Chapter 10

Predicting the Ecosystem Consequences of Biodiversity Loss: the Biomerge Framework

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10.1 Biodiversity and Ecosystem Functioning: a Synthesis

10.1.1 Why Biodiversity Matters to Global Change Ecology

Global change ecology has become increasingly concerned with understanding how linkages between changes in biological diversity (henceforth, *biodiversity*) affect ecosystem functioning (Chapin et al. 2000; Loreau et al. 2001; Hooper et al. 2005). By biodiversity we mean, "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." This definition, because it has been adopted by the Convention on Biological Diversity and the Millennium Assessment probably has the broadest subscription in comparison to the many other definitions proposed for biodiversity (Duraiappah and Naeem 2005). It clearly defines biodiversity as more than just species or taxonomic diversity ("variability of living organisms from all sources"). It includes variability in biotic interactions ("ecological complexes") and geography (diversity within and among populations, species, and ecosystems).

The relationship between biodiversity and ecosystem functioning is important in global change ecology for several reasons. First, biodiversity is experiencing unprecedented declines in virtually all ecosystems due predominantly to anthropogenic processes such as the conversion of natural ecosystems to less diverse managed systems (e.g., farms, plantations, aquaculture), biological invasions, enhanced rates of N deposition, habitat fragmentation, and climate change (Ehrlich 1988; Wilson 1988; Soulé 1991; Groombridge 1992; Hawksworth 1995; Heywood 1995; Wilcove et al. 1998; Sala et al. 2000; Balmford et al. 2002; Raven 2002). Several studies have shown that biodiversity loss can significantly lower primary production, which is critical to all other ecosystem functions (e.g., Naeem et al.1994; Tilman et al. 1996; Hector et al. 1999).

Second, biosphere-geosphere feedbacks in Earth System processes are a critical component of climate change biology (Díaz et al. 1993; Mooney et al. 1993; Walker and Steffan 1996; Woodwell 1995; Andreae 2002), thus understanding what roles biodiversity may play in these feedbacks is important given widespread declines in biodiversity. For example, carbon sequestration by terrestrial plants represents an important feedback in climate change, and CO_2 impacts on production are affected by plant species composition and diversity (e.g., Bolker et al. 1995; Zavaleta et al. 2003; Reich et al. 2004).

Third, the Convention on Biological Diversity (CBD), signed and ratified in the early 1990s by the vast majority of the world's nations, declared that biodiversity underpins Earth's ecosystems and that biodiversity conservation is fundamental to achieving environmental sustainability and sustainable development (http://www.biodiv.org/). Establishing a scientific basis for the relationship between biodiversity and ecosystem functioning would facilitate the development and implementation of science-based policy for the CBD to achieve its goals of biodiversity conservation and, ultimately, sustainable development.

An additional consideration of the importance of biodiversity in global change ecology is its relationship to ecosystem services, most of which are governed by ecosystem functions. Ecosystem services are defined as the benefits people obtain from ecosystems (Daily et al. 1997; Costanza et al. 1997; Naeem 2001a). The importance of biodiversity to ecosystem services is highlighted in the Millennium Assessment (MA), a consensus of nearly 1 400 experts from 95 countries, by the following statement:

> Biodiversity represents the foundation of ecosystems that, through the services they provide, affect human well-being. These include provisioning services such as food, water, timber, and fiber; regulating services such as the regulation of climate, floods, disease, wastes, and water quality; cultural services such as recreation, aesthetic enjoyment, and spiritual fulfillment; and supporting services such as soil formation, photosynthesis, and nutrient cycling. The MA considers human well-being to consist of five main components: the basic material needs for a good life, health, good social relations, security, and freedom and choice and action. Human well-being is the result of many factors, many directly or indirectly linked to biodiversity and ecosystem services while others are independent of these.

10.1.2 Linking Change in Biodiversity with Change in Ecosystem Functioning

In spite of the logical inseparability of biodiversity and ecosystem functioning, in that neither exists in the absence of the other, little theoretical or empirical work prior to 1992 had explicitly addressed whether changes in biodiversity could have predictable impacts on ecosystem function. Traditionally, biodiversity was largely considered an epiphenomenon or dependent function of abiotic factors, such as climate, greography, or edaphic factors (Naeem 2002; Naeem et al. 2002). Intercropping studies (e.g., Vandermeer 1989; Vandermeer et al. 2002), the study of keystone species (e.g., Power et al. 1996, and studies of ecosystem engineers (e.g., Jones et al. 1994; Wright et al. 2002), had demonstrated that species could potentially have large impacts on ecosystem function (Statzner and Moss 2004), but these were viewed as local or secondary effects. Over the last decade, however, this view has changed. Theoretical and small-scale (e.g., <10 m^2) experimental studies have introduced the idea that biodiversity can regulate abiotic factors through its control over ecosystem function, although whether these findings apply at larger scales (>1 km^2) typical of natural systems remains unclear (Naeem 2002; Loreau et al. 2002; Hooper et al. 2005).

That biodiversity was seldom linked to ecosystem functioning prior to the 1990s is not surprising in light of the fact that the study of biodiversity and the study of ecosystem functioning have been, and continue to be, largely independent lines of ecological research (McIntosh 1985; Likens 1992; Schulze and Mooney 1993; Grimm 1995; Díaz and Cabido 2001). To link biodiversity with ecosystem functioning, in particular making the latter a dependent function of the former, required a synthesis that would bring together community and ecosystem ecology.

10.1.3 Lessons Learned from Early Debates

Like syntheses in most scientific disciplines (Kuhn 1962), considerable debate surrounded early findings (Naeem et al. 2002). Three important lessons emerged from this debate, arising mostly from sources of confusion. First, the idea that ecosystem function is controlled, at least in part, by biodiversity does not imply that taxonomic or species richness, in and of itself, somehow controls ecosystem function. Biodiversity refers to both taxonomic (e.g., species or genetic) *and* ecological (e.g., life history or functional) diversity over all spatial and temporal scales and of these components, it is functional diversity that matters. Functional diversity refers to the diversity of species traits rather than taxonomic diversity, where traits are those that either govern how a species responds to environmental change or how it effects ecosystem processes. For example, a grassland may have 200 species of herbaceous plant species, but with respect to nitrogen fixation, it may be considered to have only two functional types – legumes (N fixers) and non-legumes (see Chap. 7 and 13). Thus, biodiversity can control ecosystem function when changes in biodiversity involve changes in functional diversity (number and relative abundance of functional types) over space or time (Smith et al. 1997; Hooper and Vitousek 1998; Díaz and Cabido 2001; Lavorel and Garnier 2002; Petchey and Gaston 2002; Naeem and Wright 2003; Symstad and Tilman 2001). Change in taxonomic diversity affects ecosystem functioning only in so much as it correlates with change in functional diversity.

Second, because biodiversity and biomass are often related, in the sense that larger expanses of ecosystems often contain more individuals and more species than smaller expanses, there is an additional conflation of biodiversity loss with biomass loss. For example, removal of a forest by clear cutting will significantly alter watershed discharge, but it is not the loss of biodiversity *per se* that is responsible for this change in ecosystem function – it is the loss of vegetation, or more simply, the loss of biomass. If, however, one replaced a functionally diverse forest with an equivalent biomass of a monoculture plantation and watershed discharge was affected, then in this case, the change in biodiversity led to the change in ecosystem function.

Third, the associations between biodiversity and ecosystem functioning derived from large-scale observational studies are often different both in magnitude and sign from those derived from small-scale experimental studies. Many of the debates have concerned seeming conflicts between findings from within-ecosystem experiments and those of cross-ecosystem correlational studies (e.g., Levine 2000; Naeem 2001b). Such contrasts in findings are not surprising given that larger scale studies include variation in ecosystem function due not only to variation in biodiversity, but variation in many other factors, such as climate, nutrient supply rate, and history, that are held constant in experimental systems (Troumbis et al. 2000; Troumbis and Memtas 2000; Chase and Leibold 2002; Fridley 2003). The lesson learned is that if one wants to predict ecosystem response to change in biodiversity across large scales, one has to understand how other factors (controlled in experiments and uncontrolled in observational studies) affect both biodiversity and ecosystem function.

These sources of confusion that fueled the early debates have since become active research areas in the study of how biodiversity and ecosystem functioning are linked. Indeed, the framework we discuss below is an outcome of research in theses areas.

10.1.4 What We Have Learned about the Relationship between Biodiversity and Ecosystem Function

Although the history of research on biodiversity and ecosystem functioning (BEF) is one of point-counterpoint debate, a consensus has emerged (Loreau and Hector 2001) and syntheses and directions for future research identified (Loreau et al. 2002; Hooper et al. 2005). Numerous experiments and much theory have accumulated over the last decade and BEF research continues to be one of the most active areas in ecological research. Space does not permit reviewing this enormous literature, but much of it is covered in several reviews (Chapin III et al. 2000; Loreau et al. 2002; Hooper et al. 2005). Briefely, however, BEF research has demonstrated that

- change in biodiversity has significantly altered ecosystem functioning and the services it provides in many well-documented studies,
- species' functional characteristics strongly influence ecosystem functioning,
- the mechanisms and pathways by which biodiversity loss impacts ecosystem functioning vary among systems,
- species vary in their impact on ecosystem functioning from slight to relatively subtantial,
- and, whereas a small number of species may provide levels of ecosystem functioning similar to species-rich communities, more species are needed to insure continued provisioning of ecosystem function over longer periods of time (Hoppe et al. 2005).

For this chapter, it is important to note that while theory (e.g., Hughes et al. 2002; Loreau 2004; Petchey et al. 2004), grassland experiments (e.g., Fridley 2003; Foster and Dickson 2004; Zavaleta and Hulvey 2004; Roscher et al. 2005; Spehn et al. 2005), microcosm research (e.g., Fox 2004; Heemsbergen et al. 2004; Wohl et al. 2004), and marine/aquatic studies (e.g., Duffy et al. 2001; Emmerson et al. 2001; Stachowicz et al. 2002; Solan et al. 2004), have all contributed significantly to advancing the frontiers of BEF research, only a few have considered the implications of applying BEF to the scales typical of most ecosystems (e.g., Emmerson and Raffaelli 2000; Troumbis and Memtas 2000; Bai et al. 2004; Cardinale et al. 2004; Statzner and Moss 2004). The purpose of this chapter is to establish a framework by which BEF research can expand to larger scale investigations.

10.1.5 The Scientific Framework for Linking Biodiversity and Ecosystem Functioning

The initial BEF framework was developed over a decade ago, but has stimulated a tremendous amount of research. Vitousek and Hooper (1993) developed a graphical framework for linking biodiversity and ecosystem functioning that captured the heart of the synthesis, but was insufficiently detailed to avoid the controversy that would eventually emerge. They plotted biodiversity on the *x*-axis and ecosystem functioning on the *y*-axis then postulated several possible relationships between the two. As simple as this might seem, it represented a radical departure from traditional ecology. By plotting biodiversity on the *x*-axis, it portrayed biodiversity as the *independent* factor while portraying ecosystem functioning as the *dependent* factor, traditionally the *y*-axis. Almost always, in ecology, one plots biodiversity as a dependent function, usually of abiotic factors such as temperature, precipitation, or productivity (e.g., Gaston 2000). A wide variety of relationships between biodiversity and ecosystem functioning have been proposed in accordance with the Vitousek-Hooper framework (Martinez 1996; Schläpfer and Schmid 1999; Naeem 2002).

Graphical approaches such as the Vitousek-Hooper framework are heuristic devices that motivate and facilitate scientific discourse, but adapting such frameworks to the real world is seldom straightforward (Naeem et al. 2002). In particular, the most significant challenge to adapting abstract frameworks to the real world requires dealing with scale (Naeem 2001b; Symstad et al. 2003). Both biodiversity and ecosystem functioning are complex, scale-dependent terms that are not readily quantified by single variables and therefore not readily related to each other by simple bivariate plots. "Ecosystem function" refers to a virtually limitless set of processes associated with ecosystems ranging from global (e.g., global sequestration of atmospheric CO_2) to local processes (e.g., grassland productivity). Likewise, "biodiversity" refers to an equally limitless set of ecological measures that quantify biodiversity from large-scale (e.g., biome) to small-scale (e.g., genotypic variability within a population for the expression of a single gene) properties of ecological systems. Consider Fig. 10.1 in which the scales of biodiversity and ecosystem functioning are presented as a bivariate plot. Plotting ecosystem function against biodiversity across such a plot would yield an enigmatic figure that is almost impossible to interpret mechanistically even though conceptually it captures the central idea.

When experimental tests of the Vitousek-Hooper framework were conducted, in reality, only a small region of the bivariate plot shown in Fig. 10.1 was explored, but interpretations of these studies were seldom constrained to the region explored. Much of this experimental research crossed out "biodiversity" and wrote in "plant species richness," crossed out "ecosystem functioning" and wrote in "primary production," and then plotted data collected from combinatorial experiments whose units (pots and plots) were seldom more than a few meters on a side and seldom conducted for more than one or a few years (Naeem et al. 1994; Naeem and Li 1997; Hooper and Vitousek 1997; Tilman et al. 1996; Tilman et al. 1997;

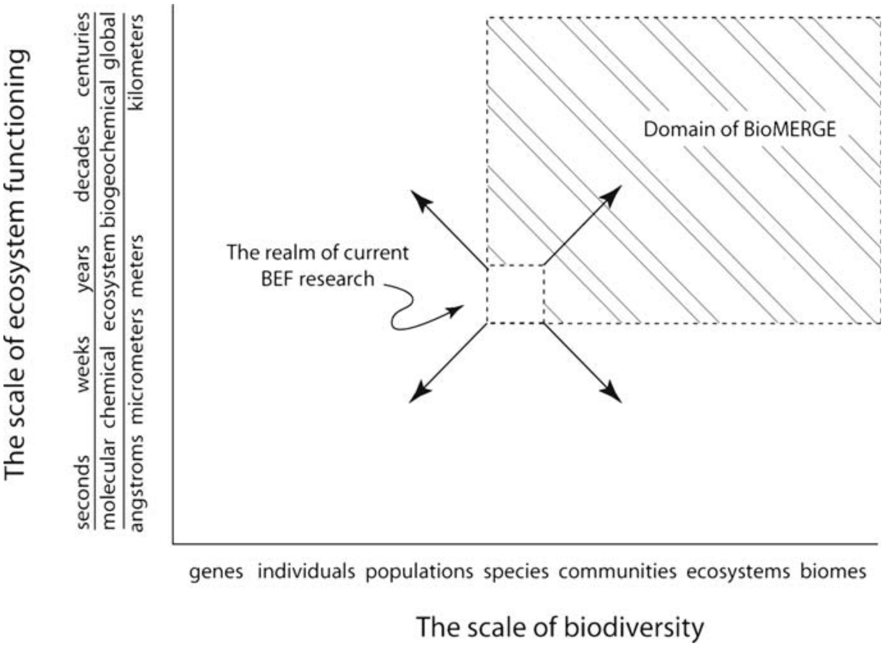

Fig. 10.1.
The realm of current research in Biodiversity and Ecosystem Functioning (BEF) and the realm of BioMERGE. Each *axis* abstractly and approximately represents the scales of biodiversity and ecosystem functioning, illustrating the latter as a dependent function of the former. The *center box* 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). The *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

Wardle et al. 1997; Symstad et al. 1998; Hector et al. 1999; Mulder et al. 1999; Sankaran and McNaughton 1999; Spehn et al. 2000; Symstad 2000; Symstad and Tilman 2001; Engelhardt and Ritchie 2001; Hooper et al. 2002; Petchey et al. 2002; Schmid 2002; Schmid et al. 2002; Fukami and Morin 2003). Microcosm studies (e.g., Naeem and Li 1997; McGrady-Steed and Morin 2000; Petchey et al. 2002; Fukami and Morin 2003) were often conducted for longer periods of time in terms of numbers of generations, but they were still small in spatial scale (small with respect to the typical size of aquatic ecosystems, though in terms of organism size, the spatial scale was probably larger than most experimental studies).

In spite of the limited scope of this research, because a positive, saturating or asymptotic (or linear in a semi-logarithmic plot) relationship between biodiversity and ecosystem functioning was often found (e.g., Naeem et al. 1994; Tilman et al. 1996; Hector et al. 1999), the claim was made that biodiversity enhances ecosystem functioning. This claim ignited a strong debate (Guterman 2000; Kaiser 2000). Even though the findings themselves were not questioned, the mechanisms were unclear, the use of species richness as a proxy for biodiversity and primary production as a proxy for ecosystem functioning seemed questionable, and the findings often appeared to be the inverse of what was known from correlative studies of biodiversity and ecosystem functioning conducted at larger scales (e.g., Wardle et al. 2000). Finally, these early experiments lacked considerations of functional diversity and trophic structure. Although later experiments would examine these issues, the initial lack of treatment of these issues offered only limited applicability of such findings to worlds that were functionally (not just taxonomically) diverse, multitrophic, and much larger in scale.

The new framework we discuss here brings biogeography into the picture, and by so doing, allows for the expansion of BEF research beyond its currently limited domain of small-scale studies to large-scale evaluations of ecosystems and environmental consequences of biodiversity loss (Fig. 10.1). Biogeography, broadly defined, is the study of past and present distributions of species and populations. As such, it encompasses many topics including evolutionary ecology, community assembly, species saturation, species area curves, ecogeographic rules, zonation, endemism, environmental heterogeneity, allometry and scaling rules, historical factors and paleoecology, and much more. In this framework we use the term *biogeography* in a narrow sense to specifically refer to geographic patterns of distribution and abundance, and we use the term macroecology (*sensu* Brown 1995) to refer more specifically to allometry and scaling rules, though the biogeography and macroecology are closely linked (Blackburn and Gaston 2003).

This chapter reviews the most recent conceptual framework for BEF research. The framework we discuss is being developed by a research coordinating network (RCN) whose acronym is BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment). For convenience, we simply refer to this framework as the BioMERGE framework.

It is important to note at the outset that *BioMERGE is not a research agenda*, such as those periodically established by the Ecological Society of America (Lubchenco et al. 1991; Palmer et al. 2004) or by international agencies such as GCTE or DIVERSITAS. Rather, it is a synthetic research framework that develops and evolves through participation by any and all interested individuals.

10.2 The BioMERGE Framework

The BioMERGE framework consists of three sub-frameworks. The first framework is structural, one that links species (taxonomic diversity), trophic groups, and functional diversity with ecosystem functioning. The second is an expansion of the Vitousek-Hooper BEF framework to include biogeographic principles. The third is a research implementation framework that serves as a guide for conducting an effective large-scale BEF research program. These three sub-frameworks reflect a summary of the previous decade of BEF research, identify existing bodies of ecological knowledge that can be brought into the BEF synthesis, and point to needed research and future directions that will enable us to better understand the ecosystem consequences of biodiversity loss.

10.2.1 The BioMERGE Structural Sub-Framework

The structural framework for BioMERGE outlines how species and ecosystems are linked and provides the ecological foundation for the conceptual and empirical frameworks discussed below. This structural framework differs little from previous frameworks and serves only to focus attention on the key elements of BEF research. An ecosystem is considered to be a collection of species representing four trophic groups (autotrophic species, autotrophically-derived species, decomposer, or decomposer-derived species, see Fig. 10.2) that cycle material between organic and inorganic forms. Omnivory or other complex trophic interactions are acknowledged, but left out of the graphic for simplicity.

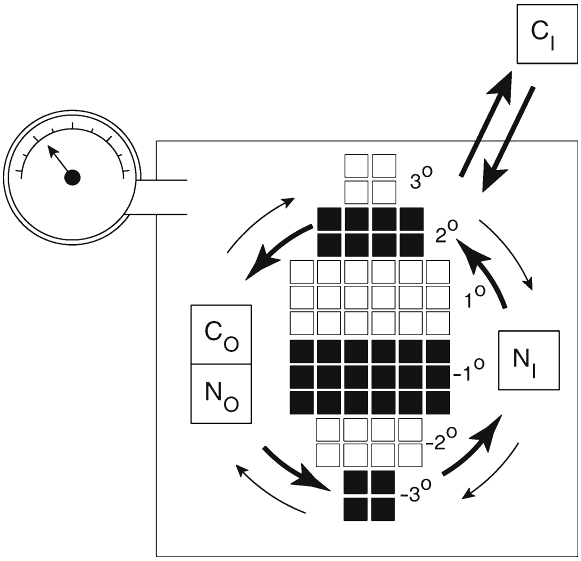

Fig. 10.2. The BioMERGE conceptual framework. Species are represented by *small squares* that are either autotrophs (here limited to photo-autotrophs or 1° producers), and either autotrophically derived heterotrophs (2° and 3° consumers) or microbial decomposers (–1°) or consumers of microbial decomposers (–2° and –3°). The autotrophs draw down inorganic carbon (C_I) (e.g., atmospheric CO_2 for terrestrial plants) and uptake inorganic nutrients to produce organic material that is distributed throughout the trophic groups of species. All contribute through mortality to a pool of dead organic material (C_O and N_O) that is decomposed into its inorganic constituents. There are many other routes (*thinner arrows*), but the overall pattern consists of internal cycling and carbon exchange that tracks energy acquisition through photosynthesis. Ecosystem functioning therefore involves any of the *broad arrows* while biodiversity represents taxonomic diversity, trophic structure, and functional diversity (not shown) within trophic groups

Graphically, this framework is illustrated by portraying an ecosystem as a box within which an assemblage of species with a specific trophic structure resides. Within this box, nutrients are represented as two organic (living species and dead organic matter) and one inorganic pool. The box (ecosystem) draws down and returns inorganic carbon (CO_2) to the atmosphere, but much of the nutrient cycling is considered to be confined to the ecosystem itself. To this system, a meter or measuring device that monitors ecosystem function (e.g., net primary production or total ecosystem respiration) is connected. This framework illustrates BEF research as the study of how ecosystem function, or the attached meter, responds to species loss. Traditional ecosystem ecology would not pay much attention to the species within the box, but would instead focus primarily on how changes in cycles and fluxes affected the meter, whereas traditional community ecology would pay little attention to the cycles, fluxes, or the meter associated with the system.

The main points of this structural framework are,

- it draws significant attention to the decomposer community, which is frequently ignored,
- traditionally defined trophic groups, such as primary consumers, herbivores, and carnivores, are not considered functional groups,
- ecosystem function refers only to organic-inorganic matter transformation (i.e., not invasion resistance or aesthetic properties).

10.2.2 The BioMERGE BEF Sub-Framework: an Expansion of the Vitousek-Hooper Framework

The Vitousek-Hooper BEF framework presented a number of alternative trajectories that ecosystem function could trace (e.g., linear, asymptotic, or logistic) as biodiversity declines. In contrast, the BioMERGE framework assumes an asymptotic trajectory that represents an average for a range of possible trajectories that ecosystem function could follow as biodiversity declines (Fig. 10.3). The asymptotic curve reflects the perspective that the loss of species does not, on average, dramatically impact ecosystem function until functional (*F*) and taxonomic diversity (*S*) are equal (i.e., species are singular rather

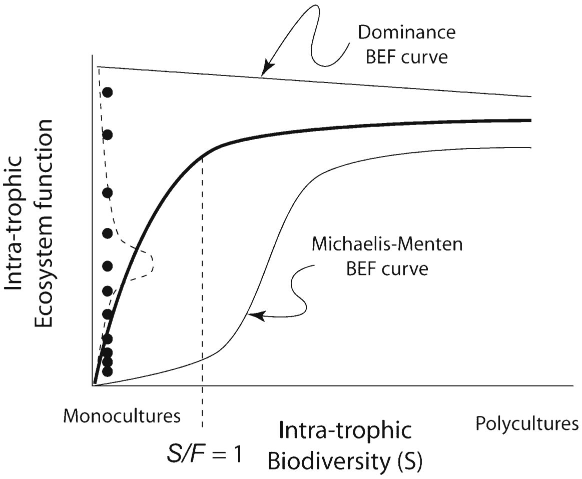

Fig. 10.3. The BioMERGE expansion of the Vitousek and Hooper framework. At the monoculture end, the majority of species (each represented as a *closed circle*) exhibit small levels of functioning whereas a few exhibit high levels following a general log-normal like pattern. The x-axis plots biodiversity as intra-trophic species richness (S), such as species richness of plants or species richness of herbivores. The maximum species richness (*right-most portion of curve*) represents an ecosystem in which species richness is stable and high. The asymptotic, *solid line*, represents the general BEF relationship based on the assumption that a significant portion of the species in an ecosystem are redundant with respect to specific ecosystem functions. That is, once at least one species is present per functional group ($S/F = 1$, where $F =$ the number of functional groups), additional species have significantly smaller impacts on ecosystem functioning. The *dashed lines* indicate boundaries of combinatorial variants in species composition. The lower boundary is based on a Michaelis-Menten like model of ecosystem function, which assumes that biodiversity acts like a catalyst for biogeochemical processes. The upper boundary is based on a dominance model in which no species can achieve higher ecosystem functioning than that of the species with the dominant level of functioning among the monocultures. The *line* is illustrated as a slightly negative slope to allow for the fact that in multi-species assemblages, at least some of the resources are controlled by other species, no matter how rare they are. These boundaries represent the range of possible expressions of ecosystem functioning for a specific level of species richness. Note that many alternative boundaries are possible

than redundant)(Naeem 1998). The "elbow" in the curve therefore occurs when $S/F = 1$.

The rationale for using a range of trajectories rather than a single trajectory is to acknowledge the fact that different sequences of biodiversity loss will result in different patterns of change in ecosystem functioning. A community will trace a specific path through the diversity-by-function bivariate space for a specific sequence of biodiversity loss, but there are many different paths possible – that is, history, or the pattern of disassembly (or assembly) matters (Fukami and Morin 2003).

The multiplicity of pathways a trajectory can take in biodiversity-function space therefore describes two distinct, but important properties of biodiversity change. The first property is the combinatorial nature of change. A step towards decreasing (or increasing) biodiversity implies an enormous number of possible changes in community structure and composition. The second property is temporal contingency or the historical component of disassembly (or assembly). One can get to any community composition or structure from another by an enormous number of possible pathways and how one gets there affects ecosystem function. Consider, for example, that a BEF experiment that constructs replicate communities of 1, 8, and 16 species to determine the relationship between biodiversity and ecosystem function, there are 26 292 possible species combinations between a 16 species community and an 8 species community and 26 316 between an 8 species community and a monoculture. Thus, the problems are not simply the inability to replicate all 8 species communities, of which there are 12 870 different kinds, but the inability to know how the ecosystem functioning observed for 8 species communities might have been affected if they were the result of a staggering number of possible disassembly (or assembly) pathways. Obviously, for practical reasons, unless the community itself is very small (<10 spp.), experimental studies can only explore such an enormous number of possible communities in a very limited way.

The BioMERGE framework also considers that among the possible single species (or monoculture) treatments only a few species exhibit high levels of ecosystem function while the rest show lower levels (Fig. 10.3). That is, species with higher abundance (in terms of biomass) are assumed to make larger contributions to ecosystem functioning. This portion of the framework derives from the common, lognormal-like pattern of distribution and abundance observed at the large spatial scales more appropriate for communities than what has been typically employed in experimental research (Preston 1962; May 1975; Hughes 1986; Adler 2004). While debate continues concerning whether the canonical lognormal (Preston 1962), sequential breakage (Sugihara 1980), neutral (Bell 2000; Hubbell 2001) or other models best explain biogeographical patterns in relative abundance at larger scales, the fact remains that lognormal-like abundance patterns are common. An important part of this exercise, which we discuss below, is to use species traits to derive relative abundance. It is at this point that biogeography, in the form of incorporating patterns of commonness and rarity, enters the BioMERGE framework. There are many other aspects of biogeography that could be included, but they are beyond the scope of our chapter.

Using a lognormal-like distribution of abundance to describe the distribution of monoculture ecosystem functions leads to the null expectation that only a few species will dominate ecosystem function while many others (the rare species) will make lesser contributions. For example, in the case of plants, the null expectation would be that dominant species in polyculture will be the most productive species in monoculture and rare species in polyculture would have the smallest abundance as monocultures. In the absence of experimentation, of course, one cannot know for certain if a rare species in polyculture is rare because of suppression by competitive dominants, but could be quite abundant if released from suppression by extinction of the dominants. For example, while it is difficult to imagine that a rare orchid in a tropical rainforest would completely replace the biomass of the rainforest if it were the only species left, it is less clear whether any one of 900 species of trees in an Amazonian rainforest would replace the bulk of the biomass of that forest in the absence of the other 899.

The issues surrounding dominance, relative growth rates, and the relationship between monoculture and polyculture production are many and complex and have been a central part of the debates surrounding BEF literature (Garnier et al. 1997; Hodgson et al. 1998; Lepš et al. 2001; Loreau and Hector 2001; Adler and Bradford 2002; Schmid 2002). We will not review these issues here, but they do point to the need for a contemporary BEF framework to explicitly include dominance.

The main points of this expanded Vitousek-Hooper BEF framework are,

- an emphasis on a *range* of possible pathways ecosystem function can take in the face of biodiversity loss rather than a single pathway
- the inclusion of both functional and taxonomic diversity reflected by an average asymptotic trajectory, with the asymptote occurring where ecological redundancy is lost
- dominance (commonness and rarity) is integrated into the framework by the assumption of a lognormal-like distribution of function among the monocultures

Like previous BEF research, this framework assumes that environmental influences over community composition and structure (e.g., gradients, frequency of disturbance, seasonality, and so forth) are constant.

10.2.3 The BioMERGE Research Implementation Sub-Framework

The third BioMERGE sub-framework is one in which we have outlined the necessary steps in an evaluation of the ecosystem consequences of biodiversity loss at scales much larger than experimental work generally encompasses. There are three steps. First, establish an operational biota using what is known to set the stage and using ecological principles to estimate what is unknown (i.e., fill in the missing species, their abundance, and their function). Second, establish diversity-function transition matrices for estimating changes in ecosystem function given changes in diversity. Third, select an extinction scenario to determine the realm of possible expressions of ecosystem function that could occur during the course of biodiversity loss. These steps are detailed below.

Step 1: Establish an Operational Biota

Virtually no biota for any ecosystem is fully known nor is likely to be known in the near future if for no other reason than the fact that microbial diversity remains, in spite of many advances in molecular methods, still impossible to determine fully (Øvreås 2000; Torsvik et al. 2002). Given a location on Earth, however, one can establish an *operational* biota, or a biota derived inventories, surveys, and from ecological principles such as biogeographic theories of relative abundance solely for the purposes of BEF analyses. Like climate modeling to understand ecosystem or Earth System responses to elevated CO_2, understanding the range of responses of ecosystems or Earth Systems to biodiversity loss provides valuable insights into the potential consequences of such change. We propose several steps.

Step 1.1. Estimate species richness for major taxa in the community. Global patterns in biodiversity are not random so, at least in principle, there are some predictable elements for species richness and relative abundance given the geographical position of the ecosystem. For example, even in the absence of taxonomic information, such as floral and faunal surveys, we can estimate species richness for various taxa (plants and vertebrates) using the environmental correlates of species richness such as potential evapotranspiration, elevation, latitude, and so forth). This information provides an approximate magnitude for the biodiversity axis on the BEF curve.

Step 1.2. Establish relative abundance. This step requires employing a lognormal-like distribution, as discussed earlier, to derive the expected relative abundance for the number of species in the ecosystems. For example, to derive the relative abundance of an ecosystem containing S species (N_i, where N equals the maximum number of individuals of the i^{th} species supported by the ecosystem) we draw S numbers from a log normal distribution with its shape determining coefficients (mean and variance) based on what is known for the region, what is known from similar regions, or from the estimated S from step 1.1.

To derive the relative biomass of species based on abundance we could use the allometric scaling formula,

$$M_i = 9\,191\, N_i^{-1.341}$$

(Enquist et al. 1998), where M_i is the biomass and N_i the density of the i^{th} species. This is not necessarily a universal law, but it is a strong, empirically robust relationship that can be used to approximate relative biomass.

While use of such methods has long been a tradition in ecology (Horn 2004; Statzner and Moss 2004), they are not without its controversies (e.g., Cyr and Walker

2004; Li et al. 2004; Marquet et al. 2004; Tilman et al. 2004). For example, allometric coefficients from the metabolic theory of ecology (MTE) (Brown et al. 2004), such as that used for M_i above, are often derived across enormous taxonomic (e.g., cyanobacteria to giant redwood trees), spatial (across biomes), and temporal scales (data collected over decades). Not surprisingly, the predictive power of scaling rules based on MTE declines rapidly as one reduces the taxonomic, spatial, and temporal scales of investigation. Indeed, they may be practically useless for predicting function for a small system typical for most ecological research (Tilman et al. 2004). The BioMERGE approach is at an intermediate scale – providing predictions at the ecosystem level for multitrophic communities over moderate time scales – thus such caution in applying MTE is appropriate.

Step 1.3. Establish species relationships to ecosystem functioning. Step 1.1 and 1.2 provide species richness and relative abundances, but response- and effect-functional traits (*sensu* Lavorel and Garnier 2002) are needed to convert changes in the estimated biota to changes in ecosystem functioning. Response traits are species traits that govern ecosystem response to environmental change (e.g., drought tolerance traits), whereas effect traits are traits that govern change in ecosystem function as a consequence of change in species abundance or metabolic activities (e.g., hosting symbiotic N-fixing prokaryotes). The study of functional traits and functional diversity is a rapidly growing field (Smith et al. 1997; Hooper and Vitousek 1998; Díaz and Cabido 2001; Symstad and Tilman 2001; Lavorel and Garnier 2002; Petchey and Gaston 2002; Naeem and Wright 2003), but acquisition of this information is still difficult. Even in the absence of any information, an extensive and rapidly growing list of ecological patterns may be usable for providing, at least to a first approximation, trait information for estimating BEF relationships. For example, leaf, stem, and root biomass are strongly correlated with one another, often with regression r^2 values >0.80 (Enquist and Niklas 2002). This means one can estimate biomass allocations for species even if they have not been determined empirically.

Another example of the utility of allometric traits comes from Wright et al.(2004) who found that leaf mass per area, photosynthetic assimilation rates, leaf nitrogen, leaf phosphorus, dark respiration rate, and leaf lifespan all showed strong patterns of associations for plants from an enormous range of habitats covering most of the range of conditions experienced in terrestrial ecosystems. Once again, even if the only information available is from herbarium sheets, one might be able to estimate important plant traits such as those studied by Wright et al. (2004).

One final example is the estimation of biomass production (primary or secondary) from growth rates using the following allometric scaling formula:

$$G_i = M_i^{0.763}$$

(Niklas and Enquist 2002), where G is the growth rate of the i^{th} species in kg dry matter yr^{-1}. There are many other examples for which physiological or functional traits of species may be estimated from density or biomass data.

While these examples are illustrative, we repeat a caution we raised earlier. The scales over which scaling coefficients are derived should match the scales over which predictions are being made. If they do not, then prediction errors associated with such mismatches (e.g., Tilman et al. 2004) should be stated.

Step 1.4. Establish patterns for trophic structure. Again, for many ecosystems, trophic structure is unlikely to be known, but even so, some efforts can be taken to include this important aspect of an ecosystem's biota. Given autotrophic biomass, one can use empirically derived relationships between the biomasses of different trophic groups or, in the absence of any empirical information, use approximate efficiencies of energy transfer across trophic groups. In many ecosystems, for example, carnivore diversity and even abundance are likely to be known, and Carbone and Gittleman (2002) have shown that about 10 000 kg of prey supports about 90 kg of a given species of carnivore for a wide range of species. The purpose of this step is to determine how much autotrophic biomass is being consumed by herbivores and how much herbivores are regulated by carnivores, an important aspect of ecosystems studied since the 1960s (e.g., Hairston et al. 1960; Polis and Strong 1996).

Below-ground food webs are much tougher to deal with, especially microbes, which may represent the dominant biomass and diversity in many ecosystems (Torsvik et al. 2002). Some studies argue that soil organisms occur in functionally redundant assemblages (Andren et al. 1995; Beare et al. 1995; Liiri et al. 2002), while others argue that redundancy may not be prevalent in stressed systems (e.g., Freckman and Virginia 1997) or in microbial communities (Cavigelli and Robertson 2000). Experimental studies argue for idiosyncratic responses or no response to biodiversity loss in soil communities (Mikola and Setälä 1998) while studies of mycorrhizal fungi argue the opposite (Van der Heijden et al. 1998). The linkages between plant diversity and soil communities and processes are also complex (Setälä and Huhta 1991; Harte and Kinzig 1993; Wardle and Nicholson 1996; De Mazancourt et al. 1998; Bardgett and Shine 1999; Naeem et al. 2000; Mikola et al. 2000; Spehn et al. 2000; Joffre and Ågren 2001; Mikola et al. 2001; Stephan et al. 2001; Mulder et al. 2003; Wardle et al. 2004). In the BioMERGE framework, we assume that the linkage is positive – that soil communities positively affect plants by mineralizing nutrients and that their diversity-function relationships follow the same pattern for other trophic levels (i.e., a positive, asymptotic BEF curve). This is an untested assumption with important consequences and requires considerable caution in interpreting results. One can relax this assumption by using several different BEF curves, but perhaps the most important point to make here is the need to find out if biodiversity in other trophic groups follows patterns similar to what has been observed for plants.

Step 2: Establish Diversity-Function Transition Matrices

A common approach to relating species to ecosystem functioning is to classify species into functional groups, but the wide variety and somewhat eclectic classification schemes make them difficult to use in BEF research (Lavorel and Garnier 2002; Naeem and Wright 2003). Rather than using functional groups, we propose directly using the functional traits of species that are the basis for forming functional groups in the first place (Lavorel and Garnier 2002; Naeem and Wright 2003).

Every organism possesses traits that characterize its response to environmental change and its effect on ecosystem processes. For example, in the face of a drought, plants with traits such as tap roots, persistent dormant seeds, thick cuticles, and greater water-use efficiency are more likely to persist than species that lack these traits. With respect to nitrogen cycling, plants with traits that facilitate microbial fixation of atmospheric nitrogen, either by harboring *Rhizobia* in nodules or supplying carbon to N-fixing bacteria in soils, impact soil N and N cycling in a variety of ways. If legumes lacked drought-tolerant traits in an ecosystem, then, based on response-traits, we could predict that a drought might negatively impact net N fixation.

To translate changes in biodiversity to changes in ecosystem functioning at large spatial scales requires four steps, each of which is illustrated in Fig. 10.4. First, a matrix of environmental variables and a matrix of species' abundances is constructed that reflects conditions prior to the application of a driver. Second, formulae are derived for adjusting each species' density or biomass according to its response functional trait. Third, using the effect functional traits, changes in ecosystem functioning are derived. Fourth, each trophic group is treated separately and the influence of one trophic group upon another is applied (see discussion above). These trophically adjusted, post-biotic-change abundances are then used to estimate what the resulting impacts on ecosystem function would be. Steps 2–4 yield the post biotic-change environmental matrix.

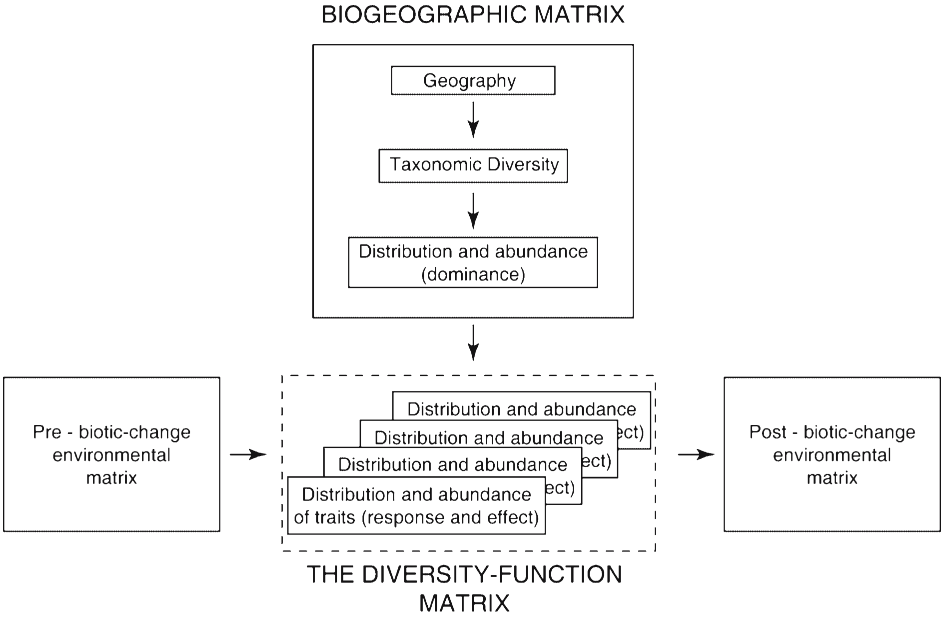

Fig. 10.4. The BioMERGE BEF implementation framework. BioMERGE develops methods of expanding from small-scale BEF research to landscape level predictions of the ecosystem consequences of changes in biodiversity. There are four basic steps; *(1)* designation or construction of a biota, *(2)* development of diversity-function transformation matrices, *(3)* application of driver scenarios for biodiversity change (most often local-extinction scenarios), and *(4)* estimation of the post-driver consequences of the selected driver(s). Constructing a biota (*top most box*) consists of using biodiversity information (i.e., species richness) developed for specific geographic locations. If distribution and abundance patterns (i.e., dominance patterns) are unavailable, then biogeographic principles are used to estimate likely patterns of distribution and abundance. Under the assumption that dominance patterns apply to all trophic levels, diversity-function matrices are developed (*boxes within dashed box on bottom*). These matrices consist of response- and effect-functional trait transformation matrices developed for each trophic group. The right most-box consists of the driver selected for investigation of ecosystem response to biodiversity change (e.g., drought, fire, increasing habitat fragmentation, elevated levels of N deposition, etc.) while the right-most box consists of the predictions for the outcome of the driver applied to the model system

Step 3: Select a Trait-Based Extinction Scenario for Change in Biodiversity

Once one has the model for converting changes in the environment to changes in ecosystem functioning (Fig. 10.4), one can explore how this model behaves when biodiversity is lost, but one has to chose a scenario for how biodiversity loss will occur. One can choose two routes for exploring biodiversity loss. First, as is done in experimental and theoretical BEF research, one can employ a neutral scenario, a combinatorial approach in which all possible compositions due to all possible sequences of species loss are examined. This neutral approach treats extinction probabilities for all species as a random variable.

The second is to employ trait-based extinction scenarios. By this we mean selecting an extinction driver (e.g., climate change, habitat fragmentation, or invasion) and varying extinction probabilities based on species' traits. For example, if the driver is habitat fragmentation, higher probabilities of extinction might be applied to rare species, species with small range sizes, species with small body size, or species in higher trophic levels. Extinction scenarios (based on expert opinion) were used by Sala et al. (2000) to derive predictions for the future of global biodiversity. This framework both extends and narrows this approach by using field-derived data rather than expert opinion on species' traits and drivers to predict specific changes in biodiversity for specific ecosystems rather than the globe. Note that it is at this point that environmental change, when treated as a driver, is incorporated into the analyses.

The main points of this implementation BEF framework are,

- instead of functional groups, response and effect traits are used
- biodiversity is as an explicit part of the conversion of changes in environmental factors to changes in ecosystem functioning through trait-based extinction scenarios

10.3 Discussion: Towards a Large Scale BEF

Initial work in biodiversity and ecosystem functioning focused on simply demonstrating that changes in biodiversity, however defined by researchers, could, in fact, change ecosystem functioning even if all other conditions were held constant. Confirmation of the hypothesis, formalized by the Vitousek-Hooper framework, was a critical first step in bringing biodiversity into our considerations of global change ecology. The next phase, to go beyond the confirmation of the Vitiousek-Hooper framework to one in which predictive applications of BEF principles can be employed in environmental problem solving, is even more critical. The BioMERGE framework is a suggestion for how to pursue this second phase. It does so by embedding much more ecology into its frameworks. By "more ecology," we mean that the BioMERGE framework

- uses patterns from biogeography (i.e., log-normal like projections) to estimate to estimate relative abundance,
- uses allometric scaling and macroecological principles to ascribe function to species,
- uses material and energy-efficiency transfer rates and trophic dynamics to estimate the influence of trophic structure on ecosystem function
- and uses trait-based extinction scenarios to link environmental change with changes in biodiversity.

Rather than supplying specific predictions of ecosystem response to biodiversity loss, it provides boundaries and central tendencies of ecosystem response to biodiversity loss. It also allows for different scenarios of biodiversity loss.

Like other synthetic frameworks, BioMERGE brings with it both the strengths and the limitations of the individual frameworks it incorporates. BioMERGE follows in the footsteps of many other synthetic frameworks, such as the Vitousek-Hooper framework, ecological stoichiometry (Elser and Sterner 2002), the unified neutral theory of biodiversity and biogeography (Hubbell 2001), the metabolic theory of ecology (Brown et al. 2004), island biogeography (MacArthur and Wilson 1967), each of which have tremendous predictive power, but whose limitations have made them each sources of much controversy. For example, in plant ecology, the continuum concept (Austin 1985) is a synthetic framework that combines autecology and biogeography to predict ecosystem function from biodiversity (Austin 1985, 1999). This framework, however, stands in conflict with frameworks that emphasize biotic interactions and system complexity (e.g., trophic-level dynamics, competition, facilitation and indirect and higher-order interactions) (Austin 1985; Callaway 1997). The inclusion of interactions in empirical work based on the continuum concept, however, is readily achieved (e.g., Garnier et al. 1997; Navas et al. 1999; Groves et al. 2003). The way forward is to embrace more complexity when necessary, but resist it when the gains in predictive power outweigh the costs of the added complexity. The BioMERGE framework goes beyond the continuum concept by the inclusion of intra- and inter-trophic interactions, metabolic theory, and biodiversity and ecosystem functioning, thereby incorporating the strengths of the continuum concept and other frameworks but at the cost of increased complexity.

For the reader, and to be honest, for the authors as well, the BioMERGE frameworks require us to conduct research that seems at first glance to be broad, imprecise, and far afield from traditional ecology. We urge, however, that ecologists not be deterred. Consider that early attempts to model global climate and the global carbon cycle began with equally coarse approximations, but the desire as well as the need to understand global warming led to concerted efforts by researchers to model climate change as best they could. Over time, data, models, and methods improved, and while climate change research is still not a precise science, it provides valuable insights into the potentials for anthropogenic forcing of climate processes to lead to significant and detrimental climate change. Given this history for climate change research, certainly understanding "biodiversity change" warrants equal attention.

The experimental and theoretical BEF research spurred by the growth of global change ecology led to a robust set of results that strongly suggest that within-trophic level changes in diversity are associated with changes in the magnitude and variability of ecosystem processes (Loreau et al. 2002; Loreau and Hector 2001). To be sure, many questions remain unanswered. To what extent are experimental results due to facilitation, niche complementarity, or sampling? Which components of biodiversity (is it functional diversity, the identity of species, or dominance) are the most important in determining the impacts of biodiversity loss? Compared to abiotic controls, do biodiversity controls over ecosystem functions matter? Is stability (low variability in ecosystem function in high diversity treatments) due to insurance (Yachi and Loreau 1999), statistical averaging (Doak et al. 1998), or other causes? These questions are not readily addressable by the small-scale experimental approaches that have typified BEF research, but large-scale experiments are impractical. Perhaps answers to these questions may come using observational studies and the BioMERGE frameworks.

Lessons learned from the controversies surrounding early phases of BEF research warn against indiscriminate employment of the BioMERGE framework. The BioMERGE framework has been partially and successfully employed by Solan et al. (2004) to predict ecosystem function (specifically, biogenic mixing) in a marine (estuarine) ecosystem. Similar studies are under way for North American and European grasslands and New World tropical rainforests. Clearly, BEF is scaling up. Perhaps the next step should be to combine a traditional combinatorial BEF experiment with a BioMERGE study and compare their findings.

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References

Adler PB (2004) Neutral models fail to reproduce observed species-area relationships in Kansas grasslands. Ecology 85:1265–1272

Adler PB, Bradford JB (2002) Compensation: an alternative method for analyzing diversity-productivity experiments. Oikos 96:411–420

Andreae MO (2002) Humanity: Passenger or pilot on Spaceship Earth? In: Global Change Newsletter. International Geosphere Biosphere Program, Stockholm, pp 2–6

Andren O, Bengtsson J, Clarholm M (1995) Biodiversity and species redundancy among litter decomposers. In: Collins HP, Robertson GP, Klug MJ (eds) The significance and regualtion of soil biodiversity. Kluwer Academic Publishers, Amsterdam, Netherlands, pp 141–151

Austin MP (1982) Use of a relative physiological performance value in the prediction of performance in multi species mixtures from monoculture performance. Journal of Ecology 70:559–570

Austin MP (1985) Continuum concept, ordination methods, and niche theory. Annual Review of Ecology, Evolution, snd Systematics 16:39–61

Austin MP (1999) The potential contribution of vegetation ecology to biodiversity research. Ecography 22:465–484

Bai Y, Han X, Wu J, Chen Z, Li L (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181–184

Balmford A, Bruner A, Cooper P, Costanza R, Farber S, Green RE, Jenkins M, Jefferiss P, Jessamy V, Madden J, Munro K, Myers N, Naeem S, Paavola J, Rayment M, Rosendo S Roughgarden J, Trumper K, Turner KR (2002) Economic reasons for conserving wild nature. Science 297:950–953

Bardgett RD, Shine A (1999) Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. Soil Biology and Biochemistry 31:317–321

Beare MH, Coleman DC, Crossley DA, Hendrix PF, Odum EP (1995) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant and Soil 170:5–122

Bell G (2000) The distribution of abundance in neutral communities. American Naturalist 155:606–617

Blackburn TM, Gaston KJ (eds) (2003) Macroecology: Concepts and Consequences. Blackwell Publishing, Malden, Massachusetts

Bolker BM, Pacala SW, Bazzaz FA, Canham CD, Levin SA (1995) Species diversity and ecosystem response to carbon dioxide fertizliation: conclusions form a temperate forest model. Global Change Biology 1:373–381

Brown JH (1995) Macroecology. University of Chicago Press, Chicago

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004a) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Brown JH, Gillooly JE, Allen AP, Savage VM, West GB (2004b) Response to forum commentary on "toward a metabolic theory of ecology". Ecology 85:1818–1821

Callaway RM (1997) Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112:143–149

Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. Science 295:2273–2276

Cardinale BJ, Ives AR, Inchausti P (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos 104:437–450

Cavigelli MA, Robertson GP (2000) The functional significance of denitrifier community composition in a terrestrial ecosystem. Ecology 81:1402–1414

Chapin III FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234–242

Chase JM, Leibold MA (2002) Spatial scale dictates the productivity-biodiversity relationship. Nature 416:427–430

Costanza R, R. d' Arge, Groot Rd, Farber S, Grasso M, B. Hannon, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, Belt. MVd (1997) The value of the world's ecosystem services and natural capital. Nature 357:253–260

Cyr H, Walker SC (2004) An illusion of mechanistic understanding. Ecology 85:1802–1804

Daily GC, Alexander S, Ehrlich PR, Goulder L, Lubchenco J, Matson PA, Mooney HA, Postel S, Schneider SH, Tilman D, Woodwell GM (1997) Ecosystem services: Benefits supplied to human societies by natural ecosystems. Issues in Ecology 2:1–18

De Mazancourt C, Loreau M, Abbadie L (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79:2242–2252

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evoluition 16:646–655

Díaz S, Grime JP, Harris J, McPherson E (1993) Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. Nature 364:616–617

Doak DF, Bigger D, Harding-Smith E, Marvier MA, O'Malley R, Thomson D (1998) The statistical inevitability of stability-diversity relationships in community ecology. American Naturalist 151:264–276

Duffy JE, McDonald SK, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagress beds: An experimental test. Ecology 82:2417–2434

Duraiappah AK, Naeem S (2005) Synthesis Report on Biodiversity. M. Assessment, Island Press

Ehrlich PR (1988) The loss of biodiversity: causes and consequences. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC, pp 21–27

Elser JJ, Sterner R (2002) Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press, Princeton

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

Engelhardt KAM, Ritchie ME (2001) Effects of macrophyte species richness on wetland ecosystem functionng and services. Nature 411:687–689

Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. Science 295:1517–1520

Enquist BJ, Brown JH, West GB (1998) Allometric scaling of plant energetics and population density. Nature 395:163–165

Foster BL, Dickson TL (2004) Grassland diversity and productivity: The interplay of resource availability and propagule pools. Ecology 85:1541–1547

Fox JW (2004) Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. Ecology 85:549–559

Freckman DW, Virginia RA (1997) Low-diversity antarctic soil nematode communities: distribution and response to disturbance. Ecology 78:363–369

Fridley JD (2003) Diversity effects on production in different light and fertility environments: an experiment with communities of annual plants. J Ecology 91:396–406

Fukami T, Morin PJ (2003) Productivity–biodiversity relationships depend on the history of community assembly. Nature 424:423–426

Garnier E, Navas M-L, Austin MP, Lilley JM, Gifford RM (1997) A problem for biodiversity-productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? Acta Oecologica 18:657–670

Gaston K (2000) Global patterns in biodiversity. Nature 405: 220–227

Grimm NB (1995) Why link species and ecosystems? A perspective from ecosystem ecology. In: Jones CG, Lawton JH (eds) Linking Species and Ecosystems. International Thomson Publishing, New York, pp 5–15

Groombridge B (ed) (1992) Global biodiversity. Chapman and Hall, London, United Kingdom

Groves RH, Austin MP, Kaye PE (2003) Competition between Australian native and introduced grasses along a nutrient gradient. Austral Ecology 28:491–498

Guterman L (2000) Have ecologists oversold biodiversity? Some scientists question experiments on how numerous species help ecosystems. The Chronicle of Higher Education 47:A24–26

Hairston NGS, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. American Naturalist 106:249–257

Harte J, Kinzig AP (1993) Mutualism and competition between plants and decomposers: implicatins for nutrient allocation in ecosystems. American Naturalist 141:829–846

Hawksworth DL (ed) (1995) Biodiversity measurement and estimation. Chapman and Hall, London

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder PH, Donovan GO, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze MD, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127

Heemsbergen DA, Berg MP, Loreau M, van Hal JR, Faber JH, Verhoef HA (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306:1019–1020

Heywood VH (ed) (1995) Global biodiversity assessment. UNEP and Cambridge University Press, Cambridge

Hodgson JG, Thompson K, Bogaard A, Wilson PJ (1998) Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. Functional Ecology 12:843–848

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nturient cycling. Ecological Monographs 68: 121–149

Hooper DU, Solan M, Symstad A, Díaz S, Gessner MO, Buchmann N, Degrange V, Grime P, Hulot F, Mermillod-Blondin F, Roy J, Spehn E, van Peer L (2002) Species diversity, functional diversity and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and Ecosystem Functioning. Oxford University Press, Oxford, pp 195–208

Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. Ecological Applications 75:3–35

Horn HS (2004) Commentary on Brown et al.'s "toward a metabolic theory of ecology". Ecology 85:1816–1818

Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton

Hughes RG (1986) Theories and models of species abundance. The American Naturalist 128:879–899

Hughes JB, Ives AR, Norberg J (2002) Do species interactios buffer environmental variation (in theory)? In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and Ecosystem Functioning: Synthesis and perspectives. Oxford University Press, Oxford, pp 92–101

Joffre R, Ågren GI (2001) From plant to soil: Litter production and decomposition. In: Roy J, Saugier B, Mooney HA (eds) Terrestral Productivity. Academic Press, San Diego, CA, USA, pp 83–99

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kaiser J (2000) Rift over biodiversity divides ecologists. Science 289:1282–1283

Kuhn TS (1962) The structure of scientific revolutions. The University of Chicago Press, Chicago

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556

Lepš J, Brown VK, Díaz Len TA, Gormsen D, Hedlund K, Kailová J, Korthals GW, Mortimer SR, Rodriguez-Barrueco C, Roy J, Santa Regina I, van Dijk C,van der Putten WH (2001) Separating the chance effect from other diversity effects in the functioning of plant communities. Oikos 92:123–134

Levine JM (2000) Complex interactions in a streamside plant community. Ecology 81:3431–3444

Li B-a, Gorshkov VG, Makarieva AM (2004) Energy partitioning between different-sized organisms and ecosystem stability. Ecology 85:1811–1813

Liiri M, Setälä H, Haimi J, Pennanen T, Fritze H (2002) Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed. Oikos 96:137–149

Likens GE (1992) The Ecosystem Approach: Its Use and Abuse. Ecology Institute, Oldendorf/Luhe, Germany

Loreau M (2004) Does functional redundancy exist? Oikos 104:606–611

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

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:806–808

Loreau M, Naeem S, Inchausti P (eds) (2002) Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford

Lubchenco J, Olson AM, Brubacker LB, Carpenter SR, Holland MM, Hubbell SP, Levin SA, MacMahon JA, Matson PA, Melillo JM, Mooney HA, Pulliam HR, Real LA, Regal PJ, Risser PG (1991) The sustainable biosphere initiative: an ecological research agenda. Ecology 72:371–412

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, N.J

Marquet PA, Labra FA, Maurer BA (2004) Metabolic ecology: Linking individuals to ecosystems. Ecology 85:1794–1796

Martinez ND (1996) Defining and measuring functional aspects of biodiversity. In: Gaston K (ed) Biodiversity: A biology of numbers and difference. Blackwell Science Ltd., Oxford, pp 114–148

May RM (1975) Patterns of species abundance and diversity. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap Press of Harvard University, Cambridge, MA, pp 81–120

McGrady-Steed J, Morin PJ (2000) Biodiversity, density compensation, and the dynamics of populations and functional groups. Ecology 81:361–373

McIntosh RP (1985) The background of ecology. Cambridge University Press, Cambridge, United Kingdom

Mikola J, Setälä H (1998) Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. Oikos 83

Mikola J, Barker GM, Wardle DA (2000) Linking above-ground and below-ground effects in autotrophic microcosms: effects of shading and defoliation on plant and soil properties. Oikos 89:577–587

Mikola J, Yeates GW, Barker GM, Wardle DA, Bonnre KI (2001) Effects of defoliation intensity on soil food-web proerties in an experimental grassland community. Oikos 92:333–343

Mooney HA, Fuentes ER, Kronberg BI (eds) (1993) Earth System responses to global change: contrasts between North and South America. Academic Press, San Diego

Mulder CPH, Koricheva J, Huss-Danell K, Högberg P, Joshi J (1999) Insects affect relationships between plant species richness and ecosystem processes. Ecology Letters 2:237–246

Mulder C, Breure AM, Joosten JHJ (2003) Fungal functional diversity inferred along Ellenberg's abiotic gradients: Palynological evidence from different soil microbiota. Granna 42:55–64

Naeem S (1998) Species redundancy and ecosystem reliability. Conservation Biology 12:39–45

Naeem S (2001a) How changes in biodiversity may affect the provision of ecosystem services. In: Hollowell VC (ed) Managing Human Dominated Ecosystems. Missouri Botanical Garden Press, St. Louis, pp 3–33

Naeem S (2001b) 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, pp 223–250

Naeem S (2002) Ecosystem consequences of biodiversity loss: The evolution of a paradigm. Ecology 83:1537–1552

Naeem S, Li S (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. Ecology Letters 6:567–579

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737

Naeem S, Hahn D, Schuurman G (2000) Producer-decomposer codependency modulates biodiversity effects. Nature 403: 762–764

Naeem S, Loreau M, Inchausti P (2002) Biodiversity and Ecosystem Functioning: The emergence of a synthetic ecological framework. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning:synthesis and perspectives. Oxford University Press, Oxford, pp 3–11

Navas M-L, Garnier E, Austin MP, Gifford RM (1999) Effect of competition on the responses of grasses and legumes to elevated atmospheric CO_2 along a nitrogen gradient: differences between isolated plants, monocultures and multi-species mixtures. New Phytologist 143:323–331

Niklas KJ, Enquist BJ (2002) Invariant scaling relationships for interspecific plant biomass production rates and body size. Proceedings of the National Academy of Sciences of the United States of America 98:2922–2927

Øvreås L (2000) Population and community level approaches for analysing microbial diversity in natural environments. Ecology Letters 3:236–251

Palmer M, Bernhardt E, Chornesky E, Collins S, Dobson A, Duke C, Gold B, Jacobson R, Kingsland S, Kranz R, Mappin M, Martinez ML, Micheli F, Morse J, Pace M, Pascual M, Palumbi S, Reichman OJ, Simons A, Townsend A, Turner M (2004) Ecology for a Crowded Planet. Science 304:1251–1252

Petchey OL, Gaston K (2002) Functional diversity (FD), species richness and community composition. Ecology Letters 5: 402–411

Petchey OL, Morin PJ, Hulot F, Loreau M, McGrady-Steed J, Lacroix G, Naeem S (2002) Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds). Oxford University Press, UK, Oxford, pp 127–138

Petchey OL, Downing AL, Mittelbach GG, Persson L, Steiner CF, Warren PH, Woodward G (2004) Species loss and the structure and functioning of multitrophic aquatic systems. Oikos 104:467–478

Polis GA, Strong DR (1996) Food web complexity and community dynamics. American Naturalist 147:813–846

Power ME (1996) Challenges in the quest for keystones. BioScience 46:609–620

Preston FW (1962) The canonical distribution of commonness and rarity. Ecology 43:185–215, 410–432

Raven PH (2002) Science, sustainability, and the human prospect. Science 297:954–958

Reich PB, Tilman D, Naeem S, Ellsworth DS, Knops J, Craine J, Wedin D, Trost J (2004) Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N. Proceedings of the National Academy of Sciences of the United States of America 101:10101–10106

Roscher C, Temperton VM, Scherer-Lorenzen M, Schmit M, Schumacher J, Schmid B, Buchmann N, Weisser WW, Schulze ED (2005) Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. Ecol Letters 8:419–429

Sala OE, Chapin FS, III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774

Sankaran M, McNaughton SJ (1999) Determinants of biodiversity regulate compositional stabitliy of communities. Nature 401: 691–693

Schläpfer F, Schmid B (1999) Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. Ecological Applications 9:893–912

Schmid B (2002) The species richness-productivity controversy. Trends in Ecology and Evolution 17:113–114

Schmid B, Joshi J, Schläpfer F (2002) Empirical evidence for biodiversity-ecosystem functioning relationships. In: Kinzig A, Pacala SW, Tilman D (eds) The functional consequences of biodiversity. Princeton University Press, Princeton, New Jersey

Schulze ED, Mooney HA (eds) (1993) Biodiversity and Ecosystem Function. Springer-Verlag, New York

Setälä H, Huhta V (1991) Soil fauna increase *Betula pendula* growth: laboratory experiments with coniferous forest floor. Ecology 72:665–671

Smith TM, Shugart HH, Woodward FI (eds) (1997) Plant functional types. Cambridge University Press, Cambridge

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

Soulé ME (1991) Conservation: tactics for a constant crisis. Science 253:744–750

Spehn EM, Joshi J, Schmid B, Alphei J, Körner C (2000) Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. Plant and Soil 224:217–230

Spehn EM, Hector A, Joshi J, Scherer-Lorenzen M, Schmid B, Bazeley-White E, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Jumpponen A, Koricheva J, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Palmborg C, Pereira JS, Pfisterer AB, Prinz A, Read DJ, Schulze ED, Siamantziouras ASD, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (2005) Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37–63

Stachowicz JJ, Fried H, Osman RW, Whitllatch 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 & Applied Ecology 5:97–106

Stephan A, Meyer A, Schmid B (2001) Plant diversity affects culturable soil bacteria in experimental grassland communities. Journal of Ecology 88:988–998

Sugihara G (1980) Minimal community structure: an explanation of species abundance patterns. American Naturalist 116:770–787

Symstad AJ (2000) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99–109

Symstad AJ, Tilman D (2001) Diversity loss, recruitment limitation, and ecosystem functioning: Lessons learned from a removal experiment. Oikos 92:424–435

Symstad AJ, Tilman D, Wilson J, Knops J (1998) Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81:389–397

Symstad AJ, Chapin III FS, Wall DH, Gross KL, Huenneke LF, Mittelbach GG, Peters DPC, Tilman D (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. Bioscience 53:89–98

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379: 718–720

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Sieman E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Tilman D, HillerRisLambers J, Harpole S, Dybzinski R, Fargione J, Clark C, Lehman C (2004) Does metabolic theory apply to community ecology? It's a matter of scale. Ecology 85:1797–1799

Torsvik V, Øvreås L, Thingstad TF (2002) Prokaryotic diversity – magnitude, dynamics, and controlling factors. Science 296: 1064–1066

Troumbis AY, Memtas D (2000) Observational evidence that diversity may increase productivity in Mediterranean shrublands. Oecologia 125:101–108

Troumbis AY, Dimitrakopoulous PG, Siamantziouras A-SD, Memtsas D (2000) Hidden diversity and productivity patterns in mixed Mediterranean grasslands. Oikos 90:549–559

Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders R (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

Vandermeer J (1989) The ecology of intercropping. Cambridge University Press, Cambridge, U.K

Vandermeer J, Lawrence D, Symstad A, Hobbie S (2002) Effect of biodiversity on ecosystem functioning in managed ecosystems. In: Naeem S, Loreau M, Inchausti P (eds) Biodiversity and ecosystem functioning:synthesis and perspectives. Oxford University Press, Oxford, pp 221–233

Vitousek PM, Hooper DU (1993) Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze ED, Mooney HA (eds) Biodiversity and Ecosystem Function. Springer-Verlag, New York, pp 3–14

Walker B, Steffan W (eds) (1996) Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, U.K

Wardle DA, Nicholson S (1996) Synergistic effects of grassland plant species on soil microbial biomass and activity: implications for ecosystem-level effects of enriched plant diversity. Functional Ecology 10:410–416

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258

Wardle DA, Huston MA, Grime JP, Berendse F, Garnier E, Laurenroth WK, Setälä H, Wilson SD (2000) Biodiversity and ecosystem function: an issue in ecology. Bulletin of the Ecological Society of America 81:235–239

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH (2004) Ecological Linkages Between Aboveground and Belowground Biota. Science 304:1629–1633

Wilcove DS, Rothstein D, Dubow J, Philips A, Losos E (1998) Quantifying threats to imperiled species in the United States. BioScience 48:607–615

Wilson EO (1988) The current state of biological diversity. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, D.C., pp 3–18

Wohl DL, Arora S, Gladstone JR (2004) Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. Ecology 85:1534–1540

Woodwell GM (1995) Biotic feedbacks from the warming of the Earth. In: Woodwell GM, Mackenzie FT (eds) Biotic Feedbacks in the Global Climate System. Oxford University Press, New York, pp 3–21

Wright J, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas E, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Yachi S, Loreau M (1999) Biodiversity and ecosystem functioning in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America 96:1463–1468

Zavaleta ES, Hulvey KB (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. Science 306:1175–1177

Zavaleta ES, Shaw MR, Chiariello NR, Mooney HA, Field CB (2003) Additive effects of simulated climate changes, elevated CO_2, and nitrogen deposition on grassland diversity. PNAS 100:7650–7654