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## The role of conservation in expanding biodiversity research

*Diane S. Srivastava, Dept of Zoology, Univ. of British Columbia, 6270 University Blvd, Vancouver, B.C. Canada V6T 1Z4 (srivast@zoology.ubc.ca).*

It has been suggested that current reductions in global biodiversity may impair the functioning of ecosystems. This biodiversity-ecosystem function (BD-EF) hypothesis represents a new avenue of ecological research originating from conservation concerns. However, the subsequent evolution of BD-EF research has reflected academic concerns more than conservation priorities. I suggest three questions for BD-EF research, which would benefit both ecological theory and conservation. (1) Is biodiversity the main driver of ecosystem function? Several experiments show that biodiversity loss is a minor link between habitat change and ecosystem function. (2) How will extinction patterns change BD-EF relationships? Biased extinctions may have additional impacts on ecosystem function, which can be deduced by comparison with random-loss models. (3) Will conserving regional biodiversity conserve local ecosystem function? The answer to this question may differ between saturated and unsaturated communities, and may depend on whether the magnitude or stability of ecosystem function is measured.

The world is currently experiencing exceptionally high rates of species extinctions, largely because of human activity (Lawton and May 1995). While the loss of biodiversity is in itself a tragedy, there may be more practical consequences for humankind. Approximately a decade ago, several ecologists proposed that reductions in current species diversity would lead to reductions in the functioning of ecosystems; that is, in the biogeochemical processes carried out by the Earth's biota (di Castri and Younes 1990, Ehrlich and Wilson 1991, Lubchenco et al. 1991, Walker 1992, Schulze and Mooney 1993). The motivation for this biodiversity-ecosystem function ("BD-EF") hypothesis is clearly rooted in conservation concerns. For example, the Ecological Society of America, in launching its Sustainable Biosphere Initiative, urged researchers to examine biodiversity effects on ecosystem function because "ecologists are increasingly asked to justify the benefits of biological diversity compared to the human benefits that might be derived from economic development" (Lubchenco et al. 1991, p. 390).

The role of conservation in formulating the BD-EF hypothesis is a reversal of the usual relationship be-

tween community ecology and conservation. Traditionally, conservation biologists have been quick to adapt general ecological theories to particular applied issues. A classic example is the application of island biogeography theory to the design of nature reserves. Community ecologists, by contrast, have been slow to convert conservation issues into new areas of ecological theory.

Given the importance of conservation for the origin of the BD-EF hypothesis, one would imagine that as BD-EF research evolved, it would expand along lines relevant to conservation. This has been only partially true. In the last decade, BD-EF research has expanded in three main areas: methodology, measures of ecosystem function, and modeling of mechanisms. Vigorous debates around experimental methodology, especially regarding spurious results, have resulted in increasingly sophisticated experiments and analysis (Huston 1997, Loreau 1998a, 1998b, Wardle 1999, Huston et al. 2000). The original rather vague concept of reduced functioning has been replaced by a more precise understanding of the key components of ecosystem functioning: magnitude, resilience and resistance to disturbance, constancy in space and time, and resistance to invasions by exotic species (Case 1990, Tilman 1996, Doak et al. 1998, Naeem 1998). The theoretical foundation for the BD-EF hypothesis, once meager, has been buttressed and expanded by recent modeling studies (Tilman et al. 1997, 1998, Ives et al. 1999, Loreau 2000, McCann 2000). While all of these areas are academically important, and indeed essential for the development of the discipline, few have direct relevance to conservation (a notable exception being interest in stability benefits of biodiversity: Schwartz et al. 2000). Nor has BD-EF research crossed over to any degree into the conservation literature (as evidenced by the concentration of this research in academic ecology journals: see reference list of this paper). The purpose of this paper is to suggest several new directions for BD-EF research that would make it more useful to conservation. However, making

BD-EF research more useful for conservation need not come at the expense of ecological generality. Indeed, the research questions outlined in this paper also point the way to how existing ecological theory can be integrated into a BD-EF framework. I begin by discussing how applied goals can be accommodated within academic ecology.

### **Are academic and applied goals compatible in biodiversity research?**

Conservation and community ecology have different goals for biodiversity research (Takacs 1996). The ecological or academic goal for BD-EF research is to determine the *presence* of biodiversity effects on ecosystem function. The conservation or applied goal for BD-EF research is to determine the *importance* and predict the *likelihood* of such a biodiversity effect. These academic and applied goals are occasionally in conflict, as illustrated by a recent debate in the literature. The “sampling effect” debate can be summarized briefly as follows. In many BD-EF experiments, communities of differing diversity are randomly assembled from a species pool. As diversity increases, the probability of any given species occurring in the community also increases. If one particular species has a disproportionate effect on the ecosystem function being measured, any increase in ecosystem function with diversity could simply reflect the increasing probability of including this species (a “sampling” or “selection probability” effect) rather than a true biodiversity effect (Aarssen 1997, Huston 1997, Wardle 1999). This is an academic argument, which questions the presence of a biodiversity effect once external, non-ecological mechanisms (sampling probability) are accounted for. The most common counter-argument, by contrast, is based in applied concerns and is as follows. Even if the underlying mechanism behind BD-EF correlations turns out to be probability rather than ecology, this does not invalidate the conclusion that declining biodiversity will affect ecosystem function. The experiments mimic how humankind is reducing biodiversity: randomly, without regard to any particular species’ effect on ecosystem function (Lawton et al. 1998, van der Heijden 1999, Hector et al. 2000). Although sampling probability is not an academically exciting mechanism, it may be an important mechanism in the real world.

The “sampling effect” debate also illustrates how academic and applied goals can be reconciled. Recent methods allow ecologists to assess the contribution of sampling effects to BD-EF relationships (Hector 1998, Loreau 1998a, 1998b). These methods allow academic goals to be met, as correcting for sampling effects allows us to search for more ecologically-interesting processes. It also satisfies applied goals, as it allows us

to assess the relative contribution of different mechanisms to an overall biodiversity effect. Once these goals are recognized as distinct from each other, conflict disappears (as has recently been witnessed: Hughes and Petchey 2001, Loreau et al. 2001).

I now turn to several specific examples of how BD-EF research could be expanded in ways that satisfy both academic and applied goals. In these examples, academic goals are met by linking current BD-EF theory with other ecological theory, such as species saturation theory or life history correlates of extinction risk. Applied goals are met by asking questions about the importance of biodiversity effects in the context of other environmental changes, and by linking local biodiversity effects with regional conservation policies.

### **Is biodiversity the main driver of ecosystem function?**

Many BD-EF experiments have shown that biodiversity has some effect on ecosystem function (reviewed by Schwartz et al. 2000). It is not clear, however, whether this biodiversity effect is important in comparison to the more direct effects of habitat change on ecosystem function (Hughes and Petchey 2001).

Habitat change is generally agreed to be the primary reason for the current wave of species extinctions (Diamond 1989, Lawton and May 1995). Close on its heels are species invasions and over-exploitation (Diamond 1989). Climate change is poised to become a fourth major cause of contemporary extinctions (Sala et al. 2000). Clearly, the only way to prevent further biodiversity loss is by ameliorating these factors. At some point, therefore, BD-EF research needs to explicitly examine whether changes in human action (e.g. conserving intact habitat) intended to protect biodiversity will also preserve ecosystem function.

The links between habitat change, biodiversity loss and ecosystem function are surprisingly complex. Consider the case of habitat fragmentation. There would appear to be a solid case for reducing habitat fragmentation if it is conclusively shown both that habitat fragmentation leads to lower local diversity, and that lower local diversity leads to reduced ecosystem function. However, this argument is not logically complete as it assumes that there is no direct (i.e., non-biodiversity) effect of habitat fragmentation on ecosystem function (Fig. 1). This is unlikely to be the case. Habitat fragmentation can cause a variety of edaphic changes, such as increased wind exposure, higher evaporation rates, and greater light penetration (Murcia 1995), all of which could directly affect any number of ecosystem functions. The key questions will be the sign and magnitude of such direct effects of habitat change on ecosystem function, relative to biodiversity effects on ecosystem function.

There are a number of experiments which suggest that direct effects between habitat changes and ecosystem function can be of greater magnitude than biodiversity effects on ecosystem function, and even counteract the effects of biodiversity loss. Petchey et al. (1999) used aquatic micro-organisms in experimental microcosms to examine the effect of environmental warming on primary production. Warming increased primary production in two ways, directly through increasing physiological rates, and indirectly through changing biodiversity and trophic structure (Fig. 1b). The gradual 14°C increase in temperature roughly doubled primary production; about 2/3 of this increase could be attributed simply to increased physiological rates (using standard  $Q_{10}$  equations), leaving up to 1/3 due to food-web changes (e.g. increased species extinctions and fewer trophic levels) (O. Petchey, pers. comm.). Other treatments in this experiment confirm that reduced biodiversity in this system can lead to increased primary production, independent of temperature change. Wardle et al. (1997) present observational evidence that several ecosystem functions (notably decomposition and nitrogen mineralization) are positively correlated with island area. At first glance, one might expect that this correlation could be explained by biodiversity effects alone; after all, islands are well-known to have strong species-area relationships. In this case, however, these island biogeography effects are com-

pletely overwhelmed by a positive correlation between island area and fire frequency (from lightning strikes). The higher fire frequency on large islands not only depresses species diversity below that on small islands but, more importantly, radically shifts the composition of the leaf litter to faster-decomposing species (Fig. 1c). Finally, in an experiment described by Gonzalez and Chaneton (2002), fragmentation of moss habitat reduced micro-arthropod productivity, but only 10% of this ecosystem function effect was due to reduced species richness; the remainder was due to decreases in total abundance through dispersal limitation (Fig. 1d).

All of these studies allowed biodiversity to be naturally affected by an extrinsic factor (simulated global warming in Petchey et al. 1999; habitat area in Wardle et al. 1997; fragmentation in Gonzalez et al. 1998). This particular design feature allowed biodiversity effects on ecosystem function to be compared with direct effects of the factor. By contrast, most BD-EF studies reduce biodiversity independently of any extrinsic factor. Although the latter approach is valuable in determining the *presence* of biodiversity effect on ecosystem function, it does not allow us to determine the *importance* of that biodiversity effect relative to other effects. These two approaches should thus be seen as complementary, and it is particularly valuable when both approaches are integrated to a single study (as in Petchey et al. 1999, Levine 2000). Ultimately, to fully understand the

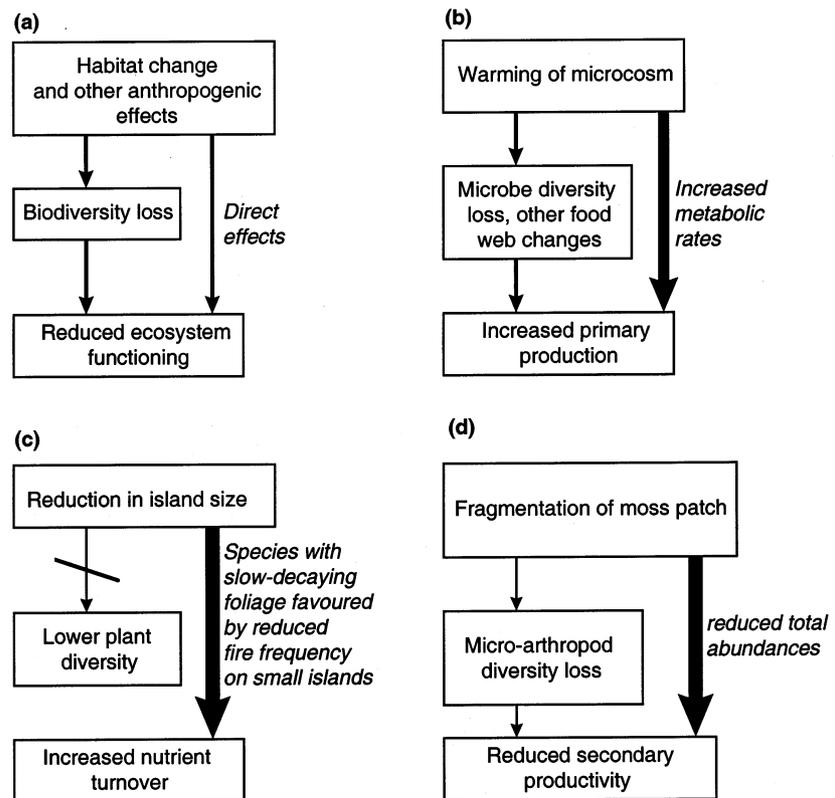


Fig. 1. (a) Habitat changes can affect ecosystem functioning both directly and indirectly via biodiversity effects. Specific examples of this phenomenon are evident in: (b) aquatic microbial communities experimentally manipulated by Petchey et al. (1999), (c) boreal island vegetation studied by Wardle et al. (1997), and (d) micro-arthropods in moss in an experiment described in Gonzalez and Chaneton (2002). The width of each arrow approximates the relative strength of the effect as determined by the authors.

repercussions of human activity on the functioning of ecosystems, we need to understand the importance of all intermediate pathways, including but not restricted to biodiversity loss.

### **How will extinction patterns change BD-EF relationships?**

All species may go extinct, but some species are more likely to go extinct than others. Particularly vulnerable to extinction are large-bodied, K-selected species which occupy high trophic positions in food webs and occur at low abundance (Lawton and May 1995). For example, there is clear evidence that for at least the last 30 years, humans have been consistently “fishing down food webs”; that is, harvesting fish species in top trophic levels under they reach economic extinction, then moving to species at progressively lower trophic levels (Pauly et al. 1998). By contrast, many BD-EF experiments assume random loss of species, and have been criticized as not representing real extinction biases between species (Wardle 1999, Griffiths et al. 2000). The counter-argument is that, if experiments were designed with some species being preferentially lost over others, then any general effect of biodiversity on ecosystem function would be confounded by a systematic change in species composition (Huston 1997, Lawton et al. 1998, Hector et al. 2000). In many ways, this is a debate reminiscent of the “sampling effect” debate: a conflict between pragmatic, conservation concerns and a more academic viewpoint striving for unbiased effects. There is a middle way to view this debate. Random-loss experiments could provide the critical null-model for examining the effects of biased extinction.

For example, suppose we wanted to look at the effect of rarity on modifying BD-EF relationships. If we assumed that the probability of a species' extinction exponentially declines with population size, we could use information on the natural abundances of species to estimate the relative probability of each species going extinct (Fig. 2). Experimental communities of varying diversities could then be assembled using these species-specific probabilities: these communities represent a biased-extinction scenario. At the same time, we could assemble a second series of communities that would represent a true random-loss scenario: each species would have an equal probability of inclusion in a community. By comparing how ecosystem function is affected by biodiversity loss in each scenario, we could separate the effect of losing biodiversity per se from the effect of losing rare species preferentially. In other words, we ask the question whether the absolute effect of biodiversity loss (random-loss scenario) differs from the likely effect of biodiversity loss (biased-loss sce-

nario). Any attempts to translate BD-EF findings into public policy will need to consider such disparities between theory and practice.

One can even go a step further here, and allow diversity to be naturally decreased in a BD-EF experiment by a habitat change, such as fertilization (Tilman 1996), warming (Petchey et al. 1999) or pollution (Griffiths et al. 2000), as discussed earlier. This will cause biased extinctions. Such an approach, when coupled with appropriate random-loss and biased-loss experiments run at the same time, could potentially tease apart (1) the biodiversity-caused effects on ecosystem function from more direct effects of the perturbation, and (2) the contributions of biased loss versus random loss to this biodiversity effect.

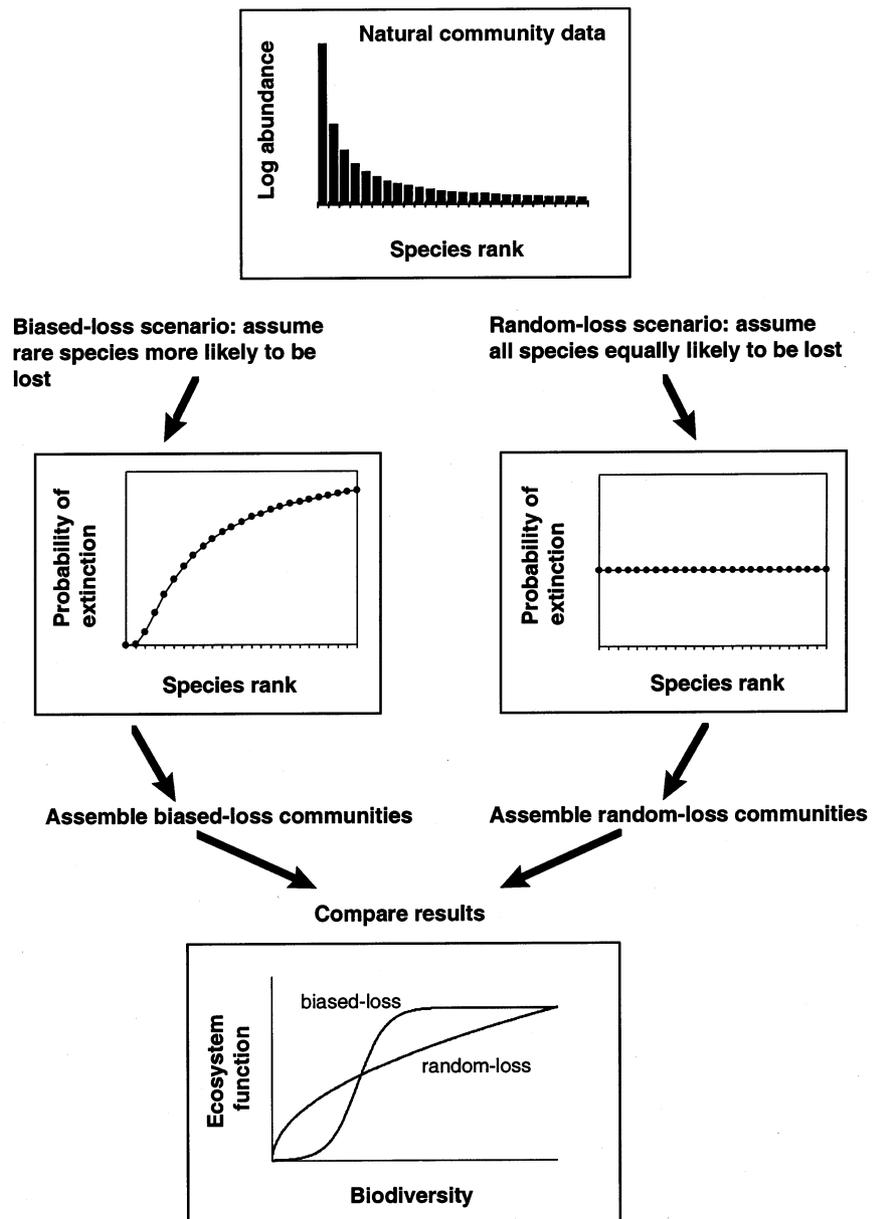
### **Will conserving regional biodiversity conserve local ecosystem function?**

Biodiversity-ecosystem function experiments are typically carried out on small spatial scales, as small as a single Petri dish for a protist community, or a 1 × 1 m plot for a plant community. Such experiments link changes in local diversity with changes in local function, where “local” is defined as the scale at which ecological interactions between species occur (Cornell and Lawton 1992, Ricklefs and Schluter 1993).

In the real world, however, biodiversity loss is occurring at a variety of spatial scales: at the small scale of local communities, at the larger scale of regional species pools, and ultimately at the scale of the entire globe. There are valid conservation concerns for biodiversity loss at all of these scales. However, as the scale of biodiversity loss increases – from local to regional to global extinctions – concern generally mounts. Most conservation guidelines prioritize species at risk of large-scale extinction over those at risk of local extinction (e.g. International Union for the Conservation of Nature guidelines). In the few countries which have formal protection for endangered species, the legislation is enacted by federal or provincial governments and concerns only nationally- or provincially-threatened species (Ray and Ginsberg 1999). At some stage, therefore, BD-EF research will need to examine the effects of biodiversity loss at these larger scales. The next challenge for ecologists is to link regional-level extinctions with changes in ecosystem function.

There are several steps in the pathway between regional biodiversity and local ecosystem function (Fig. 3a). First, changes in regional biodiversity may or may not affect local biodiversity. Secondly, changes in local biodiversity may or may not affect local ecosystem function (the more familiar question). I will examine each of these links in turn, and argue that both links depend on whether communities are “saturated” or “unsaturated” with species.

Fig. 2. An experimental design allowing the functional consequences of biased species loss to be compared to random species loss. To generate the biased-loss extinction probabilities, I simply assumed the probability of species survival was exponentially related to its population size; more complex models could be used here. The relative probability of excluding a species from an experimental community would be equivalent to its relative probability of extinction.



Let us begin with the first question: whether loss of regional diversity will necessarily result in loss of local diversity. Obviously, if any species goes regionally extinct, it is lost from all localities in that region, leading to an instantaneous decrease in local diversity. However, this reduction in local diversity may simply be a transient effect (Grime 1998). Species from other locations in the region may well invade the depauperate communities, returning local richness to its previous level. This replacement process will tend to decouple local diversity from regional diversity. In fact, this replacement process could allow substantial reductions in regional diversity with no effect on local diversity, as

long as species remain in the species pool with the right attributes to quickly fill each niche as it becomes vacant. At some point, however, the pool will become exhausted of suitable replacement species, and local diversity will begin to fall with regional diversity (Fig. 4a).

The effect of regional extinctions on local diversity therefore depends on where the original community falls on this local-regional richness trajectory. Ecologists already distinguish communities according to such effects of regional diversity on local diversity: “unsaturated” communities exhibit strong effects of regional diversity on local diversity whereas the local diversity of

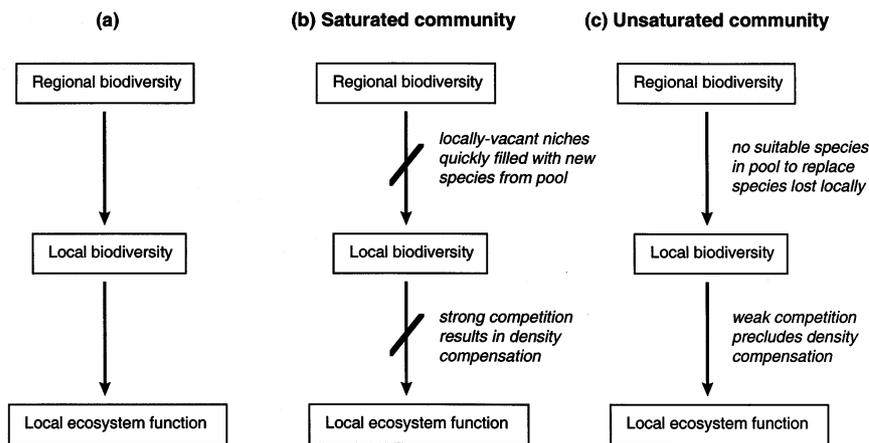


Fig. 3. (a) Changes in regional biodiversity are predicted to affect local ecosystem function via effects on local biodiversity. The strength of these links will differ between (b) saturated and (c) unsaturated communities.

“saturated” communities is relatively independent of variations in regional-level diversity (Fig. 4a). Although the concept of saturation has traditionally been used in discussing the accumulation and maintenance of local diversity, it can also apply to the process of biodiversity loss.

Saturated and unsaturated communities will differ not only in the effect of regional diversity on local diversity, but also in the effect of local diversity on ecosystem function. The latter effect depends on differences in interaction strengths between saturated and unsaturated communities. Recall that in saturated communities, lost species are quickly replaced with new species because the species pool generally contains numerous species able to fill any particular niche. Such a high species: niche ratio is predicted to lead to strong interspecific competition (Cornell and Lawton 1992, but see Fox et al. 2000). Therefore, even if local diversity was successfully reduced in a saturated community, such strong competitive interactions would likely lead to an increase in the abundance of the remaining species; i.e. density compensation. This compensatory effect would diminish any effect of species loss on ecosystem function (Ruesink and Srivastava 2001).

By contrast, in unsaturated communities, there are few if any competitors for a given niche (this is why lost species are generally not replaced). In such weakly-interactive communities, density compensation is not predicted for lost species. Thus, unsaturated/weakly-interactive communities are likely to show strong effects of local diversity on ecosystem function (Ruesink and Srivastava 2001). This conclusion agrees with several theoretical models for BD-EF relationships. The “niche differentiation” or “efficiency” effect (Tilman et al. 1997, Loreau 1998a, 1998b, 2000) is predicted to result in strong BD-EF correlations when niche overlap is minimal between species, as in unsaturated, weakly-interactive communities.

If we combine all the above effects, saturated communities should exhibit minimal effects of reduced re-

gional richness on local ecosystem function; not only is regional richness decoupled from local richness but local richness itself is not linked to ecosystem function

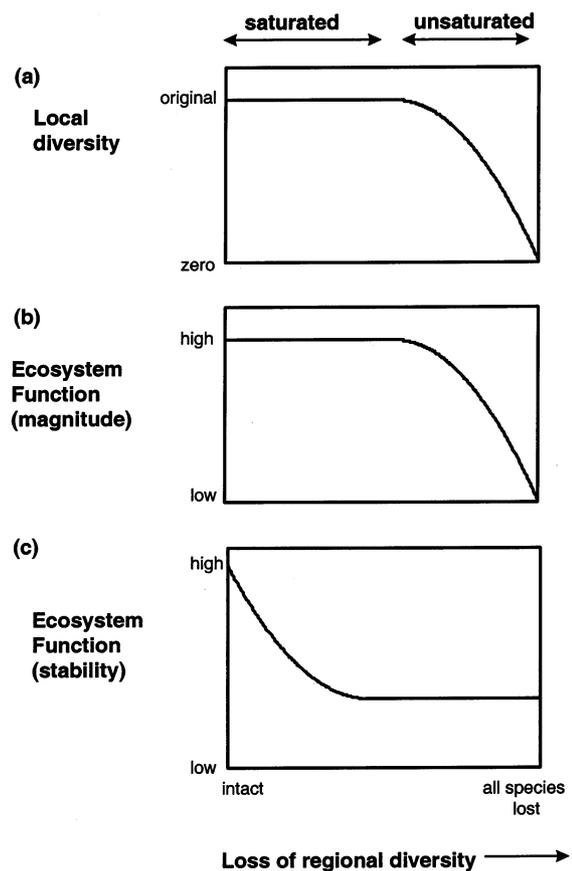


Fig. 4. (a) Loss of regional diversity may have minimal affect on local diversity as long as communities are saturated with species. When communities become unsaturated with species, local diversity will fall, reducing (b) local ecosystem function. (c) Stability is predicted to show the opposite relationship with regional diversity. The exact shapes of these relationships are unclear.

because of strong interspecific competition (Fig. 3b). Conversely, in unsaturated communities strong links from regional richness to local richness through to ecosystem function should ensure a strong role for regional richness in determining ecosystem function (Fig. 3c). Note that here I am considering ecosystem consequences of extinctions in a single region, rather than simply variance in richness between regions; in the latter case, ecosystem functions likely become drivers not responders of diversity (Huston 1997, Hector et al. 1999, Loreau 2000). Given that the consequences of reduced regional biodiversity for ecosystem function will differ between saturated and unsaturated communities, it seems imperative that ecologists begin to distinguish between these types of communities in both BD-EF theory and experiments. There are a number of ways to test for saturation, including biogeographical comparisons, evidence of competition and density compensation, and monitoring invasion effects (Ricklefs and Schluter 1993, Srivastava 1999).

It should be clear by now that BD-EF experiments carried out at the local scale cannot simply be “scaled-up” to the regional scale. There is no straightforward link between regional extinctions and changes in ecosystem function; rather, regional extinctions must be translated to biodiversity changes at the local scale before ecosystem function can be altered. Nor can we ignore the importance of regional-level changes in biodiversity. Ecologists will do conservation a great disservice if we do not make clear that the effects of biodiversity loss depend on scale. Some forestry companies are already describing clear cuts as having biodiversity value because they contain more species per hectare than the original forest. If we only value biodiversity at the local scale, the forest companies may be right; however, if we view clear cuts as replacing regionally-rare old-growth species with common secondary-growth species, the logic no longer holds. There is also a superb opportunity for ecological theory here, to construct a truly multi-scale theory of biodiversity which integrates regional and landscape-level processes with the effects of small-scale interactions between species.

### **Regional biodiversity and ecosystem stability**

Biodiversity may be critical not only for maintaining the current *magnitude* of ecosystem function, but also its *stability* over time. Stability has much value for human society. Unexpected drops or surges in ecological processes can destabilize local economies, disrupt social systems, and discourage investment. Recent examples of catastrophic ecosystem failure include the crash of Eastern Canada’s cod stocks, landslides in deforested areas of Central America, and the drying-up

of the Aral Sea. Regional biodiversity can be linked to the stability of ecosystem function in two ways: by providing an adequate species pool for strongly-interactive communities, and by providing a reservoir of potentially important species for the future.

Most hypotheses which link biodiversity to the stability of ecosystem function require strong interspecific interactions (Ruesink and Srivastava 2001). To give one example, the competition hypothesis (Tilman 1996, Naeem and Li 1997) suggests that reduction in the abundance of any species in high diversity communities is likely to be matched by an increase in the abundance of a competitor. Thus strong competitive interactions result in dampened variation in total abundance, and hence ecosystem function. (Low diversity communities, by contrast, are less likely to contain appropriate competitors, so have greater variation). This hypothesis has been supported by some models (Tilman et al. 1997, 1998) but not others (Ives et al. 1999, Loreau and Behara 1999). According to the logic of the previous section, we would expect saturated communities to have the strong competitive interactions required for stability. Ironically, in saturated communities, local biodiversity may be strongly correlated with the stability of ecosystem function but weakly correlated with its magnitude (see also Ruesink and Srivastava 2001). As species go regionally extinct, local communities will tend to be less and less saturated with species, and have increasingly less stable ecosystem functions (Fig. 4c).

High regional richness may also stabilize ecosystem functions in periods of dramatic environmental change. The “insurance hypothesis” (Tilman 1996, Yachi and Loreau 1999) proposes that communities depauperate in species are less likely to contain a species critical to maintaining ecosystem function under different environmental conditions in the future. If we expand this argument to the regional scale, then regions depauperate in species are less likely to be able to contain a species critical for maintaining local ecosystems in the future. Thus, even if reductions in regional richness do not affect local richness today (for example, because local communities are saturated with species), there may be consequences for future ecosystem function. This interpretation of the insurance hypothesis confers a local stability benefit to regional scale biodiversity, and draws attention to the value of beta diversity, that is, spatial differences in species composition.

### **How can regional diversity be manipulated?**

Regional extinctions need to be explicitly incorporated into experiments and models. Of course, it is very difficult in practice to manipulate biodiversity at the regional level. This scale constraint could be circumvented in a variety of ways. First of all, changes in

regional diversity can be simulated by supplying local experimental plots with propagules representing different numbers of species (i.e., different “species pools”), not all of which will establish. In some ways, this experiment is already being conducted by plant ecologists. Recent experiments as part of the BIODEPTH project (e.g. Hector et al. 1999) and Cedar Creek program (e.g. Tilman et al. 1996) involved seeding plots with a constant mass of seeds representing different numbers of species (different species pools), only some of which survived in the plots (different local diversities). In both cases, there were strong links between planned and actual local diversity and between planned diversity and ecosystem function, implying strong effects of the species pool on ecosystem function. In a similar vein, Levine (2000) described how landscape-level variation in plant propagule supply affected native plant diversity on river tussocks, which in turn affected (in controlled experiments) the invasion resistance of each tussock to exotic species.

A second approach is to use small-bodied species in appropriately small-sized landscapes to make manipulations of regional diversity manageable. Ideal candidates for this type of experiment are protist communities and micro-arthropod communities. In protist communities, correlations between local and regional diversity have been shown (Fox et al. 2000), and between local diversity and ecosystem function (Naeem and Li 1997, Petchey et al. 1999), but not yet between true regional diversity and ecosystem function. In the micro-arthropod communities on moss, secondary productivity appears to be linked to local richness (Gonzalez and Chaneton 2002). We (A. Gonzalez and D. Srivastava) are now conducting experiments in which we manipulate the regional richness of moss micro-arthropods by changing the size of large patches of moss (“regions”), to examine the effect first on local diversity and then on ecosystem function.

A third approach is to use various “natural experiments”, such as are provided by recent regional extinctions or declines (for example, bird species on Guam), species invasions (Vitousek 1990), or biogeographic effects on diversity (Feinsinger et al. 1982, Wardle et al. 1997). I provide examples of each of these in turn. The *rapid population decline* of Aleutian island sea otters triggered a trophic cascade resulting in an order of magnitude decline in kelp productivity, an important marine ecosystem function (Estes et al., 1998). By contrast, the sudden loss of North American chestnut trees due to blight had remarkably little effect on the Lepidopteran species which formerly fed upon this tree: only 7 of 56 Lepidopteran species went extinct (Pimm 1991). *Invading species* occasionally have dramatic effects on ecosystem functions. For example, invasion of Hawaii by the exotic shrub *Myrica faya* has quadrupled nitrogen inputs in early-succession ecosystems (Vitousek 1990). Many other invasive species, by contrast,

may have little effect on ecosystems (Vitousek 1990). It is also still not clear if the ecosystem effects of adding an exotic species are expected to be symmetrical to the effects of losing a native species. *Island biogeographic effects* are particularly well-documented for the Caribbean islands. The island of Tobago has a smaller regional species pool of hummingbirds (5 species) than the island of Trinidad (16 species), presumably because of its smaller size and longer period of isolation. This difference in regional diversity appears to have resulted in lower (and more variable) pollination rates of many flower species on Tobago relative to Trinidad (Feinsinger et al. 1982).

## Conclusion

The origin of the BD-EF hypothesis represents a tremendous opportunity to link the disciplines of community ecology and conservation. This is, however, not a natural partnership. Community ecologists are trained to ask questions about mechanism and, to do so, abstract communities from complicating external factors. This makes ecologists excellent detectives, but poor forecasters. Without knowing the relative importance of these “externalities” it is difficult to predict how important a particular mechanism (in this case biodiversity loss) will be in the future. Unfortunately, conservation requires precisely this type of forecasting ability: policymakers generally decide on conservation measures by weighing the likelihood of success against the costs. I have outlined how BD-EF research could incorporate three “externalities”: causes of extinctions, patterns of extinctions, and the spatial scale of extinctions. Each of these directions would make biodiversity research more applicable to conservation. Furthermore, each direction is made possible by integrating existing ecological theory into the current BD-EF framework, creating a more comprehensive theory of biodiversity. Both ecology and conservation would benefit by such an expansion of the scope of BD-EF research.

Biodiversity is a challenging phenomenon to study, for it reflects the confluence of ecological, evolutionary and anthropogenic processes, many of which operate on different spatial and temporal scales. Some of the most exciting recent advances in biodiversity research reflect links made between these different processes and scales (Ricklefs and Schluter 1993, Gaston 2000, Schluter 2000). Ecologists are now on the brink of linking human activity with the functional effects of biodiversity. Our success in this endeavor will depend on our creativity in translating conservation concerns into testable ecological hypotheses.

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