et al.'s (2002) estimates of biome reductions of 1.2 to 11.4% over the previous decade (see discussion above), significant declines in global biomass and global biodiversity are very likely during the next century. What are the consequences of such loss? The simplest conclusion would be that for every 10 Gt of global biomass lost, roughly 1.1 Gt of C will not cycle per year, which can be readily translated into reductions in other ecosystem functions. But what would happen if the bulk of the biomass lost consists of standing rather than growing biomass, or consists entirely of rare species, or the loss occurs predominantly in the oceans rather than terrestrial systems, or consists of declines in heterotrophic biomass rather than autotrophic biomass? Clearly, global changes in biomass have impacts, but how biodiversity changes (e.g. the spatial, trophic, taxonomic, and other components of biomass) is equally important. If we wish to understand how Earth, its biomes, or its ecosystems are shifting

between the biogeochemically active systems they are now towards depauperate, predominantly geochemical systems (i.e. uninfluenced by biology), intense ecological research is necessary now and in the near future (Naeem et al. 2000, Hooper et al. 2005).

Certainly there is evidence that both biodiversity and biomass are declining on large scales. If we consider global changes to major biome types as an indicator of changing biomass, with the exception of boreal forests, Balmford et al. (2002) estimated that between 1992 and 2002, the Earth's major biomes shrunk in area or extent at an annual rate of 1.2 to 11.4%. Given that species occurrences and biomass are positively related to area, then there is little doubt that biodiversity (at least locally) and biomass have declined on a global scale. Although such large-scale changes suggest correlated changes in biomass and biodiversity in natural systems, and paleoecologically the 2 seem to have been correlated for a long time (Rothman 2001), there is no *a priori* reason to believe that they are causally coupled in any way (Falkowski & Rosenthal 2001). From the standpoint of conservation, for example, a biodiversity hotspot (e.g. Myers et al. 2000, e.g. Rodrigues et al. 2004) or marine protected area (e.g. Balmford et al. 2004, Browman & Stergiou 2004) can contain a significant fraction of the Earth's taxonomic diversity, yet represent an insignificant portion of the global biomass. From the standpoint of unsustainable use, when humans construct managed systems, such as fish or shrimp farms, they often locally increase biomass well beyond anything previously observed in the system, but at extraordinarily low levels of biodiversity (although this is generally achieved by subsidization Naylor et al. 1998). One can legitimately ask whether either activity is desirable—creating a landscape with small areas that contain tremendous biodiversity, but show next to no biogeochemical activity, to large subsidized areas that show a tremendous amount of biogeochemical activity, but contain almost no biodiversity (Millennium Ecosystem Assessment 2003).

Clearly, changes in biomass lead to changes in biogeochemistry, but less clear is whether changes in biodiversity, beyond the trivial point of no biodiversity, are of any biogeochemical significance. Scientific exploration of the biogeochemical or ecosystem consequences of changes in biodiversity began a little over a decade ago (Schulze & Mooney 1993). This research is dominated by terrestrial studies, all small in spatial and temporal scale. With the exception of Steinberg & Geller's (1993) contribution on plankton diversity and ecosystem processes, virtually no treatment of marine biodiversity and marine ecosystem functioning was covered in the founding volume on the topic by Schulze & Mooney (1993). A decade later, only a handful of experimental studies have examined the ecosystem con-

sequences of biodiversity loss in marine systems (e.g. Emmerson & Raffaelli 2000, Duffy et al. 2001, Emmerson et al. 2001, Stachowicz et al. 2002, Callaway et al. 2003, Covich et al. 2004, Solan et al. 2004).

The need to address the terrestrial bias of biodiversity and ecosystem functioning (henceforth, BEF) research is clear (Emmerson & Huxhan 2002). Given that widespread alteration of the Earth's biota is undoubtedly at least as significant for marine ecosystems (Roberts & Hawkins 1999, Jackson et al. 2001, Myers & Worm 2003) as it is for terrestrial ecosystems, the motivation for terrestrial biodiversity and ecosystem functioning research applies to both marine and terrestrial systems. Given that the biosphere is 71% marine in surface area and probably much more in terms of volume (Groombridge & Jenkins 2000), that it is responsible for nearly half of the Earth's net primary production (NPP) (Schlesinger 1997b), that more than half the world's population lives within 60 km of the sea, and that marine fisheries consume 24 to 35% of the NPP (Roberts & Hawkins 1999), a terrestrial bias in BEF research limits its ability to address global environmental issues.

The primary challenge for marine BEF research is that of scaling up, which is actually the same challenge terrestrial BEF faces, but because of fewer logistical constraints, terrestrial systems have had more options. BEF studies will continue in the foreseeable future to be small in scale and short in duration, and are critical for the evolution of theory and testing of mechanisms in BEF research (Loreau et al. 2001, Naeem 2001, Bengtsson et al. 2002). To meet the challenge of going beyond the limited scales of current BEF studies, a research-coordinating network known as BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment) was created (see [www.columbia.edu/cu/biomerge/](http://www.columbia.edu/cu/biomerge/) and Naeem & Wright 2003). The majority of BEF studies to date, including the few marine studies, have all explored only a limited portion of the spatial, temporal, and biological realm of biodiversity and ecosystem functioning (Fig. 1). BioMERGE's mission is to coordinate efforts that lead to the development of BEF methods that allow exploration of a greater range of ecosystems over much larger scales than have currently been achieved.

The focus of the present paper is the framework developed by BioMERGE developed for scaling up BEF research by the participants of the research-coordinating network (note, henceforth, when referring to BioMERGE it will be explicitly in refer-

ence to its framework). This framework is explicitly non-experimental, aiming to provide insights on the relationship between biodiversity and ecosystem functioning by making use of the wealth of past, existing, and planned studies of biodiversity and ecosystem functioning. Using this framework, I will offer some suggestions for possible directions for future marine BEF research that can address the needs for working at large scales with limited information about both biomass and biodiversity in marine ecosystems.

### GLOBAL BIODIVERSITY AND ECOSYSTEM FUNCTIONING IN TERRESTRIAL AND MARINE SYSTEMS

#### Terrestrial BEF research as a springboard for marine research

Even though BEF research is currently largely terrestrial in nature, there are sufficient similarities between marine and terrestrial systems that enable current BEF research to serve as a springboard for developing ideas concerning the scaling up of marine BEF research. For starters, there are many similarities at the global scale between marine and terrestrial environmental concerns. For example, in many cases

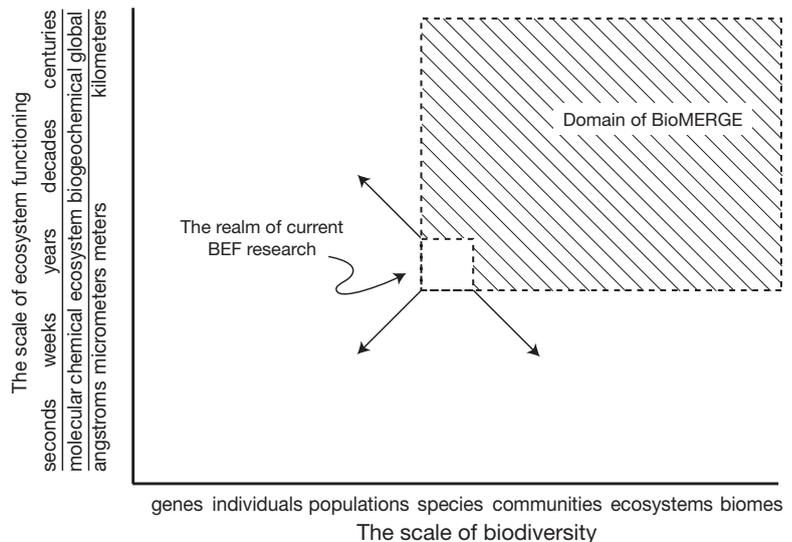


Fig. 1. The realms of current research in biodiversity and ecosystem functioning (BEF) and BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment). Each axis abstractly and approximately represents the scales of biodiversity and ecosystem functioning, illustrating the latter as a dependent function of the former. The center box illustrates the average domain of current BEF research, which has focused on relating species diversity to ecosystem functioning at small spatial (in the realm of square meters) and temporal scales (in the realm of weeks to years). Arrows indicate directions of new research necessary for the expansion of BEF research. The larger box encompassing the upper right quadrant represents the domain of BioMERGE, which seeks to extend BEF research to larger scales (after Naeem et al. in press)

marine zooplankton and phytoplankton show unimodal relationships with their own biomass (Irigoien et al. 2004), much like what is seen in terrestrial systems (Mittelbach et al. 2003). Marine ecosystems are experiencing rates of change similar to major terrestrial biomes (Balmford et al. 2002). And both terrestrial (e.g. Purvis et al. 2000) and marine ecosystems have proportionally larger percentages of top predators or carnivores threatened or vulnerable than species at lower trophic levels (e.g. Myers & Worm 2003, e.g. Hutchings & Reynolds 2004). Furthermore, marine NPP, estimated at  $48.5 \times 10^{15}$  g C, is similar to terrestrial NPP, estimated at  $56.4 \times 10^{15}$  g C (Schlesinger 1997b).

Estimates for both terrestrial and marine biodiversity are completely lacking, because of the difficulties of documenting the many dimensions of biodiversity (e.g. functional diversity, and spatial and temporal patterns of distribution), but to the extent that taxonomic diversity may serve as a crude proxy (Naeem 2002a, Petchey & Gaston 2002), marine and terrestrial systems may be similar. Deep-sea macrofaunal diversity, based on box-core samples, has been estimated to be as high as 10 million species (Grassle & Maciolek 1992), but the uncertainty surrounding this number is similar to the uncertainty surrounding the estimate of 30 million species of terrestrial insects estimated by Erwin (1982). Conservatively, dismissing some of the very high estimates for species richness, the global total is more likely to be about 14 million species (Groombridge & Jenkins 2000), with a sense that marine taxonomic diversity is lower (in species), but certainly larger in phyla.

Perhaps the greatest uncertainty surrounds microbial species richness (Tiedje 1995, Pace 1997, Torsvik et al. 2002, Nee 2004), which, given that microbes dominate biogeochemical processes (Fenchel et al. 1998), represents a major gap in our knowledge of taxonomic diversity. For example, one of the most thorough molecular estimates of prokaryotic diversity is that of Venter et al. (2004) in which they estimated 1800 genomic species in the samples they collected from the Sargasso Sea. Analyses of their data, however, suggest that a 12-fold greater depth of sampling is needed before they would be within 95% of the likely diversity. This study illustrates the difficulty in attempting to quantify prokaryotic diversity, even from 1 marine site.

One interesting difference between terrestrial and marine systems, however, is that vast though the marine realm is, it may contain a smaller proportion of the global biomass. Total marine biomass (in terms of carbon) is estimated at 5 to  $10 \times 10^{15}$  g C, while land contains  $560 \times 10^{15}$  g C—or almost 2 orders of magnitude more biomass (Groombridge & Jenkins 2000). Nevertheless this does not affect the way the question of how biodiversity and ecosystem functioning are related (see next section).

## Diversifying the slime

At one level, it is not uncommon in ecology to treat the biosphere or an ecosystem as simply autotrophic biomass—the equivalent of a homogeneous, photon-fuelled slime coating the Earth or an ecosystem. Likewise, microbial biomass (a brown slime) in sediment and soil is often associated with decomposition, mineralization, and other ecosystem functions without consideration of microbial diversity.

Crude though it is, this slime approach provides a means of determining the role our biota play in governing biogeochemical processes or ecosystem functioning by a simple formula that might look like this:

$$E = BR \quad (1)$$

in which some measure of ecosystem function ( $E$ ) is equal to the product of the biomass ( $B$ ) of the biological community in the ecosystem and the per unit biomass rate of biogeochemical activity ( $R$ ). Note that there are many possible metrics or currencies one could use for biomass, such as C, N, and P for all biomass (though dead biomass would have to be removed) or RNA and ATP for active biomass. As mentioned previously, one can also divide biomass into standing, growing, and reproductive biomass (e.g. Reekie & Bazzaz 1987a,b,c), but for simplicity, I ignore these divisions here.

This slime, however, is made up of individuals whose body sizes range from  $10^{-6}$  cm (e.g. viruses) to nearly  $10^4$  cm (e.g. blue whale *Balaenoptera musculus*), though the vast majority of such organisms are very small ( $10^{-5}$  to  $10^{-3}$  cm, such as prokaryotes and protists) (Fenchel 1987, Nee 2004) and their individual densities range from substantially <1 individual (e.g. vertebrates) to trillions (e.g. microbes) per square meter. Each unit of biodiversity, such as a species, a group of organisms sharing functional traits, or ecosystem type, represents some portion of community biomass. By calculating the sum of the biomass of all individuals in the unit of diversity, we can determine its relative role in ecosystem processes by comparing it to the sum of the biomass of all individuals across all units of diversity in the ecosystem. Adding diversity to the equation, or diversifying the slime, changes the formula to:

$$E = \sum_{i=1}^D B_i R_i \quad (2)$$

or simply the sum of biomass  $\times$  function for each unit ( $i$ ) of diversity (e.g. species, functional group, ecosystem type, or other unit of biodiversity) for all the units of diversity in the estimate ( $D$ ).

Solan et al. (2004) followed this approach to model ecosystem functioning relevant for a benthic marine community. The function was biogenic mixing depth (BMD), or the depth to which animals burrow from the

sediment surface, and Solan et al. related this to biodiversity by the simple formula:

$$\text{BMD} = 0.719 \log \left( \sum_{i=1}^D \bar{B}_i^{0.5} R_i \right) + 4.55 \quad (3)$$

where  $\bar{B}_i$  is the mean biomass of the  $i$ th unit of diversity, and  $R_i$  for their system was defined as the product of the propensity to move and the reworking mode (the functional sediment mixing class of the organism such as surface modifier, burrower, excavator, or other class of impact on the sediment) of the  $i$ th unit of diversity, and for their system the unit of diversity,  $i$ , is a species and  $D$  is the total number of species in the community or ecosystem. The constants and log transformation were derived from curve-fitting a formula that bounded BMD to observed depths (see Solan et al. 2004, supplementary information, for further details). One can see the similarity between Eqs. (2) & (3) and also appreciate how relatively simple the task can be for relating biodiversity and biomass to ecosystem functioning. Admittedly, BMD may represent a case in which ecosystem functioning was readily related to biodiversity and biomass. Complications arise when ecosystem functioning is not so readily related to biomass, and other factors must be included in the formulation.

Additional complications arise when attempting to use units of diversity that are not as readily defined or obtained as taxonomic diversity. For example, one can define the unit of diversity as a group of organisms clustered by similarities in their phenotypes (e.g. body size, morphology, physiology, behavior, biochemistry, reproductive rates and dispersal patterns) or by their functional traits (e.g. traits related to the ecosystem function of interest) (Díaz & Cabido 2001, Lavorel & Garnier 2002, Naeem 2002b, Petchey & Gaston 2002). Such classification schemes tend to be hierarchical in nature, the basic unit being the species in taxonomic classifications and individuals sharing functional traits in functional classifications. With respect to the latter, as noted by Lavorel & Garnier (2002), one must further distinguish between traits that are associated with the ecosystem function and traits associated with responses to environmental change, a fact that is particularly important when considering extinction scenarios (see 'Modeling biodiversity, loss: extinction drivers and scenarios' section).

### Adding macroecology

The units of diversity are not randomly, uniformly spread over space and time, which allows for the possibility of using patterns of association between diversity and biotic and abiotic factors in developing BEF mod-

els. Statzner & Moss (2004) point to the long history in ecology of studying allometric relationships among biodiversity, ecosystem function, habitat properties (e.g. area, structure, and abiotic factors), and species properties (e.g. body size, longevity), much of which constitutes the current field of macroecology (Brown 1995, Gaston 2000, Blackburn & Gaston 2003a,b), as a source for guiding the development of BEF studies at larger scales than our current experiments permit. These macroecological relationships provide, not only a foundation for structuring and testing descriptive models of the relationship between biodiversity and ecosystem functioning, but may serve as a means for approximating BEF variables when data are lacking.

As an example of the utility of macroecology, consider attempting to apply the method developed by Solan et al. (2004) described above to another marine system in which only the taxa are known. One needs estimates of relative abundance of species which Solan et al. derived from actual photographs of the fauna, but one seldom has such data to hand. In the absence of such information about distribution and abundance, however, macroecology provides useful insights into what the patterns of relative abundance might be and how one might estimate a biologically plausible range of relative abundances for a given biota (Brown 1995, Gaston 2000, Blackburn & Gaston 2003a,b). Species within trophic groups, for example, often show predictable patterns with respect to area, productivity, climate, and other geographical features, and relative abundance typically exhibits log-normal like distributions (Preston 1962, Sugihara 1980, Hubbell 2001, Hubbell & Lake 2003, Nee 2003), in which many species are rare and a few dominant. Hypothetically, it is possible to approximate abundance of other species using macroecological methods in terrestrial systems (and hypothetically all systems for the neutral, unified model), even if one has only limited information on such aspects as presence/absence data and total biomass (or density) of the community, as well as some knowledge about relative abundance (e.g. which species are rare and which are numerically dominant). In comparison to terrestrial ecosystems, macroecology is less well developed for marine systems, but some studies suggest macroecological principles may be usefully employed in marine studies (McKinney 1998, Belgrano et al. 2002, Li 2002, Foggo et al. 2003, Statzner & Moss 2004).

### Modeling biodiversity loss: extinction drivers and scenarios

Achieving the primary goal of BEF research requires knowing how biodiversity will change over time in order to predict how ecosystem functioning will

change as biodiversity changes. Empirical studies, with few exceptions (e.g. Zavaleta & Hulvey 2004, e.g. Schlapfer et al. 2005), have largely sidestepped the issue by exploring all possible patterns of loss of biodiversity, which effectively involves employing a scenario in which every unit of diversity (e.g. species, functional group, or some other unit of biodiversity) has a uniform, random probability of going extinct. This is the most general approach one can take that will lead to results that can relate to all possible extinction scenarios. It is also the most difficult to employ, however, because of the large number of replicate communities one would have to construct to explore biodiversity loss. Further, the relationship between a specific path of biodiversity loss and ecosystem functioning may be masked by the large number of pathways of loss that come from random-extinction models. Even more disturbing for some is the fact that random-extinction models lead to the construction or modeling of communities that are unlikely to exist in nature. For example, in a random-extinction grassland experiment (e.g. Tilman et al. 1996, Naeem et al. 1999) one constructs communities that completely lack grasses—fine for theory, but troublesome for those concerned explicitly with the loss of biodiversity in grasslands. One might take comfort in knowing that somewhere in the hodge-podge of results from a combinatorial BEF experiment lies the pattern of biodiversity loss of interest, but one will also be dismayed by the fact that identifying it in a cloud of data may be impossible.

In reality, biodiversity loss involves local (or global) extinctions that follow trait-based probabilities of loss based on the extinction driver or ecological, evolutionary, or anthropogenic process that governs extinction. How does one incorporate such trait-based extinction drivers into the BioMERGE framework? The framework uses extinction scenarios. 'Extinction scenarios' were used by Sala et al. (2000) in which the authors explored scenarios for how loss would shape biodiversity by the year 2100. They used expert opinion, not data, in which anthropogenic drivers that lead to biodiversity loss were ranked separately for each biome. These extinction drivers included land use, climate change, nitrogen deposition, invasion or biotic exchange, and elevated atmospheric CO<sub>2</sub>. They explored 3 kinds of scenarios based on these 5 extinction drivers. In the first case, all drivers had additive effects. In the second, the dominant driver governed the change. In the third, the drivers interacted synergistically such that each driver's effect was multiplied by the other. Rather than using expert opinion, however, scenarios in which extinction drivers (e.g. increasing pollution in an estuary) are explicitly associated with trait-based extinction probabilities (e.g. marine invertebrate sensitivity to pollution) provide a more direct way of assess-

ing the realm of possible ecosystem responses to biodiversity loss than expert opinion. Below, I review Solan et al. (2004) as an example.

There are many extinction scenarios one could employ. The first study to employ extinction scenarios in an observational BEF study was, again, that of Solan et al. (2004). The authors employed 4 extinction scenarios for their marine system: (1) random, (2) body size (smaller has a higher extinction probability), (3) population size (smaller has a higher extinction probability), and (4) sensitivity to pollution. Zavaleta & Hulvey (2004), in contrast, employed a single nested extinction scenario (all depauperate communities were taxonomically nested sets of higher diversity communities) without stipulating what extinction driver would produce such a pattern. The defense of using a nested scenario of biodiversity loss is that nestedness is widely observed in nature (Patterson & Atmar 1986, Atmar & Patterson 1993). One could additionally use trophic position, home range size, population growth rates, or other traits identified by comparative methods (e.g. Purvis et al. 2003) that allow one to relate diversity loss with extinction drivers.

In summary, an extinction scenario describes the realm of possible biodiversities likely to be obtained based on probabilities of extinction that are governed by species traits and their sensitivities to extinction drivers, or the ecological, evolutionary, or anthropogenic processes that drive units of diversity to extinction.

### **The BioMERGE framework for scaling up BEF**

The BioMERGE framework for scaling up BEF research (Naeem & Wright 2003, Naeem et al. in press) is one in which fundamental ecological principles can be employed to provide first approximations of the role of biodiversity in ecosystem functioning. The most extreme version of the BioMERGE approach involves being able to indicate what the biogeochemical or ecosystem consequences of biodiversity loss would be for a region in which the only information one has is a list of the existing taxa and the global positioning system (GPS) coordinate. A more feasible BioMERGE approach involves having, not only the taxa and geography, but the relative growth rates of all species, their relative abundance (e.g. commonness and rarity), the trophic interactions that structure the community, the dynamics of the different populations, and spatial and temporal patterns of both the biota and ecosystem functions and properties. In such a case, however, one hardly needs the BioMERGE framework, since traditional community and ecosystem ecology can be combined to model the relationship between biodiversity and functioning and how changes in community composition change ecosystem functioning.

Every study will fall somewhere between these 2 extremes—having just a list of taxa and GPS coordinates to having a well-documented study of biodiversity and ecosystem functioning (empirical and observational) over space and time. There will be a tradeoff in the precision with which one can predict the ecosystem consequences of biodiversity loss with the degree of information one employs in the analysis, but the BioMERGE goal is to not be paralyzed by a lack of information that could require far too many resources or far too long to provide answers.

### The 3 step BioMERGE framework

As the above outlines, there are essentially 3 major steps in the BioMERGE framework. The assumption is that one has the biota, basic ecosystem measures, and a specific ecosystem function selected for investigation (Naeem & Wright 2003, Naeem et al. in press). From there, 3 steps are important:

(1) *Diversify the slime*. As described above, ecosystem functions are often readily related to biomass; thus, one has to estimate biomass and structure it according to known or observed relationships between a unit of diversity, the amount of biomass in that unit, and the function that converts that biomass to a unit of ecosystem function. For NPP in pelagic marine systems, this requires determining phytoplankton biomass and phytoplankton diversity which can, again, be taxonomic, functional, or some other unit. In coral reef systems, calcium carbonate production and coral diversity may be the function–diversity pair of interest. In an estuary, BMD and infaunal (sediment-dwelling animal) diversity may be the function–diversity pair of interest. In most cases, allometric relationships between body size and metabolic rates or other physiological functions may be used to derive the relationship between unit biomass and ecosystem functioning, a suggestion for BEF research first made by Steinberg & Geller (1993).

(2) *Determine the macroecology*. Depending on the unit of diversity, biomass (or densities), patterns of distribution and abundance become important for weighting each unit's contribution to ecosystem functioning. If the diversity unit is species, then one would expect that many species are probably rare and a few domi-

nant, as described above. Either way, this necessitates biotic inventories that go beyond taxonomic diversity—they need to include, at a minimum, relative abundance and, ideally, measures of traits relevant to extinction drivers.

(3) *Develop extinction scenarios*. The BioMERGE approach combines extinction drivers with trait-based extinction probabilities which are referred to as extinction scenarios. Again, we may borrow from Roberts & Hawkins (1999) whose review of marine extinctions identified natural causes (e.g. disease), biotic exchange, unsustainable harvest, habitat alteration or destruction, and multiple causes as drivers that are associated with known marine extinctions. As in Sala et al. (2000), one has to determine whether the scenario considers single drivers, the additive effects of drivers, or the multiplicative effects of drivers. For marine systems, we can begin with Roberts & Hawkins (1999) whose list of traits that relate to threats of extinction for marine species can be used in scenarios (Table 1). What marine ecologists need to do is to identify which drivers warrant investigation (e.g. unsustainable harvest, climate change, or pollution), which traits are relevant to which drivers, and to document these traits for the species in the ecosystems being modeled.

After completing these steps, one can plot ecosystem functioning against biodiversity loss for as many communities as one wishes to model, for as many scenarios as one wishes to explore. The results one obtains would look something like that shown in Fig. 2 in which the scenario determines the gradient of biodiversity, the empirically derived formula relating biomass, biodiversity, and function provides the estimate

Table 1. Three classes of traits of marine species that can be used for extinction scenarios in BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment) modeling based on expert opinion. Parenthetical classifications describe end of spectrum for possible values that would describe species at greater risk of extinction (adapted from Roberts & Hawkins 1999)

Life history or ecological traits	Capacity for recovery	Range and distribution
Longevity (short)	Regeneration from fragments (does not occur)	Horizontal distribution (nearshore)
Growth rate (slow)	Dispersal (short distance)	Vertical depth range (narrow)
Natural mortality rate (low)	Competitive ability (poor)	Geographic range (small)
Production biomass (low)	Colonizing ability (poor)	Patchiness of population within range (high)
Reproductive effort (low)	Adult mobility (low)	Habitat specificity (high)
Reproductive frequency (semilparity)	Recruitment by larval settlement (irregular or low-level)	Habitat vulnerability to people (high)
Age or size at sexual maturity (old or large)	Allee effects on recovery (strong)	Commonness and/or rarity (rare)
Sex change occurs (occurs)		
Spawning (aggregations at predictable locations and time)		
Allee effects on reproduction (strong)		
Trophic level (high)		

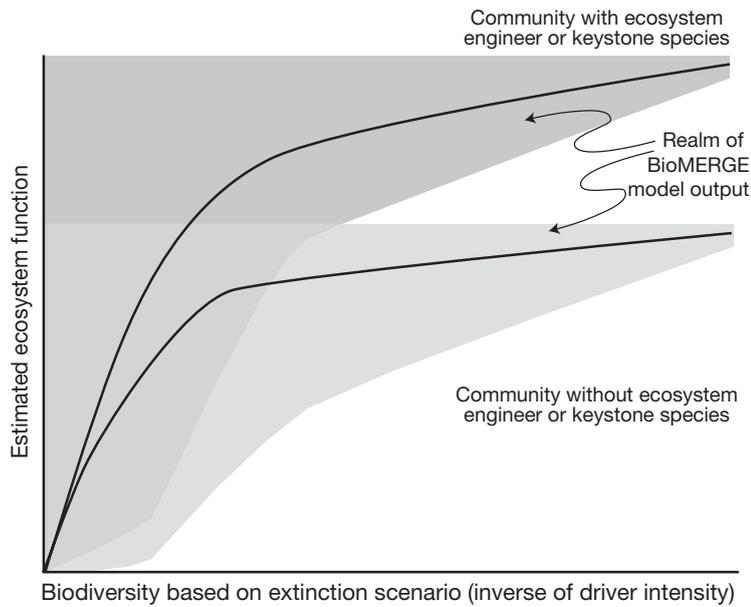


Fig. 2. Example outcomes from a BioMERGE model exploring the ecosystem consequences of biodiversity loss. The x-axis describes biodiversity as quantified by the model, which may be species, functional, landscape, or some other measure of biodiversity. The y-axis describes a single selected function that is modeled by the BioMERGE framework. The lines represent the central tendencies of the model output. Model output would reflect multiple iterations in which maximum diversity is driven to lower levels by incremental changes in extinction driver intensity. The higher the intensity, the lower the biodiversity; hence, the x-axis also represents the inverse of driver intensity. If there are ecosystem engineers or keystone species the presence of which dramatically alters ecosystem functioning, then multiple curves are possible. Here, only 2 possible curves are shown, each surrounded by gray areas indicating the range of possible values. This range may be considered the inverse of biological insurance as larger areas imply greater uncertainty with respect to biodiversity loss

for ecosystem functioning for any simulated community, and the scatter of points around any given level of biodiversity provides an estimate of the variability (instability) or biological insurance (inverse of the spread) associated with a level of biodiversity. As the study of Solan et al. (2004) revealed, it is possible that some species can have such dramatic impacts on ecosystem functioning and that several curves are likely. Such multiple curves would indicate the possible existence of ecosystem engineers, keystone species, or other species with distinct, strong impacts on ecosystems.

In reality, ecosystem functioning is more than just the sum of biomass  $\times$  function for each unit of diversity. Biotic interactions (e.g. competition, predation, disease) are incredibly important in governing how populations will fluctuate, which, in turn, determines compensatory growth and system stability (McNaughton 1977, Grover & Loreau 1996, Yachi & Loreau 1999, McCann 2000, Hughes et al. 2002, Loreau et al. 2002).

Niche partitioning, redundancy, and complementarity are also very important to separate out selection and complementarity effects (Hooper 1998, Naeem 1998, Duffy et al. 2001, Emmerson et al. 2001, Loreau & Hector 2001, Pfisterer & Schmid 2002). But to tackle such dimensions requires obtaining relative growth rates, interaction coefficients (strengths and directions), niche breadth, carrying capacities, and much more—all well-developed fields in ecology, but generally never known to any degree of sufficiency for ecosystems to relate biodiversity to ecosystem function at large scales. The BioMERGE framework motivates the necessary synthesis and unification of many existing ecological disciplines (i.e. population, community, macro-, ecosystem, biogeographical, physiological, and functional ecology) to address BEF issues by observational means. The end result may be fairly complex models of ecosystems, but in the same way that climate modelers have not been dissuaded by the complexity necessary to address global warming in climate models and contend with the uncertainties that surround such approaches (e.g. Murphy et al. 2004), ecologists should not be dissuaded from developing complex models. Meeting the challenge is especially important for marine systems in which biotic changes due to anthropogenic influences are widespread and large scale (e.g. Roemmich & McGowan 1995, Kleypas et al. 1999, Sanford 1999, Jackson et al. 2001, Baum et al. 2003, Abram et al. 2004, Coleman et al. 2004, Hutchings & Reynolds 2004, e.g. Richardson & Schoeman 2004, Duraiappah & Naeem 2005).

## CONCLUSIONS

Scaling up the findings of ecological research to larger and longer scales has been a challenge to mathematical and experimental ecology since its beginning (e.g. Levin et al. 1997, Gardner et al. 2001), and BEF is no exception (Naeem 2001, Bengtsson et al. 2002). Experimental approaches will always be limited in size, replication, and duration, and theory will always employ simplifying assumptions. Principles learned from such approaches, however, in combination with observational work, can be combined in BioMERGE-type models that will provide insights into the ecosystem consequences of biodiversity loss both in terrestrial (Emmerson et al. 2001, Stachowicz et al. 2002, Solan et al. 2004) and marine systems.

Given the urgency of many marine conservation and management issues concerning biodiversity (Roberts & Hawkins 1999), we should not shy away from providing scientific insights to managers and policy makers. The range of options spans using little more than expert opinion (e.g. Sala et al. 2000) to data-rich models (Solan et al. 2004). The more work done in this area, the stronger the case, the more we can identify general principles, and the more precise we can be in our recommendations. One thing that is certain is that if we do nothing, then the options to sustainably manage, protect, or restore degraded marine ecosystems and the services they provide will continue to be dominated by species- or ecosystem-oriented approaches although the proper approach is to integrate both.

*Acknowledgements.* I thank M. Solan, B. Schmid, S. F. Tjossem, and 2 anonymous reviewers for critically evaluating the manuscript and all members of the BioMERGE network for the development of the framework reviewed in this paper. BioMERGE is supported by NSF DEB 0435178.

#### LITERATURE CITED

- Abram NJ, Gagan MK, McCulloch MT, Chappell J, Hantoro WS (2004) Coral reef death during the 1997 Indian Ocean Dipole linked to Indonesian wildfires. *Science* 301: 952–955
- Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382
- Balmford A, Bruner A, Cooper P, Costanza R and 15 others (2002) Economic reasons for conserving wild nature. *Science* 297:950–953
- Balmford A, Gravestock P, Hockley N, McClean CJ, Roberts CM (2004) The worldwide costs of marine protected areas. *Proc Natl Acad Sci USA* 101:9694–9697
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299:389–392
- Belgrano A, Allen AP, Enquist BJ, Gillooly JF (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecol Lett* 5:611–613
- Bengtsson J, Engelhardt K, Giller P, Hobbie S, Lawrence D, Levine JM, Vilà M, Wolters V (2002) Slippin' and slidin' between the scales: the scaling components of biodiversity–ecosystem functioning relations. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: syntheses and perspectives*. Oxford University Press, Oxford, p 209–220
- Blackburn TM, Gaston KJ (2003a) Introduction: Why macroecology? In: Blackburn TM, Gaston KJ (eds) *Macroecology: concepts and consequences*. Blackwell Publishing, Malden, MA, p 1–14
- Blackburn TM, Gaston KJ (eds) (2003b) *Macroecology: concepts and consequences*. Blackwell Publishing, Malden, MA
- Browman HI, Stergiou KI (2004) Marine Protected Areas as a central element of ecosystem-based management: defining their location, size and number. *Mar Ecol Prog Ser* 274: 271–272
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, IL
- Callaway JC, Sullivan G, Zedler JB (2003) Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecol Appl* 13:1626–1639
- Coleman FC, Figueira WF, Ueland JS, Crowder LB (2004) The impact of United States recreational fisheries on marine fish populations. *Science* 305:1958–1960
- Covich AP, Austen MC, Barlocher F, Chauvet E and 8 others (2004) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54: 767–775
- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Duffy JE, McDonald SK, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–2434
- Duraiappah AK, Naeem S (2005) *Ecosystems and human well-being: biodiversity synthesis*. World Resources Institute, Washington, DC
- Emmerson MC, Huxhan M (2002) How can marine ecology contribute to the biodiversity–ecosystem functioning debate? In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: syntheses and perspectives*. Oxford University Press, Oxford, p 139–146
- Emmerson MC, Raffaelli DG (2000) Detecting the effects of diversity on measures of ecosystem functioning: experimental design, null models and empirical observations. *Oikos* 91:195–203
- Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli DG (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411:73–77
- Ernst WG (2000) The Earth's place in the solar system. In: Ernst WG (ed) *Earth systems: processes and issues*. Cambridge University Press, Cambridge, p 45–58
- Erwin TL (1982) Tropical forests: their richness in *Coleoptera* and other arthropod species. *Coleopterists Bull* 36:74–75
- Falkowski PG, Rosenthal Y (2001) Biological diversity and resource plunder in the geological record: Casual correlations or causal relationships? *Proc Natl Acad Sci USA* 98: 4290–4292
- Fenchel T (1987) *Ecology of protozoa*. Springer-Verlag, Berlin
- Fenchel T, King GM, Blackburn TH (1998) Bacterial biogeochemistry: the ecophysiology of mineral cycling. Academic Press, San Diego, CA
- Foggo A, Frost MT, Attrill MJ (2003) Abundance–occupancy patterns in British estuarine macroinvertebrates. *Mar Ecol Prog Ser* 265:297–302
- Gardner RH, Kemp M, Kennedy VS, Petersen JE (eds) (2001) *Scaling relations in experimental ecology*. Columbia University Press, New York
- Gaston K (2000) Global patterns in biodiversity. *Nature* 405: 220–227
- Grassle JF, Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am Nat* 139:313–341
- Groombridge B, Jenkins MD (2000) *Global biodiversity: Earth's living resources in the 21st century*. World Conservation Press, Cambridge
- Grover JP, Loreau M (1996) Linking communities and ecosystems: trophic interactions as nutrient cycling pathways. In: Hochberg ME, Clobert J, Barbault R (eds) *Aspects of the genesis and maintenance of biological diversity*. Oxford University Press, Oxford, p 180–193
- Hollowell VC (ed) (2001) *Managing human dominated ecosystems*. Missouri Botanical Garden Press, St. Louis, MO

- Hooper DU (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* 79:704–719
- Hooper DU, Ewel JJ, Hector A, Inchausti P and 10 others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. *Ecol Appl* 15:3–35
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ
- Hubbell SP, Lake JK (2003) The neutral theory of biodiversity and biogeography, and beyond. In: Blackburn TM, Gaston KJ (eds) *Macroecology: concepts and consequences*. Blackwell Publishing, Malden, MA, p 45–63
- Hughes JB, Ives AR, Norberg J (2002) Do species interactions buffer environmental variation (in theory)? In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, p 92–101
- Hutchings JA, Reynolds JD (2004) Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 54:297–309
- Irigoin X, Huisman J, Harris RP (2004) Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429:863–867
- Jackson JBC, Kirby MX, Bergre WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Kasting JF, Siefert JL (2002) Life and the evolution of Earth's atmosphere. *Science* 296:1066–1067
- Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–120
- 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
- Levin SA, Grenfell B, Hastings A, Perelson AS (1997) Mathematical and computational challenges in population biology and ecosystem science. *Science* 275:334–343
- Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419:154–157
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Loreau M, Naeem S, Inchausti P, Bengtsson J and 8 others (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:806–808
- Loreau M, Downing AL, Emmerson MC, Gonzalez A and 5 others (2002) A new look at the relationship between diversity and stability. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, p 79–91
- Lovelock J (1979) *Gaia*. Oxford University Press, Oxford
- Mathez EA, Webster JD (2004) Life and conditions on early Earth. Columbia University Press, New York, p 37–48
- McCann KS (2000) The diversity–stability debate. *Nature* 405:228–233
- McKinney M (1998) On predicting biotic homogenization: species–area patterns in marine biota. *Global Ecol Biogeogr Lett* 7:297–301
- McNaughton SJ (1977) Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am Nat* 111:515–525
- Millennium Ecosystem Assessment (2003) *Ecosystems and human well-being*. Island Press, Washington, DC
- Mittelbach GG, Scheiner SM, Steiner CF (2003) What is the observed relationship between species richness and productivity? Reply. *Ecology* 84:3390–3395
- Murphy JM, Sexton DMH, Barnett DN, Jones GS, Webb MJ, Collins M, Stainforth DA (2004) Quantification of modeling uncertainties in a large ensemble of climate change simulations. *Nature* 430:768–772
- Myers N, Mittermeier RA, Mittermeier CG, De Fonesca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Naeem S (1998) Species redundancy and ecosystem reliability. *Conserv Biol* 12:39–45
- Naeem S (2001) Experimental validity and ecological scale as tools for evaluating research programs. In: Gardner RH, Kemp WM, Kennedy VS, Petersen JE (eds) *Scaling relationships in experimental ecology*. Columbia University Press, New York, p 223–250
- Naeem S (2002a) Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology* 83:2925–2935
- Naeem S (2002b) Functioning of biodiversity. In: Munn T (ed) *The encyclopedia of global environmental change, Vol 2*. John Wiley & Sons, Chichester, p 20–36
- Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol Lett* 6:567–579
- Naeem S, Byers D, Tjossem SF, Bristow C, Li S (1999) Plant neighborhood diversity and production. *Ecoscience* 6:355–365
- Naeem S, Chapin FSI, Costanza R, Ehrlich P and 8 others (2000) Biodiversity and ecosystem functioning. Report No. 4, Ecological Society of America, Washington, DC
- Naeem S, Colwell R, Dias S, Hughes J and 6 others (in press) Predicting the ecosystem consequences of biodiversity loss at the landscape level. Island Press, Washington, DC
- Naylor RL, Goldburg RJ, Mooney H, BevrIDGE M and 6 others (1998) Nature's subsidies to shrimp and salmon farming. *Science* 282:883–884
- Nee S (2003) The unified neutral phenomenological theory of biodiversity. In: Blackburn TM, Gaston KJ (eds) *Macroecology: concepts and consequences*. Blackwell Publishing, Malden, MA, p 31–42
- Nee S (2004) More than meets the eye. *Nature* 429:804–805
- Pace NR (1997) A molecular view of microbial diversity and the biosphere. *Science* 276:734–740
- Patterson BD, Atmar W (1986) Nested sub-sets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc* 28:65–82
- Petchey OL, Gaston K (2002) Functional diversity (FD), species richness and community composition. *Ecol Lett* 5:402–411
- Pfisterer AB, Schmid B (2002) Diversity-dependent productivity can decrease the stability of ecosystem functioning. *Nature* 416:85–86
- Preston FW (1962) The canonical distribution of commonness and rarity. *Ecology* 43:185–215 & 410–432
- Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proc R Soc Lond B* 267:1947–1952
- Purvis A, Orme CDL, Dolphin K (2003) Why are most species small-bodied? A phylogenetic view. In: Blackburn TM, Gaston KJ (eds) *Macroecology: concepts and consequences*. Blackwell Publishing, Malden, MA, p 155–173
- Reekie EG, Bazzaz FA (1987a) Reproductive effort in plants. 1. Carbon allocation to reproduction. *Am Nat* 129:876–896
- Reekie EG, Bazzaz FA (1987b) Reproductive effort in plants.

2. Does carbon reflect the allocation of other resources? *Am Nat* 129:897–906
- Reekie EG, Bazzaz FA (1987c) Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *Am Nat* 129:907–919
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–1612
- Roberts CM, Hawkins JP (1999) Extinction risk in the sea. *Trends Ecol Evol* 14:241–246
- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L and 17 others (2004) Effectiveness of the global protected area network in representing species diversity. *Nature* 428: 640–643
- Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. *Science* 267:1324–1326
- Rothman DH (2001) Global biodiversity and the ancient carbon cycle. *Proc Natl Acad Sci USA* 98:4305–4310
- Sala OE, Stuart SF III, Armesto JJ, Berlow E and 15 others (2000) Biodiversity: global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–2097
- Schlapfer F, Pfisterer AB, Schmid B (2005) Non-random species extinction and plant production: implications for ecosystem functioning. *J Appl Ecol* 42:13–24
- Schlesinger WH (1997a) Introduction. In: *Biogeochemistry*, 2nd edn. Academic Press, San Diego, CA, p 3–14
- Schlesinger WH (1997b) *Biogeochemistry*, 2nd edn. Academic Press, San Diego, CA
- Schulze ED, Mooney HA (eds) (1993) *Biodiversity and ecosystem function*. Springer-Verlag, New York
- Smil V (2002) *The Earth's biosphere: evolution, dynamics, and change*. MIT Press, Cambridge, MA
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function. Reconciling pattern and process. *Ecology* 83: 2575–2590
- Statzner B, Moss B (2004) Linking ecological function, biodiversity and habitat: a mini-review focusing on older ecological literature. *Basic Appl Ecol* 5:97–106
- Steinberg CEW, Geller W (1993) Biodiversity and interactions within pelagic nutrient cycling and productivity. In: Schulze ED (ed) *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, p 43–64
- Sugihara G (1980) Minimal community structure: an explanation of species abundance patterns. *Am Nat* 116:770–787
- Tiedje JM (1995) Approaches to the comprehensive evaluation of prokaryote diversity of a habitat. In: Allsopp D, Colwell RR, Hawksworth DL (eds) *Microbial diversity and ecosystem function*. CAB International, Wallingford, p 73–87
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720
- Torsvik V, Øvreås L, Thingstad TF (2002) Prokaryotic diversity—magnitude, dynamics, and controlling factors. *Science* 296:1064–1066
- Venter JC, Remington K, Heidelberg JF, Halpern AL and 19 others (2004) Environmental genome shotgun sequencing of the Sargasso Sea. *Science* 304:66–74
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277: 494–499
- Yachi S, Loreau M (1999) Biodiversity and ecosystem functioning in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci* 96:1463–1468
- Zavaleta ES, Hulvey KB (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306:1175–1177

*Editorial responsibility: Martin Solan (Guest Editor), Newburgh, UK*

*Submitted: December 20, 2004; Accepted: October 21, 2005  
Proofs received from author(s): March 7, 2006*