# BIODIVERSITY-ECOSYSTEM FUNCTION RESEARCH:
## Is It Relevant to Conservation?

## Diane S. Srivastava[1] and Mark Vellend[2,3]

[1]Department of Zoology and Biodiversity Research Centre, University of British
Columbia, Vancouver, British Columbia, Canada V6T 1Z4; email: srivast@zoology.ubc.ca
[2]National Center for Ecological Analysis and Synthesis, Santa Barbara, California
93101-3351

[3]Current address: Departments of Botany and Zoology and Biodiversity Research Centre,
University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4;
email: mvellend@interchange.ubc.ca

■ **Abstract**  It has often been argued that conserving biodiversity is necessary for
maintaining ecosystem functioning. We critically evaluate the current evidence for
this argument. Although there is substantial evidence that diversity is able to affect
function, particularly for plant communities, it is unclear if these patterns will hold for
realistic scenarios of extinctions, multitrophic communities, or larger spatial scales.
Experiments are conducted at small spatial scales, the very scales at which diversity
tends to increase owing to exotics. Stressors may affect function by many pathways,
and diversity-mediated effects on function may be a minor pathway, except in the case
of multiple-stressor insurance effects. In general, the conservation case is stronger for
stability measures of function than stock and flux measures, in part because it is easier
to attribute value unambiguously to stability and in part because stock and flux mea-
sures of functions are anticipated to be more affected by multitrophic dynamics. Nor is
biodiversity-ecosystem function theory likely to help conservation managers in prac-
tical decisions, except in the particular case of restoration. We give recommendations
for increasing the relevance of this area of research for conservation.

## INTRODUCTION

The past decade has seen a flurry of ecological research on the effects of bio-
diversity on ecosystem functions. The biodiversity-ecosystem function (hereafter
BDEF) hypothesis posits that a reduction in biological diversity (variety of species,
genotypes, etc.) will cause a reduction in ecosystem-level processes. Although the
BDEF hypothesis has deep academic and philosophical roots (reviewed by Hector
et al. 2001, Naeem 2002), it became widely discussed by ecologists in the early
1990s as the result of seminal conferences (Schulze & Mooney 1993), interna-
tional collaborations (Heywood & Watson 1995, Jones & Lawton 1994), and

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research initiatives (Lubchenco et al. 1991). The studies that test the BDEF hypothesis differ from previous competition or facilitation experiments in that they encompass a much wider range of diversity treatments and consider ecosystem-level responses as interesting in their own right, rather than a mechanism for competitive exclusion (e.g., nutrient depletion) or assessing fitness (e.g., plant growth).

It is no coincidence that BDEF research emerged at a time when public interest in conservation was at a peak in Western countries. The term biodiversity, for example, was popularized by the 1992 United Nations Conference on Environment and Development in Rio de Janeiro. There are clear links between the BDEF hypothesis and conservation concerns. Many authors have argued that BDEF research will allow ecologists to predict the consequences of extinctions on ecosystem properties, many of which can be assigned economic value (e.g., carbon fixation, water purification). According to this rationale, the case for conserving biodiversity will be bolstered if reductions in biodiversity are shown to reduce ecosystem functions. Government policy documents have already begun to include general statements justifying conservation in order to maintain ecosystem functions (Government of Saskatchewan 2004). This review evaluates whether BDEF research is relevant for conservation and what would be needed to make it more relevant. Relevance could occur in two ways: either in the form of practical recommendations to conservation managers or as a more general justification to the public for conserving diversity. This review primarily considers the latter question, as this is the most common type of relevance mentioned in the BDEF literature. Our review builds on many past perspectives on this topic (Hector et al. 2001, Hooper et al. 2005, Lawler et al. 2002, Lepš 2004, Schmid & Hector 2004, Schwartz et al. 2000, Srivastava 2002) and also attempts to integrate the assessment of conservation relevance more fully into a broad theoretical framework.

Our assessment is based on the premise that using BDEF research to bolster the case for conservation requires posing a progressive sequence of questions, each question contingent on an affirmative to the previous one. The structure of the review is as follows. After defining biodiversity and ecosystem function, we evaluate assumptions about change in each variable: Is biodiversity decreasing at relevant spatial scales for experiments? Can we easily define desirable levels of ecosystem function? We then evaluate the potential for biodiversity to affect ecosystem function, asking if diversity is able to affect function, whether BDEF patterns are general, and if these patterns can be scaled-up to spatial scales relevant for conservation. We then ask if BDEF results can stand up to the addition of more ecological realism, such as differences in extinction risk between species and the inclusion of species in complex food webs. Finally we compare the importance of any BDEF effects on ecosystem function with other human-induced changes in ecosystem function. We conclude with a synthesis of our assessment of the above questions and recommendations for improving the relevance of BDEF research for conservation.

## DEFINITIONS: BIODIVERSITY AND ECOSYSTEM FUNCTION

Biodiversity and ecosystem function have been defined in many ways, and the choice of definition may have consequences for linking BDEF research with conservation.

### Biodiversity

Biodiversity has two fundamental levels, species diversity and genetic diversity, which are monotonic increasing functions of the number of species and genotypes, respectively, and the evenness of their relative abundances (Magurran 2004). In BDEF research, biodiversity is most often manipulated or measured as the number of species or genotypes, although a few studies have manipulated evenness (e.g., Wilsey & Polley 2002). Broader discussions of biodiversity frequently imply that any change in species composition (the identity of species present) constitutes a change in biodiversity (Chapin et al. 2000). However, in the BDEF literature, a clear distinction has been made between effects of biodiversity (as defined above) and effects of composition (e.g., Downing & Leibold 2002). In particular, BDEF researchers have attempted to remove covariance between diversity loss and composition change by randomly selecting the species that form communities of differing diversity. Although separating the effects of diversity and composition may be important in pinpointing the mechanisms underlying BDEF relationships, most realistic extinction scenarios predict directional change in composition, an issue we return to below.

### Ecosystem Function

The term ecosystem function has often been used synonymously with ecosystem services, the latter defined by Daily (1997) as "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life." Daily's (1997) list of ecosystem services includes air and water purification, maintenance of soil fertility, and aesthetic beauty. Interestingly, it also includes maintenance of biodiversity, which would be circular in BDEF studies. A more focused concept of ecosystem function is provided by Pacala & Kinzig (2002), who distinguish between three classes of ecosystem functions: stocks of energy and materials (e.g., biomass), fluxes of energy or material processing (e.g., productivity, decomposition), and the stability of rates or stocks over time. Stability of ecosystem processes has been measured as resistance to or resilience from perturbations, predictability, and the inverse of temporal variability. Many ecosystem functions measured to date fall comfortably into one of these classes, although virtually any aggregate property of an ecosystem could be considered an ecosystem function, such as invasion resistance, the community-wide prevalence of disease, or efficiency of pollination or seed dispersal.

# ARE THE CONSERVATION ASSUMPTIONS BEHIND BDEF RESEARCH JUSTIFIED?

Before we discuss the premise that biodiversity loss will lead to impoverished ecosystem functioning, we examine key assumptions implicit in the BDEF case for conservation: (*a*) Diversity is being reduced at a scale relevant to ecosystem functions and (*b*) reductions in commonly measured ecosystem variables are undesirable.

## Is Biodiversity Really Declining? A Balance of Extinctions and Invasions at Different Scales

BDEF studies of the last decade almost universally invoke the global decline in biodiversity as the primary impetus for research (Naeem et al. 1999). Conservation management and measurement of ecosystem functions (e.g., carbon credits) also occur on relatively large scales, from watersheds to nations. Most empirical studies, on the other hand, have been conducted at relatively small scales. Indeed, there is no doubt that biodiversity is decreasing globally (McKinney & Lockwood 1999), but the question of whether biodiversity is actually declining at the same spatial scales at which experiments or observations are conducted, or at the scales at which conservation policies are implemented, is much less certain.

When a forest is cleared and turned into an agricultural field, biodiversity declines. However, BDEF experiments are often designed to simulate extinction events in natural or semi-natural habitats, and the question of how biodiversity is changing in these systems has no such self-evident answer. A comprehensive multi-taxa review of this question (Sax & Gaines 2003) revealed the surprising answer that in many cases, particularly for plants, species diversity at local to regional scales is currently increasing through additions of exotic species that have not been fully offset by extinctions of natives. With the caveat that the trend in increasing local diversity may be system- or biome-specific, or transient, these data complicate conservation arguments based on small-scale BDEF experiments.

The fact that exotic species often increase local and regional species diversity underscores the importance of addressing the question raised by Levine and D'Antonio (1999): "Are native and exotic species all that different?" For example, of the 19 species used in the Cedar Creek experiments (e.g., Tilman et al. 2002), two (*Poa pratensis* and *Achillea millefolium*) are considered invasive weeds in many North American grasslands (Stubbendieck et al. 1994). Because a positive relationship between diversity and productivity was found in this system, could the results be used to suggest that exotic species should be encouraged? Of course, conservation efforts in natural habitats almost universally oppose the establishment and spread of non-native species, regardless of their impacts on productivity or nutrient cycling (Pimentel et al. 2000), and we are not attempting to suggest that there is any internal inconsistency in most conservation arguments—the goal is to protect native biodiversity from anthropogenic threats, which may include the

introduction of non-native species. Rather, we are calling attention to a potential pitfall of using BDEF research to bolster the public case for biodiversity protection. The immediate goal of conservation is often the composition of ecological communities, not just their diversity.

## Are Declines in Commonly Measured Ecosystem Variables Undesirable?

Ecosystem function is a potentially problematic concept, in part because the word function carries the unfortunate baggage of an implied purpose and an underlying assumption that particular levels can be unambiguously considered good (Lawler et al. 2002). Even when the implication of purpose is removed by defining functioning as simply showing activity (Naeem et al. 1999), the problem of value judgment remains. In intensively managed ecosystems (e.g., agriculture), it is unambiguous that high productivity is desirable, but in more natural ecosystems it is often not clear that any particular level of ecosystem function is good or bad (Vandermeer et al. 2002). Furthermore, the same ecosystem function may be valued very differently in different contexts. High productivity is often not desired in lake management but would be when managing a forest for carbon credits. In a purely scientific endeavor, the issue can be sidestepped by simply asking how ecosystem-level variables depend on biodiversity. However, any conservation implication of the BDEF hypothesis assumes that we would like to maintain or enhance the functioning of ecosystems, so a particular target level of functioning is often implied (e.g., high productivity is good), although rarely stated explicitly. Nor is it generally stated in BDEF studies which ecosystem functions are more important than others, critical to assessing the overall impact of declining diversity. We would like to emphasize that these points are not a criticism of academic BDEF research, but rather a call for more explicit considerations of what is meant by ecosystem function when deriving implications for conservation.

## THE THREE PHASES OF BIODIVERSITY RESEARCH

We distinguish between three sequential questions that BDEF research needs to answer in the affirmative before concluding that conserving biodiversity is valuable in terms of maintaining ecosystem functions. Phase 1 of BDEF research addresses whether diversity loss is able to reduce ecosystem functions. This question, which has dominated BDEF research for the last decade, concerns the existence and sign of the arrow between diversity and ecosystem function in Figure 1. Phase 2 research asks if loss in diversity is likely to reduce ecosystem functions and, in Figure 1, refers to the net effect of the arrows linking the stressor with ecosystem function via diversity and composition changes. Phase 3 research asks if biodiversity loss is an important pathway by which ecosystem functions are reduced. In Figure 1*b* and 1*c*, Phase 3 research refers to the relative importance (arrow width) of the indirect
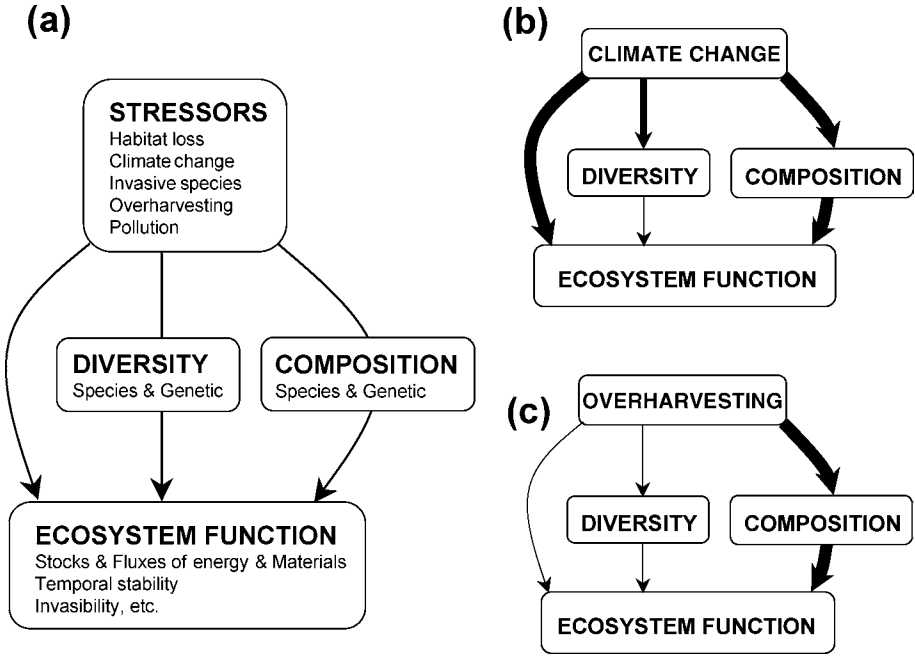
**(a)**

**STRESSORS**
Habitat loss
Climate change
Invasive species
Overharvesting
Pollution

**DIVERSITY**
Species & Genetic

**COMPOSITION**
Species & Genetic

**ECOSYSTEM FUNCTION**
Stocks & Fluxes of energy & Materials
Temporal stability
Invasibility, etc.

**(b)**

**CLIMATE CHANGE**

**DIVERSITY**     **COMPOSITION**

**ECOSYSTEM FUNCTION**

**(c)**     **OVERHARVESTING**

**DIVERSITY**     **COMPOSITION**

**ECOSYSTEM FUNCTION**

**Figure 1**     (*a*) There are many pathways between environmental stressors and ecosystem functions. Simply showing a positive effect of diversity on ecosystem function is insufficient evidence that reducing a stressor will lead to improvements in ecosystem functioning. The relative importance of each pathway (indicated by arrow width in *b,c*) may differ between specific stressors, in this case (*b*) climate change and (*c*) overharvesting.

effects of a stressor on ecosystem function, as mediated by diversity, versus other effects of stressors on ecosystem function (direct or via composition).

## PHASE 1: IS SPECIES LOSS ABLE TO REDUCE FUNCTION?

There are two questions we can ask of Phase 1 research that are particularly important for conservation. Are patterns between biodiversity and ecosystem function truly general across systems and methods? Only a general pattern can be used to make a consistent argument for conserving biodiversity. Can results from small-scale BDEF studies be scaled-up to the larger spatial scales of conservation applications? As argued above, conservation policy deals with much larger spatial scales than the norm for ecological experiments.

### How General are BDEF Relationships?

There has been heated debate about the generality of patterns between biodiversity and ecosystem function (Kaiser 2000). Earlier reviews of BDEF studies include

**TABLE 1**    Potential mechanisms behind positive effects of diversity on function in single-trophic level systems

Stocks and flux types of ecosystem functions

*Niche complementarity*: Niche differentiation between species or genotypes allows diverse communities or populations to be more efficient at exploiting resources than depauperate ones, leading to greater productivity and retention of nutrients within the ecosystem (Antonovics 1978, Loreau 2000, Tilman et al. 1997).

*Functional facilitation*: A positive effect of one species on the functional capability of another will lead to an increase in function in more diverse communities. Examples include promotion of net consumption rates in diverse aquatic insect assemblages through modifications of hydrology and detrital particle size (Cardinale et al. 2002, Heard 1994).

*Sampling effect*: Also called positive selection effect (Loreau 2000). This effect combines probability theory with species-sorting mechanisms. When there is positive covariance between the competitive ability of a species and its per capita effect on ecosystem function, the probability of including a dominant, functionally important species will increase with diversity (Holt & Loreau 2002, Huston 1997, Ives et al. 2005, Tilman et al. 1997).

*Dilution effect*: Lower densities of each species or genotype in high-diversity communities may reduce the per capita effects of specialized enemies such as pathogens (e.g., via reduced transmission efficiency) or predators (e.g., via reduced searching efficiency). In essence, specialized enemies create frequency-dependent selection among species or genotypes (e.g., Mitchell et al. 2002).

Stability of ecosystem functions

*Insurance effects*: Species that are redundant in functional roles or capacity respond differently to stressors, allowing maintenance of net community function after perturbation (Ives et al. 1999, Yachi & Loreau 1999).

*Portfolio effect*: Independent fluctuations of many individual species may show lower variability in aggregate than fluctuations of any one species (Doak et al. 1998, Tilman et al. 1998), much as a diversified stock portfolio represents a more conservative investment strategy than would any single stock. This effect does not require any interactions between species.

*Compensatory dynamic effects*: Negative temporal covariance between species abundances create lower variance in their aggregate properties, such as total biomass (Tilman et al. 1998).

a 20-study review of Schwartz et al. (2000), a 49-study review by Schmid et al. (2002), a broad overview of the field (Hooper et al. 2005), as well as reviews of specific functions (Jolliffe 1997, Levine & D'Antonio 1999) and specific systems (Covich et al. 2004, Loreau et al. 2002). We compiled a total of 100 BDEF studies (see Supplemental Table 1; follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org/). Of these studies, 71% found a positive effect of diversity on at least one ecosystem function. This strong support for the BDEF hypothesis should be tempered by several caveats. First, many studies examined multiple ecosystem functions, and it is possible that

the more functions are examined, the more likely at least one function will exhibit a positive response to diversity. If we randomly choose one function per study, then only 62% of studies found positive BDEF effects. Second, positive effects of diversity on ecosystem functions were more often log-linear relationships (53%) than linear (39%), with 8% showing other patterns (see also Schmid et al. 2002, Schwartz et al. 2000). Several authors (Schwartz et al. 2000, Wardle 2002) have argued that log-linear BDEF functions imply that many species can be lost from a system before there is much decrease in function. Other authors speculate that increasing spatial or temporal scale will change asymptotic patterns to linear (Lawler et al. 2002, Tilman 1999). It is useful to understand why BDEF studies differ in results. Various authors have pointed out that the effect of species diversity on function depends on the system studied and the function measured (Duffy 2003, Schmid et al. 2002, Schwartz et al. 2000, Wardle 2002). For example, within grassland experiments, 74% of studies showed a positive BDEF effect on primary productivity, but only 44% reported a similar effect on decomposition. Overall, studies were less likely to find positive diversity effects on stocks and flux measures of functions (67% found at least one positive effect) than measures of stability (73%) or invasion resistance (73%). System effects are also important. Half (51%) of the studies used grassland communities, mainly north-temperate, of which 78% found at least one positive BDEF effect. Only 63% of studies in other systems found at least one positive BDEF effect, suggesting that ecologists are disproportionately looking for an effect in systems where it is likely to occur.

Research design likely also explains some of the variance in results. The empirical studies making up Phase 1 research include both observational evidence and experiments. All experiments require communities of differing richness, but these have been created by either artificially assembling communities, removing species, or through perturbation (e.g., fertilization). Furthermore, species could be lost at random, according to species sensitivities or following a set order (nested). Several authors have shown that the likelihood of detecting a BDEF effect depends on these design choices (Allison 1999, Mikola et al. 2002, Zavaleta & Hulvey 2004).

The strength of BDEF effects may also depend on the level of diversity manipulated (genetic, species, or functional group). When species are clustered into functional groups, functional diversity effects generally tend to outweigh species diversity effects (Heemsbergen et al. 2004, Hooper et al. 2002, Petchey et al. 2004b). Relatively few Phase 1 studies have examined the effects of genetic diversity within species (Bell 1990; Boles et al. 2004; Booth & Grime 2003; Hughes & Stachowicz 2004; Madritch & Hunter 2002–2004; Weltzin et al. 2003), and it is difficult to generalize about results.

Phase 1 BDEF research has been useful in outlining potential mechanisms behind positive effects of diversity on function (Table 1), although it is often difficult to link patterns unequivocally to mechanisms (Ives et al. 2005, Wardle 2002). Note that most mechanisms proposed to date apply largely to diversity within trophic levels, although Ives et al. (2005) suggest that they may extend to

predator diversity effects on prey density. Below we describe the complexity that arises when one considers multiple trophic levels.

## Can We Scale-Up Results from Local BDEF Experiments?

The size of experimental units in BDEF research varies from Petri dishes (e.g., Naeem & Li 1997) to field plots of almost 100 $m^2$ (e.g., Tilman et al. 2002). Observational evidence includes sites up to several hectares in size (e.g., Aoki 2003). By contrast, conservation policies are often implemented at scales ranging from a few hectares to many square kilometers. Can we scale-up from small-scale experiments to large-scale conservation implications?

Several theoretical studies have outlined potential mechanisms linking BDEF relationships at different scales (Bond & Chase 2002; Cardinale et al. 2000, 2004; Loreau & Mouquet 1999; Loreau et al. 2003; Peterson et al. 1998; Srivastava 2002; Tilman 1999). Based on the scaling of species richness with area, Tilman (1999) argued that the 11 species needed to maintain function at the local (0.5 $m^2$) scale implied that 232 species needed to be maintained at the regional (1 $km^2$) scale. Unfortunately, species-area relationships tell us that species richness tends to be correlated across different scales but do not explain why. Without a mechanism, it is difficult to predict the exact effect of reducing regional diversity on local diversity. By contrast, species-saturation and metacommunity theory predict mechanisms by which reductions in regional richness may affect local richness. Saturation theory predicts that regional extinctions will reduce local richness only when the regional species pool (or dispersal from it) is already relatively depauperate (Cornell & Lawton 1992). At high levels of regional richness, communities should be saturated with immigrating species, and local diversity will be limited more by interspecific interactions. Thus if local diversity influences local ecosystem function, regional extinctions should result in reduced levels of ecosystem function when local communities are not saturated with species (Ruesink & Srivastava 2001, Srivastava 2002). However, the degree of saturation in most ecological communities remains unclear (Hillebrand & Blenckner 2002, Shurin & Srivastava 2005).

Metacommunity models consider a landscape composed of many local-scale patches, with dispersal among them (Leibold et al. 2004). If we assume that in a given patch some species are better than others at carrying out a function, then at the scale of this patch, increasing diversity may have a positive effect on function through an increased probability of including functionally important species (sampling effect: Table 1); however, there may also be a negative effect when additional species reduce, through interspecific competition, the abundance of functionally important species (Bond & Chase 2002, Loreau et al. 2003). At larger spatial scales, patches become increasingly different in environmental conditions and, consequently, species composition (Gilbert & Lechowicz 2004). This could have several outcomes. First, species that do not contribute to ecosystem function in one patch may become functionally important in other patches. Thus if species with a high level of functional importance in a given patch type are favored to

occur in that patch type, high regional diversity could increase the overall magnitude (Cardinale et al. 2004, Loreau et al. 2003) or variety (Bond & Chase 2002) of ecosystem function at the regional level. For example, in a system of wet and dry habitat patches, a diverse species pool will allow for greater productivity than a species pool lacking in drought-adapted species. Second, because species may be stochastically lost from individual patches, dispersal between patches may be needed both to rescue the patch population (Cardinale et al. 2004, Loreau et al. 2003) and to maintain regional richness (Loreau et al. 2003). It is important to note that this body of theory is as much about incorporating beta diversity (regardless of spatial scale) as it is about increasing spatial scale per se.

There are as yet no empirical studies that directly test the above hypotheses relating regional extinctions and local function. However, some empirical studies suggest that regional processes are important in maintaining both diversity and ecosystem function (Symstad et al. 2003). Increasing propagule pressure (i.e. increasing dispersal from the regional pool) increases productivity and diversity in grasslands under some conditions (Foster & Dickson 2004, Foster et al. 2004) but not others (Foster & Dickson 2004, Foster et al. 2004, Wilsey & Polley 2003). Isolation of habitat fragments (i.e., reduced dispersal from the regional pool) is linked to reductions in both diversity and function in studies of pollinators and coffee production (De Marco & Coelho 2004), parasitoids and pest suppression (Kruess & Tscharntke 1994), and microarthropods and secondary production (Gonzalez & Chaneton 2002). Unfortunately, it is often difficult to isolate (see Figure 1) the effect of diversity change from other effects of fragmentation on function (but see Gonzalez & Chaneton 2002), a point we return to below.

In sum, theory suggests that when local diversity is constrained by immigration from the regional species pool, changes in regional diversity could lead to changes in ecosystem function. At present, it is unknown whether this would actually happen, even in an experimental system. Thus it is too early to derive any significant conservation implications concerning links between regional-scale diversity and ecosystem function, although this line of inquiry seems promising.

## PHASE 2: IS REALISTIC SPECIES LOSS LIKELY TO REDUCE FUNCTION?

The first generation of experiments (Phase 1) explored the ecological conditions under which change in diversity is able to affect ecosystem function. This is an interesting academic question and will probably continue to be actively investigated for some time to come. However, in order to answer this question rigorously, experiments have often had to make simplifying assumptions, such as random extinction of species and single trophic-level communities. In terms of conservation, therefore, the important follow-up question (Phase 2) is whether extinctions of species or loss of genetic diversity will likely lead to change in ecosystem functioning. We first ask whether BDEF relationships still hold for more realistic patterns of

diversity loss. We then ask how BDEF relationships will be affected by extinctions occurring at, or cascading through, multiple trophic levels.

## Incorporating Non-Random Species Loss

After some of the first BDEF experiments (Naeem et al. 1994, Tilman & Downing 1994) were criticized for confounding species number with species composition (Aarssen 1997, Huston 1997, Huston & McBride 2002, Wardle 2002), researchers have been careful to assign composition randomly at each richness level. We refer to such experiments as random-loss experiments. By biased-loss we mean the non-random association of certain species with richness levels. The results of random-loss BDEF experiments could most easily be used to predict the effects of species extinctions when such extinctions naturally occur independently of species traits (Lepš 2004, Srivastava 2002). However, species extinctions do not appear to be random in either the geological record or modern time. Extinctions of fossil species are often correlated with traits such as long generation time, large body size, small geographic range, and low local density (McKinney 1997), although the strength of these correlations differs between mass extinction events and periods of background extinction (Jablonski 2001). The same suite of traits generally also characterizes modern species that have gone or are on the verge of going extinct (Lawton 1995, McKinney 1997).

Given that extinction is biased to certain types of species, can we still use the results of random-loss experiments to predict likely effects of real extinctions on ecosystem functions? If there is little difference in predicted BDEF relationships between random-loss and realistic biased-loss scenarios, random-loss experiments might still give a "general expectation in the absence of detailed predictions" (Hector et al. 2001: p. 625). However, the few studies to date that have contrasted ecosystem effects of realistic extinctions with those of random extinctions have found marked differences. These studies examine effects of marine invertebrate extinctions on bioturbation (Solan et al. 2004), terrestrial vertebrate extinctions on risk of Lyme Disease (Ostfeld & LoGiudice 2003), grassland species loss on invasion resistance (contrast Zavaleta & Hulvey 2004 with Dukes 2001) and primary production (Schläpfer et al. 2005), as well as simulations with theoretical food webs (Ives & Cardinale 2004).

These differences between real and random extinctions can be understood, in part, by examining trait correlations. If the traits that cause species to be extinction-prone are positively correlated with the traits that cause species to be functionally important, then the first species to be lost will initially cause a disproportionately large reduction in functioning (Hooper et al. 2002, Lavorel & Garnier 2002). For example, large-bodied species often have higher extinction risk, in part, because large-body size is correlated with other extinction-prone traits: small population sizes, long generation times, and high trophic positions (Cardillo & Bromham 2001, Gaston & Blackburn 1995, Gonzalez & Chaneton 2002, McKinney 1997). In the marine invertebrate study (Solan et al. 2004) described above, large-bodied

species are also among the most effective bioturbators. In the Lyme disease study (Ostfeld & LoGiudice 2003), large-bodied species such as deer and raccoons tend not to transmit the Lyme disease agent to ticks and so reduce disease prevalence. More generally, simulations of multiple data sets show that when extinctions are biased toward animal species with large-body sizes, there is a disproportionate loss of function-effect traits (Petchey & Gaston 2002). The opposite pattern may also dominate. If the traits that cause species to be extinction-prone are negatively correlated with traits that cause species to be functionally important, then the first few species to be lost will have little initial effect on ecosystem functions. For example, species at low abundance are disproportionately likely to go extinct, as they are more sensitive to environmental, demographic, and genetic stochasticity (Lawton 1995, McKinney 1997). However, such rare species often have the smallest effects on ecosystem functioning simply because they contribute very little to total community abundance (but see Lyons & Schwartz 2001). For example, in the marine invertebrate study (Solan et al. 2004), bioturbation rates could be largely maintained despite loss of rare species, as long as one of the most abundant and largest species, a brittlestar, remained. A more common pattern is for large-bodied species to have low abundance (Brown 1995), and it will be more challenging to predict the net effects of losing such species.

The above discussion relates to initial decreases in function. Longer-term effects of biased extinctions on function also depend on the strength of interspecific interactions, and whether niche complementarity, facilitation, or sampling effects (Table 1) predominate (Gross & Cardinale 2005). The potential of the community to compensate is affected by the traits of the remaining species that are, of course, also biased in biased-loss scenarios (Gross & Cardinale 2005, Solan et al. 2004). Removal experiments in grasslands demonstrate that different segments of the plant community have different capacities for functional compensation (Lyons & Schwartz 2001, Smith & Knapp 2003). For example, the study by Smith & Knapp (2003) shows that removal of the rarest species can be compensated by increased growth of the dominant species, whereas reductions in the density of the dominant species cannot be compensated by rare species.

One of the clearest extinction patterns is the preferential loss of top trophic levels. Top predators are recorded to be among the first species to go extinct in marine (Myers & Worm 2003, Pauly et al. 1998), freshwater (Petchey et al. 2004a), and terrestrial systems (Didham et al. 1998, Kruess & Tscharntke 1994). Experimental perturbations of model systems also often result in preferential loss of species at high trophic levels (Gilbert et al. 1998, Petchey et al. 1999). The reasons behind this preferential loss of predators include life-history correlates, food web dynamics, and human behavior (Holt et al. 1999, Pauly et al. 1998, Petchey et al. 2004a). Extinction of species at top trophic levels may, in turn, have disproportionately strong impacts on ecosystem functions. For example, the effects on plant biomass of removing a top trophic level (Shurin et al. 2002) have been argued to be comparable to the effects of drastic reductions in plant diversity (Duffy 2003). It should be noted that in the studies summarized in these meta-analyses, removal

of the top trophic level was generally achieved by removing one predator species, whereas the decrease in plant diversity involved a mean ($\pm$SD) loss of $10.9 \pm 8.6$ species (Duffy 2003), suggesting that the effect of losing a single species was greater when the species originated from a higher trophic level (Duffy 2003). To date, we know of only two experiments appropriate for testing this hypothesis. In seagrass mesocosms, producer (eelgrass, macroalgae, epiphyte) biomass tended to be 17 to 33% more strongly affected by loss of the only predator species than by the loss of a single grazer species (data from Duffy et al. 2005). By contrast, in plant-aphid-predator mesocosms, aphid suppression was equally affected ($\pm$15% change) when either a plant or predator species was removed (data from Aquilino et al. 2005). The capacity for functional compensation may be reduced for extinctions occurring at higher trophic levels simply because there are fewer species at the same trophic level that could potentially compensate (Duffy 2002, Vinebrooke et al. 2003). That is, species richness is inversely related to trophic level (Duffy 2002, Petchey et al. 2004a, Vinebrooke et al. 2003).

Although species at high trophic levels may strongly affect various ecosystem functions, the direction and mechanism of such effects are often difficult to predict without full knowledge of the food web (Petchey et al. 2004a, Thébault & Loreau 2003). In linear food webs, extinctions may initiate trophic cascades such that extinctions at adjacent trophic levels can have opposite effects on basal trophic levels (Carpenter & Kitchell 1993). In simulations of more complex food webs, the impact of extinctions on ecosystem biomass depends on food web shape, connectance and interaction strengths (Ives & Cardinale 2004, Petchey et al. 2004a, Thébault & Loreau 2003). We now turn to a more detailed consideration of multitrophic effects of extinctions on ecosystem function.

## Returning Species to Food Webs

Species are at risk throughout food webs. The *Exxon Valdez* oil spill in Alaska, for example, affected organisms throughout the coastal marine food web, from seaweed to orcas (Paine et al. 1996). However, the majority of BDEF experiments have considered only extinctions within a single trophic level, although there is an increasing number of multitrophic studies (reviewed by Duffy 2003, Duffy et al. 2005, Schmid et al. 2002). Whether this emphasis on single trophic level experiments and theory prevents ecologists from applying their results to real, multitrophic food webs depends on the answers to the following three questions:

1. When multiple extinctions occur at different trophic levels, do they have opposing or synergistic effects on ecosystem function? Theoretically, we might expect that ecosystem functions will be affected differently by extinctions at different trophic levels, but the direction of this interaction is unclear. To illustrate this, let us envisage the simplest possible multitrophic system, one with just producers and consumers. To make things even simpler, let us assume reductions in producer diversity lead to reductions in primary productivity, and ask whether this reduction in function is offset or exacerbated

by reduced consumer diversity (for more dynamic scenarios see Thébault & Loreau 2003). Loss of all consumers could increase primary production when producers experience a trade-off between growth rate and palatability, such that consumers lead to the dominance of slow-growing inedible species (Fox 2004b, Norberg 2000, Thébault & Loreau 2003). Alternatively, loss of all consumers could reduce primary productivity when herbivory accelerates nutrient cycling between plant matter and soil (Hik & Jefferies 1990, McNaughton et al. 1997). Reductions in consumer diversity that do not lead to loss of the entire trophic level can increase primary productivity, for example, in cases where consumers previously complemented each other in consumption efficiency (Norberg 2000, Sommer et al. 2001), or where high diversity allowed the most efficient predator species to persist (Fox 2004b, Holt & Loreau 2002), a type of sampling effect (Denoth et al. 2002, Ives et al. 2005). Alternatively, reductions in consumer diversity can reduce primary productivity, for example, in cases where the efficiency of diverse predator assemblages was reduced by intraguild predation or interference (Finke & Denno 2004). Theoretically, therefore, consumer extinctions could either amplify or buffer the effects of producer extinctions. Only a few experiments have addressed interactive effects of extinctions between two trophic levels, and results are predictably mixed. In aquatic microcosms, effects of algal richness on primary productivity and community biomass have been shown to depend also on the richness of other trophic levels (bacteria × algal richness effects, Naeem et al. 2000; herbivore × algal richness effects, Gamfeldt et al. 2005). However, in another aquatic microcosm experiment, algal productivity is independent of both algal richness and herbivore richness, although there are transient effects (Fox 2004a). In Swedish grasslands, a strong relationship between plant richness and biomass accrual depends on removal of all insects from the system (Mulder et al. 1999). However, BDEF relationships have been found in other grassland experiments despite not actively excluding insects (e.g., Tilman et al. 1996). A tritrophic study in seagrass mesocosms found eelgrass and epiphyte biomass to be strongly affected by a grazer diversity by predator presence interaction (Duffy et al. 2005). By contrast, a tritrophic study in crop-insect mesocosms found no interaction between plant diversity and predacious insect diversity on suppression of a herbivore, the pea aphid (Aquilino et al. 2005).

2. Can extinctions cascade through food webs and thus impact ecosystem function at other levels? Changes in diversity at one trophic level have often been implicated in changes in diversity at other trophic levels, either higher or lower (Dyer & Letourneau 2003, Hunter & Price 1992, Siemann 1998). The proposed mechanisms behind extinction cascades vary with the trophic role of the lost species, that is, they depend on how composition change covaries with diversity loss. In the case of predator-mediated coexistence, loss of a predator species can lead to decreases in prey diversity (Paine 1966). Reductions in diversity at basal trophic levels may also cause loss of species at

higher trophic levels through reduction in the types of resources, net amount of resources, or number of facilitative interactions (Siemann 1998, van der Heijden et al. 1998). Indirect effects can allow such extinction cascades to propagate through multiple levels in food webs (Borrvall et al. 2000, Dyer & Letourneau 2003, Morris et al. 2004). However, there is little consensus as to the conditions favoring extinction cascades. Studies with simulated food webs have found extinction cascades to be more likely with either many (Lundberg et al. 2000) or few species per trophic level (Borrvall et al. 2000) and either high (Pimm 1982) or low connectance between species (Dunne et al. 2002). The presence of cascading extinctions is important from a conservation perspective, as it suggests that the effects of losing a single species may ultimately have consequences for multiple species and their associated ecosystem functions (van der Heijden et al. 1998).

3. Do the mechanisms behind BDEF relationships depend on multitrophic interactions, including indirect effects? Several empirical studies have found that changes in diversity at one trophic level affect functions performed by a different (unmanipulated) trophic level, clearly requiring multitrophic interactions (Cardinale et al. 2003, Duffy 2003, Duffy et al. 2005, Finke & Denno 2004, Naeem et al. 2000, van der Heijden et al. 1998). Indirect effects are a special subset of multitrophic interactions that involve linked pairwise interactions. In several multitrophic BDEF experiments, indirect effects determined effects of diversity on function (Cardinale et al. 2003, Downing & Leibold 2002, Duffy et al. 2003, Finke & Denno 2004, Mikola & Setälä 1998). For example, diverse assemblages of natural enemies were more efficient in suppressing pea aphids because of apparent facilitation involving a second aphid species (Cardinale et al. 2003). Initial theoretical examinations show that indirect effects may modify BDEF relationships, although less so than previously expected (Ives et al. 2005). Increased diversity can stabilize ecosystem function through a variety of mechanisms. Several mechanisms do not require multitrophic interactions (see Table 1). However, recent simulations of food webs suggest that multitrophic interactions can create additional mechanisms to stabilize communities, for example through omnivory (McCann & Hastings 1997) or the buffering of strong interactions by weak interactions (McCann et al. 1998, McCann 2000). Low mean interaction strengths tend to stabilize food webs (Jansen & Kokkoris 2003) and, in simulations of community assembly, characterize more diverse communities (Kokkoris et al. 1999). Although the last observation suggests that extinctions result in less stable food webs and hence ecosystem functions, it should be cautioned that this conclusion is likely highly dependent on the exact pattern of extinction (Ives & Cardinale 2004, Ives et al. 2000).

In summarizing these three questions about multitrophic systems, we found that multiple extinctions at various trophic levels can affect a given ecosystem function either synergistically or antagonistically. Such multiple extinctions may occur not

only through a multitrophic stressor (such as pollution or habitat loss), but also because single extinctions can result in further cascading extinctions throughout food webs. Consequently, multitrophic interactions can have strong effects on the relationship between diversity and function, but the direction of these effects is highly context dependent (Thébault & Loreau 2003). In practice, it will be difficult to predict such BDEF effects in all but the simplest food webs. Note that many multitrophic BDEF experiments report unexpected or idiosyncratic results (Downing & Leibold 2002; Duffy et al. 2001, 2005; Mikola & Setälä 1998; Naeem et al. 2000; Norberg 2000). Thus multitrophic extinctions and interactions weaken the BDEF argument for conserving diversity in order to maintain certain levels of ecosystem stocks and fluxes. By contrast, in terms of stability of function, multitrophic effects may—at least under some extinction scenarios—exacerbate the destabilizing effects of extinctions (Ives & Cardinale 2004, McCann 2000).

## PHASE 3: IS SPECIES LOSS THE MOST IMPORTANT PATHWAY TO REDUCED FUNCTION?

Simulating realistic patterns of extinction in real food webs brings us closer to connecting BDEF research and conservation concerns, but ultimately we need to consider the underlying causes of biodiversity change and their direct effects on ecosystem function (Gonzalez & Chaneton 2002, Schmid & Hector 2004, Srivastava 2002, Wardle 2002, Figure 1). The five top reasons for changes in biodiversity are habitat loss and conversion, climate change, invasive species, pollution and enrichment, and over-harvesting (Diamond 1989, Parmesan & Yohe 2003, Sala et al. 2000). Each of these may affect ecosystem functioning directly or indirectly via changes in the biota. Indirect biotic effects on ecosystem function can be further divided into effects of composition (including shifts in abundance) and effects of diversity per se (Figure 1). If the effects of diversity per se on ecosystem function are minimal relative to the other effects, it will be difficult to justify the conservation of biodiversity on the grounds that reductions will lead to a loss of ecosystem functioning. A full examination of different drivers of biodiversity loss is beyond the scope of this review. Here we contrast two scenarios for which we can make preliminary assessments of the likely importance of the three pathways to changes in ecosystem function.

Over-harvesting generally results in the selective removal of particular species, with relatively minor direct effects on ecosystem function. For example, pelagic fisheries often focus on particular target species, and apart from an immediate reduction in the biomass of fish, direct effects on ecosystem functions such as stocks or fluxes of nutrients are likely to be minor. However, ecosystem function may be greatly altered via a cascade of effects through the food web. For example, Estes et al. (1998) have suggested that declines in fish stocks off the shores of Alaska ultimately led to the collapse of kelp forests (and associated primary production). Declining fish stocks are thought to have led to declines in pinniped

populations, which, in turn, caused killer whales to shift their primary food source
from pinnipeds to sea otters, the main regulator of kelp-eating sea urchins. This
scenario suggests a strong effect of over-harvesting on the abundances of species
in the food web (i.e., a composition effect), which ultimately reduced productivity
in kelp forests. Direct effects of fishing on kelp production, and indirect effects via
changes in diversity, were likely quite minor.

Climate change will have profound direct effects on ecosystem function. Rates
of energy and material flux depend fundamentally on temperature and moisture,
both predicted to show significant changes over the next century (Intergovernmen-
tal Panel on Climate Change 2001). Thus even if species ranges were unresponsive
to climate change, ecosystem function at all spatial scales would be dramatically
altered. Species ranges have consistently shifted in response to climate change in
the past (Delcourt & Delcourt 1991), and many species already show clear signals
of shifts in response to contemporary climate change (Parmesan & Yohe 2003,
Root et al. 2003). Species composition at particular sites is, therefore, certain to
be altered dramatically, with consequent effects on ecosystem function. Encroach-
ment of grasslands by shrubs, for example, should greatly alter carbon dynamics
(Jackson et al. 2002). Whereas global diversity is most likely to decrease with
climate change (Thomas 2004), regional and local diversity seem just as likely to
increase as decrease depending on geographic location. It is difficult to imagine
that changes in diversity resulting from climate change will translate into changes
in ecosystem function that are measurable relative to large direct effects of climate
change and indirect effects via changes in composition.

In these two scenarios of biodiversity change, one seems likely to show a
relatively weak direct effect on ecosystem function (over-harvesting), the other a
relatively strong effect (climate change). Both may show strong indirect effects
via composition, but neither show strong indirect effects via diversity. Strong indi-
rect effects via diversity change also seem unlikely for other drivers. For example,
diversity effects accounted for only a fraction of the total change in ecosystem func-
tion following experimental habitat fragmentation (6 %; Gonzalez & Chaneton
2002) or warming (<33%; O. Petchey personal communication in Srivastava
2002). However, we realize that biased-extinction scenarios represent simultaneous
changes in both composition and diversity and that our separation of composition
and diversity effects may be tenuous in many real situations.

It is also important to note that compositional change depends fundamentally
on the existence of diversity to begin with. If diversity is reduced by a driver,
the range of possible responses of the ecosystem to subsequent drivers may be
compromised; that is, biodiversity provides a kind of insurance in the face of dif-
ferent kinds of environmental perturbation (Ives et al. 1999, Naeem 1998, Yachi &
Loreau 1999). Many studies indicate that diversity promotes resilience or resistance
of ecosystem functions to stressors (McCann 2000) (see Supplemental Table 1;
follow the Supplemental Material link from the Annual Reviews home page at
http://www.annualreviews.org/) by allowing species composition to respond to
changing conditions. For example, high diversity grassland plots at Cedar Creek

were more resistant to drought because they contained key drought-tolerant species that increased in biomass as other species declined (Tilman 1996). A few studies have shown that communities experiencing high levels of one stressor have both reduced diversity and reduced resistance to a subsequent stressor (Griffiths et al. 2000, Tilman & Downing 1994), although it is difficult to unambiguously attribute resistance to diversity-mediated insurance effects. In general, such multiple-stressor insurance effects will be strongest when species tolerances to one stressor are positively correlated with tolerances to a subsequent stressor (see Vinebrooke et al. 2004 for a more comprehensive discussion). The corollary is that effects of multiple stressors will depend critically on the identity of the stressors. There are many examples of non-additive effects of multiple stressors on ecosystem states (Folt et al. 1999, Payette et al. 2000, Vinebrooke et al. 2004); it would be instructive to revisit these examples to test specifically for insurance effects (see also Vinebrooke et al. 2004).

## CONCLUSIONS

Ecological and evolutionary research provide the underpinning for our understanding of the natural world and, therefore, our ability to manage and protect it. However, particular sub-fields or studies within these disciplines may or may not have direct conservation implications. For example, it is undisputable that the functional characteristics of organisms play a central role in regulating ecosystem processes (Wardle 2002). However, as pointed out by Hooper et al. (2005), this fact was established by more than 50 years of research in ecosystem ecology long before the recent spate of BDEF studies. The key question here is whether BDEF research of the last decade or so has conservation implications above and beyond those derived from earlier work. Posing the question in this way distinguishes our approach from some previous efforts to derive conservation implications from BDEF research, which focused more broadly to include long-standing research topics such as the difference between monocultures and polycultures in agriculture or the functional importance of individual species (e.g., Chapin et al. 2000, Hooper et al. 2005).

As outlined in the introduction to this review, BDEF research may have conservation implications if (*a*) it improves our ability to manage particular ecosystems or (*b*) if it bolsters the public case for general conservation of biodiversity. The last decade of fervent activity in BDEF research was motivated by the latter possibility. Here we present four conclusions based on our review of the BDEF literature (Table 2) and our assessment of its conservation relevance.

BDEF research is most useful for conservation managers in cases where humans directly control plant diversity and where high levels of ecosystem functions are unambiguously preferred (e.g., in restoration projects). Restoration ecologists are frequently concerned with reclaiming severely disturbed sites, in which case high levels of functions such as primary productivity and nutrient retention are

**TABLE 2**    Summary of the main conclusions of this review

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ARE THE CONSERVATION ASSUMPTIONS BEHIND BDEF RESEARCH JUSTIFIED?

    Biodiversity is declining at global scales, but not always at the smaller spatial scales at
    which policies are implemented or experiments conducted.

    Target levels are often unclear for stocks and flux types of functions. However, stability of
    functions is often desirable.

PHASE 1: IS SPECIES LOSS ABLE TO REDUCE FUNCTION?

    Although many studies show positive effects of biodiversity on function, others do not.
    Generality is obscured by differences between systems, functions measured, level of
    diversity manipulated, as well as experimental approaches.

    It is not yet clear how results from small-scale BDEF experiments can be scaled-up to
    larger spatial scales relevant to conservation.

PHASE 2: IS SPECIES LOSS LIKELY TO REDUCE FUNCTION?

    Realistic patterns of species extinctions can result in BDEF effects different from those
    predicted by Phase 1 random-loss experiments.

    Preferential loss of species at top trophic levels may have particularly strong ecosystem
    effects.

    Ecosystem effects of extinctions in multitrophic food webs will be difficult to predict
    because of numerous indirect effects and the likelihood of simultaneous or cascading
    extinctions through multiple trophic levels.

PHASE 3: IS SPECIES LOSS IMPORTANT IN REDUCING FUNCTION?

    Anthropogenic drivers of extinction will also directly affect ecosystem function. Indirect
    effects of such drivers on ecosystem function, via diversity effects independent of
    composition, may often be minor by comparison.

    Extinctions caused by one stressor may reduce the potential for compositional shifts
    in response to a second stressor, reducing stability of ecosystem functioning. Such
    insurance effects depend on the particular stressors involved, and covariance in species
    tolerances.

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preferred. BDEF studies in temperate grasslands have clearly demonstrated that diverse plantings of species generally show elevated levels of productivity and nutrient uptake. In some cases, diverse plant communities are also more stable in the face of perturbations. For example, restoration of seagrass beds is most effective when diverse genotypes are planted, as genetic diversity increases resistance to goose grazing (Hughes & Stachowicz 2004). However, apart from restoration, BDEF research has little to offer in the way of practical advice for conservation managers. Many conservation managers pursue diversity as a goal unto itself. When certain ecosystem functions are desired in the course of reserve management (e.g., reduction of invasive species biomass), it can be more effective to identify functionally important types of species (e.g., biocontrol agents or native competitors) than simply to advocate increased diversity. We now shift our attention to the question of whether BDEF research bolsters the general case for conservation.

It is easier to make the general case for conservation implications of positive biodiversity effects on ecosystem stability than on stocks or fluxes of energy and materials. Many stock and flux measures of ecosystem functions are desirable in certain contexts but not others. For example, high productivity is desirable when growing forests for carbon credits but is undesirable in many lakes. By contrast, human society and economic systems generally depend on the stability of ecosystems and their functions. Although many Phase 1 studies demonstrated positive relationships between biodiversity and stocks or fluxes of energy and materials (particularly in the case of grasslands), our review indicates that once multitrophic interactions are considered explicitly it becomes challenging to predict the response of such stocks and fluxes to loss of diversity. By contrast, studies of both single trophic and multitrophic systems suggest that loss of diversity is likely to precipitate some reduction in ecosystem resistance or resilience. Furthermore, when diversity effects on stock and flux types of ecosystem functions are compared with the direct effects of stressors or species composition, diversity effects are expected to be of minor importance. However, maintaining diversity may be an important insurance strategy, ensuring the option of composition change in response to future stressors. Therefore, the case for conserving diversity in order to maintain function is generally weaker with respect to stocks and fluxes than it is for their stability.

The validity of any function-based argument for conserving diversity will depend critically on the anticipated pattern of extinctions. Compositional change is an inevitable consequence of extinctions and cannot be ignored in ecologists' predictions about the functional consequences of future extinctions. Ironically, the random-loss BDEF experiments that proved so powerful in isolating functional effects of diversity from those of composition are insufficient to yield predictions about likely biased-loss extinction scenarios. This will be particularly true when extinctions result in changes in trophic structure.

In neither the case of ecosystem stocks and fluxes nor that of stability has BDEF research yet been able to create a convincing general argument for conservation in complex systems, either because important questions have not yet been resolved or because of context-dependency of results (Table 2). This does not mean that the BDEF case for conservation cannot be strengthened in the future. Within the past few years, several studies have started to add ecological realism to BDEF research by simulating realistic extinction scenarios, using multitrophic communities and invoking larger-scale processes. We interpret this as a positive sign that the transition from Phase 1 to Phase 2 of BDEF research has begun and that the results of experiments are starting to become more relevant to conservation. However, we are not presently in a position to say that "incorporating diversity effects into policy and management is essential" (Hooper et al. 2005) with respect to maintaining ecosystem function, unless diversity is defined so broadly as to mean the biotic community (as in figure 1 of Hooper et al. 2005).

If BDEF research is to fulfill its mandate of predicting ecosystem consequences of the current and impending loss of biodiversity, we suggest that future BDEF research (*a*) use realistic scenarios of extinctions, either by trait-analysis of

endangered species or by utilizing real stressors; (*b*) expand to systems underrepresented in BDEF research, particularly multitrophic systems; (*c*) extrapolate results and theory to the larger spatial scales relevant to diversity loss and conservation; (*d*) reconcile the role of invasive species as both a response (invasibility as a function) and manipulated (contributing to biodiversity) variable; (*e*) contrast the importance of biodiversity effects on function with other pathways between stressors and functions (direct effects, effects via composition); and (*f*) in the case of multiple stressors, explore the insurance effects of diversity on future composition shifts.

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