

Long-Term and Large-Scale Perspectives on the Relationship between Biodiversity and Ecosystem Functioning

AMY J. SYMSTAD, F. STUART CHAPIN III, DIANA H. WALL, KATHERINE L. GROSS, LAURA F. HUENNEKE, GARY G. MITTELBACH, DEBRA P. C. PETERS, AND DAVID TILMAN

In a growing body of literature from a variety of ecosystems is strong evidence that various components of biodiversity have significant impacts on ecosystem functioning. However, much of this evidence comes from short-term, small-scale experiments in which communities are synthesized from relatively small species pools and conditions are highly controlled. Extrapolation of the results of such experiments to longer time scales and larger spatial scales—those of whole ecosystems—is difficult because the experiments do not incorporate natural processes such as recruitment limitation and colonization of new species. We show how long-term study of planned and accidental changes in species richness and composition suggests that the effects of biodiversity on ecosystem functioning will vary over time and space. More important, we also highlight areas of uncertainty that need to be addressed through coordinated cross-scale and cross-site research.

Keywords: biodiversity, ecosystem functioning, spatial scale, temporal scale, community–ecosystem interactions

Ecologists have historically been interested in the relationship between biodiversity and ecosystem functioning. Widespread loss of diversity caused by anthropogenic forces has heightened this interest and fostered a desire to determine the mechanisms underlying these relationships. Species diversity is expected to affect ecosystem processes, because the number and kinds of species present determine the specific traits represented in an ecosystem. Species traits may directly mediate energy and material fluxes or may alter abiotic conditions (e.g., disturbance, climate, and limiting resources) that regulate process rates. The components of species diversity that determine this expression of traits in an ecosystem include the number of species present (species richness), their relative abundances (species evenness), the particular species present (species composition), the interactions among species (nonadditive effects), and the temporal and spatial variation in these properties.

Research conducted at sites in the Long Term Ecological Research (LTER) Network provides long-term data not only from observations of natural variation but also from experimental manipulation of populations, communities, and ecosystems. This information is essential for determining the temporal and spatial scales at which species traits and species diversity exert their effects—information crucial for resolving recent debates surrounding the interpretation of experiments designed to examine the relationship between biodiversity and ecosystem functioning and the applicability of

those experiments to the “real world” (e.g., Huston 1997, Huston et al. 2000, Wardle et al. 2000). In this overview we explore how the many types of research from LTER sites contribute to our understanding of the relationship between ecosystem functioning and the components of diversity described above. Following the theme of this special section and of the LTER program, we focus on how the spatial and temporal scales of studies of diversity and ecosystem functioning may influence their results. (We use “functioning” to mean “showing activity”; this term avoids any implication that

Amy J. Symstad (e-mail: asymstad@inhs.uiuc.edu) was with the Illinois Natural History Survey in Savanna, IL, when this article was prepared; she is now a research ecologist with the US Geological Survey, Mount Rushmore National Memorial, Keystone, SD 57751-0268. F. Stuart Chapin III is a professor at the Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775. Diana H. Wall is a professor and director of the Natural Resource Ecology Laboratory at Colorado State University, Fort Collins, CO 80523. Katherine L. Gross is a professor in the Department of Plant Biology, and Gary G. Mittelbach is a professor in the Department of Zoology, at Michigan State University; Gross and Mittelbach are based at the W. K. Kellogg Biological Station in Hickory Corners, MI 49060. Laura F. Huenneke is a professor and department chair in the Department of Biology at New Mexico State University, Las Cruces, NM 88003-8001. Debra P. C. Peters is a research scientist at the US Department of Agriculture, Agricultural Research Service, Jornada Experimental Range, New Mexico State University, Las Cruces, NM 88003-0003. David Tilman is director of the Cedar Creek Natural History Area and McKnight Presidential Chair in Ecology in the Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108. © 2003 American Institute of Biological Sciences.

organisms perform purposeful roles in ecosystem-level processes.)

A first step in discerning the effects of biodiversity, including species or functional group richness and composition, on ecosystem functioning is to directly manipulate these factors in an experimental setting where other factors (climate, soil type, etc.) are held constant and the resulting effects on ecosystem functioning are measured. Such experiments are a relatively new phenomenon, which began in the early 1990s. Two such experiments at the Cedar Creek LTER site have been at the forefront of this avenue of research. The first of these, initiated in 1994, consists of 3-meter (m) \times 3 m plots planted with 1, 2, 4, 6, 8, 12, or 24 plant species. The composition of each plot was determined by a separate random draw from a pool of 24 species. The second experiment, also initiated in 1994, is similar, except that the plots are 9 m \times 9 m and planted with 1, 2, 4, 8, or 16 species randomly chosen from a pool of 18 species.

Both experiments show that, as the number of species planted increases, total community plant biomass increases and the level of unconsumed soil nitrate decreases. However, they also show that functional group composition of plots is as important as species richness in controlling these measures of ecosystem functioning (Tilman et al. 1997). These results, and those from a multiple-site experiment across Europe (BIODEPTH [BIODiversity and Ecosystem Processes in Terrestrial Herbaceous Ecosystems]; Hector et al. 1999), stimulated vigorous debate. Were these results caused by sampling effects, resulting from the higher probability that more diverse plots would contain and become dominated by a highly productive species? Or were they caused by complementarity effects: that is, did the differences in the ecological niches of species lead to more complete use of resources in more diverse plots (e.g., Huston 1997, Wardle 1999, Huston et al. 2000)? Analyses of the Cedar Creek results suggest that both mechanisms were responsible for the positive relationships found between diversity and ecosystem functioning, with sampling effects explaining much of the correlation early in the experiment (1 to 3 years) but longer-term results (5 to 6 years) being more consistent with the mechanism of complementarity (Tilman et al. 2001).

The loss of biodiversity is just one component of the changes occurring in ecosystems throughout the world. Questions about how diversity loss may interact with other aspects of global change are being addressed in a third synthetic community experiment, BioCON (Biodiversity, CO₂, and Nitrogen), at the Cedar Creek LTER site (Reich et al. 2001). In this experiment, plant diversity is manipulated in combination with atmospheric carbon dioxide (CO₂) and nitrogen (N) deposition, again in small plots. The results of the first 2 years of BioCON confirmed the diversity–biomass and diversity–soil nitrate relationships found in the other two Cedar Creek experiments. In addition, biomass accumulation in response to elevated CO₂ or N was greater in species-rich than in species-poor plots, both because the more diverse plots were more likely to contain dominant species (sampling

effect) and because of niche differentiation (complementarity effect). Continuation of this experiment will help determine whether these short-term (2-year) results will change over time as community composition shifts and soil microbial feedbacks kick in (Reich et al. 2001).

This type of research—highly controlled experimental manipulation—has been instrumental in addressing the potential consequences of biodiversity loss and generating new research ideas. In addition, some issues surrounding these experiments, particularly the relative importance of sampling and complementarity effects, are being resolved through new analyses of longer-term data. However, the relevance of these results to the real-world problem of local and global biodiversity loss still remains in question, at least partially because plots are small and the synthesized communities are assembled randomly from relatively small species pools. Ecologists need to consider how such controlled studies relate to issues raised by biodiversity changes in species-rich systems with multiple trophic levels, at large spatial scales and over long time frames.

Spatial effects on diversity–functioning relationships

The spatial scale at which an ecological study is conducted depends on the size of the organisms and the properties of the ecosystem involved, but also on logistical constraints. The size of a study also determines the level of detail at which any one component of an ecosystem can be investigated and, consequently, how the results are interpreted. No single experiment can manipulate all components of biological diversity and measure the reactions of all aspects of functioning in a single ecosystem, let alone across different ecosystems. However, the unusually complete understanding of an ecosystem that comes from long-term coordinated research at LTER sites provides valuable information for discerning the implications of diversity–functioning studies for spatial scales other than those at which they were conducted. In this section we illustrate how research designed outside the biodiversity–ecosystem functioning framework yields valuable insight as to how diversity–functioning relationships may vary across spatial scales.

Spatial patterns of soil biodiversity. Spatial patterns of soil organism richness and composition, as well as spatial relationships between soil organisms and habitat structure, illustrate how the spatial scale of a biodiversity–functioning study may influence study results. For microbes and microfauna, local diversity effects may occur at the scale of micrometers, whereas for larger invertebrates and vertebrates they occur at the scale of centimeters to meters. The diversity of these organisms is influenced by habitat properties, which also vary at different scales.

Vegetation, organic matter, and edaphic properties all affect soil diversity, but which factor is most influential differs among ecosystems. In deserts or other ecosystems where vegetation is scarce or absent, edaphic factors determine the structure of soil communities. For example, in the McMurdo

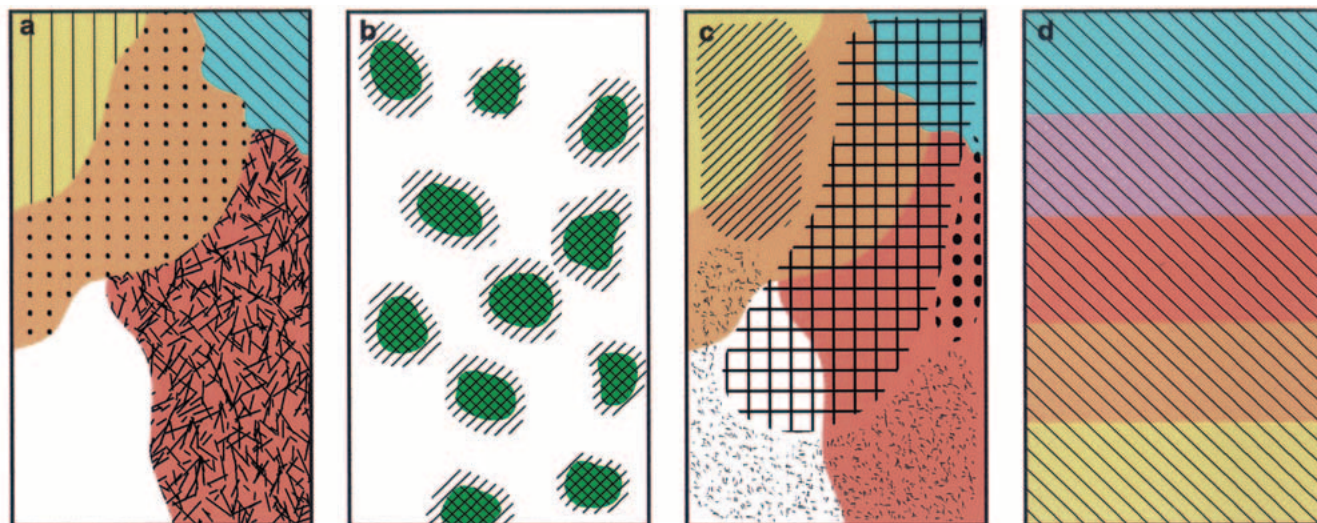


Figure 1. Spatial relationships between soil communities (patterns) and biotic or abiotic factors (colors) in the environment. (a) In desert or other environments with little or no vegetation, soil community composition corresponds closely to edaphic factors. (b) In semiarid ecosystems dominated by shrubs, soil communities are most diverse under and in the near vicinity of shrubs. (c) In productive grasslands, biotic (e.g., plant community) and edaphic factors interact to affect soil community composition and diversity in often unpredictable ways. (d) Soil community composition may be relatively insensitive to different agricultural practices if edaphic factors are consistent across treatments.

Dry Valleys LTER site in Antarctica, variation in the diversity of soil nematode communities across the landscape depends on edaphic factors such as organic carbon (C), salts, and soil moisture (figure 1a; Courtright et al. 2001). In contrast, the distribution of soil biodiversity in semiarid ecosystems, such as the Jornada Basin and Shortgrass Steppe LTER sites, is highly dependent on the patchy spatial pattern of the vegetation. At these sites, biodiversity in the soil below plants is greater than in the adjacent exposed soil. This suggests that the plants serve as “resource islands,” providing higher organic matter pools (e.g., roots and litter) and higher rates of ecosystem processes such as mineralization (figure 1b; Herman et al. 1995). In more productive ecosystems, where vegetation cover is more continuous, soil biodiversity still varies considerably across space, but the relationship to plant community or soil properties is unclear (figure 1c; Broughton and Gross 2000). At the Kellogg Biological Station LTER site, soil microbial community structure has not responded after 7 years to different management treatments ranging from conventional tilling to successional field (figure 1d; Buckley and Schmidt 2001). This may be a consequence of the historical legacy of disturbance, as seen at the Harvard Forest LTER site (Foster and Motzkin 1998), or it may be that soil characteristics that influence microbial communities—total C and N, for example—require decades or centuries to equilibrate with the plant community (Wardle 2002).

These examples show how the coupling between soil community diversity and edaphic or biotic factors differs among ecosystems. Although these studies were done in the context of understanding how these factors affect soil communities, they also suggest that the spatial scale at which soil community diversity influences ecosystem functioning differs among

ecosystems. In places like McMurdo, diversity effects may be limited at any scale because ecosystem functioning is strongly influenced by edaphic factors. In semiarid shrublands, diversity effects may depend on the spatial distribution of plants. In productive ecosystems, diversity effects of the soil community on ecosystem functioning may be more difficult to predict because of the multitude of factors involved. Few experiments directly testing the effect of soil community diversity on ecosystem functioning have been performed (but see van der Heijden et al. 1998). The LTER Network, with its variety of ecosystems, provides an excellent forum for testing these predictions and determining the mechanisms that underlie these relationships across spatial scales.

Productivity–diversity relationships. A number of experimental studies have shown significant positive effects of species richness on ecosystem productivity in relatively small experimental plots. However, as we mentioned earlier, it is unknown how these effects scale up to larger ecosystems, or to changes in species richness across natural gradients of diversity within and across communities. Studies of the reverse relationship—how species richness varies with productivity—have a much longer history in ecology (Rosenzweig 1995) and have been examined across spatial scales ranging from within communities to across entire continents. These studies demonstrate the importance of scale in determining the relationship between productivity and species diversity, and their results provide insights into how diversity influences ecosystem functioning at larger scales.

For example, a recent meta-analysis of published productivity–diversity relationships (Mittelbach et al. 2001) showed that, for vascular plants, the relationship between

productivity and species number was generally unimodal (hump-shaped) in studies conducted at local and regional geographic scales but became more linearly positive at large (continental) scales, such as the latitudinal gradient. The relationship also differed among ecological scales. For terrestrial plants, studies that crossed community types more commonly detected a unimodal relationship than studies within a single community type, possibly because studies that crossed communities tended to encompass a greater range of productivity.

The studies reviewed by Mittelbach and colleagues (2001) represent a heterogeneous collection of sampling methodologies and data types. Ideally, the collection of data across sites should be standardized to better examine the effects of scale on any ecological relationship. Gross and colleagues (2000) used data collected with similar (but not identical) methods from a number of LTER sites to more closely examine the impact of scale on productivity–diversity relationships in plant communities. Using consistent measures of diversity (number of species per m²) and productivity (peak aboveground plant biomass from clipped plots) in herb-dominated terrestrial communities from six LTER sites, Gross and colleagues (2000) found a significant unimodal relationship between productivity and diversity at the largest scale, that is, when data from individual fields were compared across a biogeographic region. The same hump-shaped pattern was found when data from all six LTER sites (including old-fields, short- and tallgrass prairies, arctic and alpine meadows) were included and when only the grassland sites were used in the analyses. However, at the smaller scale of individual fields within an LTER site, productivity and diversity were significantly related at only one site, and this relationship was negatively linear. The findings of Gross and colleagues (2000) confirm the importance of geographic and ecological scale in determining the relationship between productivity and species diversity, although the patterns differ somewhat from those reported by Mittelbach and colleagues (2001).

Recently, Chase and Leibold (2002) contrasted local and regional patterns of species diversity and productivity in aquatic (pond) communities. They found a significant unimodal productivity–diversity relationship at the local scale (among ponds) for both plants and animals, but a significant positively linear relationship at the landscape scale (among watersheds) because of decreasing similarity in species composition as productivity increased. The authors suggested that this difference in community similarity might have occurred because of differences in community assembly processes between low- and high-productivity sites, with high-productivity sites having a greater possibility for multiple stable states.

The same concepts, including competitive exclusion and niche packing, have been invoked to explain both productivity–diversity and diversity–ecosystem functioning relationships. These concepts are generally more applicable at local scales, and so have generally been successful at explaining results of small-scale biodiversity–ecosystem functioning experiments. However, larger-scale properties such as

differences in soil fertility and climate, which can also influence productivity–diversity relationships, may more strongly affect ecosystem functioning than does diversity (Huston and McBride 2002) at scales larger than the experimental plot. In addition, community assembly processes such as those mentioned by Chase and Leibold (2002), which are often affected by regional-scale properties, have not yet been incorporated into biodiversity–ecosystem functioning theory or experimentation. Clearly, we have a long way to go to determine the importance of biodiversity to ecosystem functioning at large spatial scales. Moreover, future research will need to reconcile the positive relationships between species richness and ecosystem productivity observed in experimental manipulations with the variety of productivity–diversity patterns observed in nature (Loreau et al. 2001).

Scaling up from small plots in single ecosystems. One of the difficulties in achieving this reconciliation and extrapolating results from small, controlled experiments is that experiments in which biodiversity is directly manipulated on the scale of entire ecosystems are nearly impossible to conduct. However, ecosystem simplifications that simulate anthropogenic disturbances indirectly reveal effects of species composition on ecosystem functioning. Whole-lake acidification experiments have had large effects on the species composition of food webs but comparatively small effects on ecosystem processes such as respiration and phytoplankton production (Schindler 1990). These results are at odds with the predictions of small-scale experiments showing that species loss or changes in species composition can have major effects on ecosystem functioning (e.g., Duffy et al. 2001, Downing and Leibold 2002).

Schindler and colleagues (1985) suggest that the relatively minor effects of compositional changes in the food webs of these whole-lake acidifications demonstrate the importance of species compensation and the role of colonization of new species from the regional species pool. The opportunities for species colonization and replacement in controlled laboratory or weeded field experiments are obviously limited, which may point to an important caveat in extrapolating the results of small-scale or short-term experiments to estimate the ecosystem impacts of biodiversity loss in nature. Diversity at the landscape scale will influence these colonization and replacement processes. For example, successional trajectories after fire in forested ecosystems such as at the Bonanza Creek LTER site in Alaska often depend on landscape patterns of seed availability and resprouting potential (Van Cleve et al. 1991). Integrating these landscape and community processes with actual patterns of diversity loss at different spatial scales will be necessary for making such extrapolations.

Another issue related to scaling up from meter-scale plots to kilometer-scale ecosystems is whether the patterns found in one ecosystem are relevant to other ecosystems. For example, a removal experiment has shown that the relative importance of biotic versus abiotic factors for ecosystem functioning varies among ecosystems. By excluding all soil

fauna from some litter bags and leaving the fauna intact in others, Gonzalez and Seastedt (2001) compared faunal effects on litter decomposition and N mineralization rates of the same litter among ecosystems with very different abiotic conditions: wet and dry tropical forests at the Luquillo LTER site and subalpine forests at the Niwot Ridge LTER site. They found that both the abiotic factor (climate) and the biotic factor (soil fauna presence) significantly affected ecosystem processes. However, soil fauna had a disproportionately large effect on decomposition and mineralization in the wet tropical forest, compared with the dry tropical forest and subalpine forests. Removing all soil fauna is an extreme example of diversity reduction, but this study serves as an example of how experiments on biodiversity and ecosystem functioning in different environmental conditions could yield strikingly different results. The LTER Network provides excellent opportunities for this type of cross-site comparison.

Such a cross-site experiment has been performed in the European BIODEPTH program, which manipulated plant species and functional group richness in eight grasslands from Greece to Sweden. In this experiment, plant diversity positively affected aboveground plant biomass when all sites were combined, and only one site differed from the overall pattern when sites were examined separately (Hector et al. 1999). At the Greek site, the dominance and high productivity of one species at low levels of diversity resulted in no significant relationship between plant species richness and productivity. This dominant species was one of the few perennial species in the annual-dominated community at this site, whereas all the other sites included only perennial species (Troumbis et al. 2000).

This result suggests two factors to consider when extrapolating results from one ecosystem to others. First, the addition of a different growth form to a relatively simple community (e.g., shrub invasion in a perennial grassland) may produce different diversity–functioning relationships because the range of possible interactions among species changes (Hochstrasser 2001). Second, dominant species have varying effects on the community and ecosystem depending on context. This phenomenon is illustrated by the results of a simulation model based on data from three LTER sites (Peters and Herrick 2002). An individual plant–based model (ECOTONE) was used to simulate the response of functional groups (perennial grasses, shrubs, perennial forbs, and annuals) to a multiyear drought that occurred in 1976–1977 at three grassland LTER sites (Shortgrass Steppe, Sevilleta, and Jornada Basin). At all of these sites, the dominant grass species (*Bouteloua* spp.) failed to

establish during the drought, but after the drought ended and *Bouteloua* became established, the biomass of remaining plant functional groups decreased (figure 2). Annuals suffered the greatest loss in biomass—a 73% to 94% decrease—at all three sites when the dominant species appeared, but other remaining functional groups' responses differed across sites. At the Shortgrass Steppe and Jornada Basin sites, the establishment of the dominant *Bouteloua* species caused decreases in biomass that were relatively consistent across all functional groups (figure 2a, 2b), whereas at the Sevilleta site, perennial grasses and annuals were affected more than shrubs when the two codominant *Bouteloua* species became established (figure 2c). These dominant species presumably exert large influences on ecosystem functioning, not only directly but also indirectly through their effects on the diversity of the rest of the community.

Together, these examples illustrate how the effects of diversity on ecosystem functioning may vary among ecosystems because of differences in dominant species, in abiotic conditions, and in the interactions between biotic and abiotic processes and properties. In addition, they show that, in order to successfully scale up the results of small-scale biodiversity–ecosystem functioning experiments and the theory behind them to make accurate predictions about how biodiversity loss affects functioning on the ecosystem scale, community assembly and species colonization processes need to be incorporated.

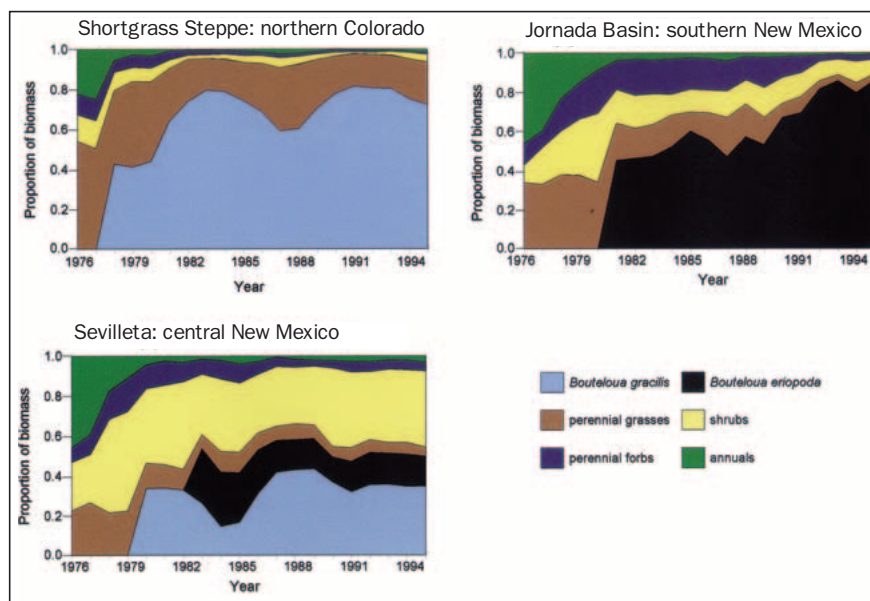


Figure 2. Proportion of total aboveground biomass through time for the dominant species (*Bouteloua gracilis*, *Bouteloua eriopoda*) and one of four species groups at three LTER sites, as simulated with ECOTONE, an individual plant–based model. The model uses daily climatic data, soil texture by depth, and species-specific recruitment, growth, and mortality parameters to simulate individual plant, population, and community responses to drought (1976–1977) while controlling for other extrinsic factors, such as disturbance. Plots were initialized without plants in the first year of the simulation. Illustration: Peters and Herrick (2002).

Temporal effects on diversity–functioning relationships

Because colonization, recruitment, and assembly processes often take a long time, long-term ecological research is often the only way to observe and understand these processes and their effects on ecosystem functioning. Most experiments explicitly designed to test the effect of biodiversity on ecosystem functioning are still relatively young and short-term. However, these and other research projects have already supplied some insight into how biodiversity affects the stability of ecosystem functioning through time, as well as into how and why the short- and long-term effects of biodiversity on ecosystem functioning may differ.

Biodiversity and stability of ecosystem functioning. One common argument made to justify efforts to preserve biodiversity is that greater diversity leads to greater stability (Naeem 1998). Whether this statement is true, however, has been a matter of strong debate since MacArthur (1955) suggested it more than four decades ago. Long-term monitoring of an LTER experiment has shed some light on the resolution of this debate and in turn inspired advancements in ecological theory that suggested mechanistic hypotheses that have subsequently been tested in other systems.

At the Cedar Creek LTER site, a long-term N-addition experiment initiated in grassland fields in 1982 resulted in plots with plant species richness levels ranging from 1 to 22 species per 0.3 m². Aboveground biomass of all individual plant species has been sampled in every plot each year since then. Analyses of these data following a major drought in 1987–1988 revealed that total plant community biomass in plots with greater plant diversity was about five times more resistant to drought than in plots with one or two plant species (Tilman and Downing 1994), in part because the low-diversity plots had the highest rates of N addition and were therefore dominated by less drought-resistant species. There was also a highly significant tendency for plots with higher diversity to have less year-to-year variation in total biomass (figure 3a; Tilman 1996), suggesting that greater plant diversity may increase the stability of total plant community biomass. These relationships remained significant even after statistically controlling for the effects of N-addition rate, subsequent changes in community biomass and composition, and other potentially confounding variables. Thus, whether stability was measured as resistance to a major perturbation or as lower year-to-year variation, greater plant diversity was associated with greater stability in total community biomass. Individual species, however, had greater year-to-year variation in abundance in higher-diversity plant communities (figure 3b; Tilman 1996).

This seeming paradox—that each member of a community was less stable, but the sum of these members was more stable, at higher diversity—is resolved by the explanation that, first, compensating shifts in the abundance of individual species stabilize the entire community (McNaughton 1977, Chapin and Shaver 1985, Tilman 1996), and, second,

averaging larger numbers of random variables reduces variability through statistical effects (Doak et al. 1998). Simple models based on data from the Cedar Creek grasslands provide theoretical backing for these mechanisms as potential causes of the observed results. Lehman and Tilman (2000) found that three different models of exploitative multispecies competition for limiting resources all predicted that the mechanisms of interspecific interaction that led to coexistence of species also caused, on average, greater total community biomass and stability, as well as lower stability of individual species, in more diverse communities.

The apparent effects of diversity on stability observed in the Cedar Creek N-addition experiment were controversial because diversity was not under direct experimental control (Huston 1997). Rather, diversity effects had to be inferred after statistical control for more than 20 different potentially confounding variables that had been measured. However,

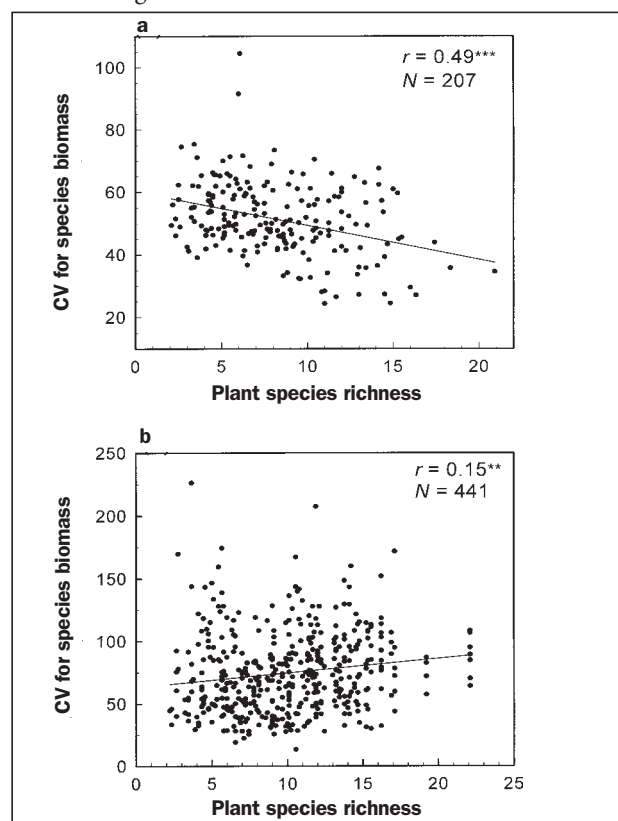


Figure 3. Stability of aboveground biomass related to plant species richness in 207 grassland plots at the Cedar Creek LTER site. (a) Relationship between coefficient of variation (CV) for community biomass and plant species richness. Each point represents a plot for which the y-axis represents the CV of biomass from 1984 to 1994, excluding the drought years of 1987 and 1988, and the x-axis is the average species richness of the plot for the same time period. Illustration modified from Tilman (1999). (b) As in (a), but CVs are determined for common individual species. r = Pearson correlation coefficient; N = sample size; ** = significant at $P < 0.01$; *** = significant at $P < 0.001$. Illustration modified from Tilman (1996).

this criticism led to new long-term experiments for which LTER sites are ideally suited, including those described at the beginning of this article. When the next drought or plague of locusts comes along, these experiments will be ready to test the diversity–stability hypothesis directly. More data are clearly needed, as recent experiments in other ecosystems have yielded conflicting results (e.g., Pfisterer and Schmid 2002).

Short-term versus long-term effects of diversity on ecosystem functioning.

Long-term data are needed to understand not only the effect of biodiversity on stability of ecosystem functioning but also the processes behind differences in short-term and long-term results of diversity–functioning experiments. In some cases, biodiversity may seem to have little effect on ecosystem functioning in the short term, but in the long term it may have significant effects. For example, late-successional boreal forests at the Bonanza Creek LTER site are typically dominated by a single tree species (white or black spruce) that has significant effects on ecosystem processes such as water and energy exchange (Chapin et al. 2000). Early successional trees, shrubs, and herbaceous species constitute only a small percentage of the production. Following fire, these early-successional species resprout and dominate the burned area. The spatial distribution and diversity of these resprouts govern the spatial pattern of tree establishment (Cater and Chapin 2000) and the long-term successional trajectory of the stand (Mann and Plug 1999). Other early-successional species that contribute substantially to two ecosystem functions—nutrient retention and productivity—of early successional stands are present only in the seed bank in the soil or recruit from other small patches of disturbance in the landscape (Vioreck 1973). Thus, species that are rare and have little effect on ecosystem functioning in one stage of the disturbance cycle may be critical to the productivity and nutrient retention at other phases, suggesting that the diversity of these forests is essential to the ecosystem's long-term functioning even when it plays a relatively minor role in the short term.

An experiment at the Jornada Basin LTER site expressly designed to investigate the effect of a dominant species on ecosystem functioning revealed that the response of even an herbaceous ecosystem can be slow, compared with the typical length of time that experiments are monitored. In this study the dominant perennial grass, *Bouteloua eriopoda*, was removed from diverse semiarid grassland plots in 1994. Even after 6 years, including both dry and wet years, the species composition and abundances of other plant species in removal plots remained virtually identical to those in control plots (Baggs 1997). Observations over the longer term are necessary to confirm the lack of response of other species to such a dramatic removal (loss of 50% or more of original cover). Responses of other ecosystem components were subtle; for example, only slight decreases in soil organic matter were observed over time, and only longer-term observations were able to detect significant effects.

This pattern also often occurs when a species or functional group is introduced to an ecosystem, as illustrated by the cascading effects of the reintroduction of a top predator into a temperate lake (Mittelbach et al. 1995). In this case, a natural event (heavy snowfall and subsequent low wintertime oxygen levels) eliminated largemouth bass (*Micropterus salmoides*) from Wintergreen Lake, Michigan. When bass were reintroduced 9 years later in 1987 (figure 4a), there was a dramatic decrease in the abundance of planktivorous fish (figure 4b), followed by the reappearance of large zooplankton (*Daphnia*; figure 4c) and a significant increase in water clarity (measured by average Secchi depth; figure 4d) caused by *Daphnia* grazing on algae. The dramatic increase in water clarity did not occur until the 5th year after the bass were reintroduced, however, apparently because the decreasing predation on *Daphnia* did not reach some lower threshold until this time. The invasion of an alien species, the rusty crayfish (*Orconectes rusticus*), into Trout Lake at the North Temperate Lakes LTER site in Wisconsin showed an even longer delay. More than 20 years elapsed from the first detection of rusty crayfish in Trout Lake to their eventual spread and dominance throughout the lake. Today, this invasion has led to a significant loss of macrophyte species diversity, declines in macroinvertebrate abundance, a shift in fish species composition, and the virtual elimination of native crayfish (Wilson 2002).

In addition to these observational studies, experiments in aquatic systems show that changes in community structure and composition significantly affect ecosystem functioning. However, the effects in these experiments occurred much more quickly. One- to three-year removals of the top trophic level from whole lakes or small enclosures within lakes resulted in significant changes in nutrient dynamics and transport (Schindler et al. 1997, Vanni et al. 1997), thermal stratification (Mazumder et al. 1990), and ecosystem productivity (Perin et al. 1996). The differences in reaction time between these observational and experimental studies, as well as the differences we discussed earlier in the context of spatial scale, illustrate the importance of understanding the remaining community's potential for compensation and the processes that affect how long it takes for that compensation to occur. These factors will determine how similar the short-term and long-term effects of biodiversity loss are.

In an experiment at the Cedar Creek LTER site, short-term effects of biodiversity reduction on ecosystem functioning were greater than long-term effects, but how long the short-term effects lasted varied among treatments. In this study, in which plant diversity and composition were manipulated by removing all possible combinations of zero, one, or two functional groups (forbs, graminoids using the C_3 photosynthetic pathway, and graminoids using the C_4 photosynthetic pathway), the response time of different treatments to the removals depended on the ability of remaining functional groups to colonize open space. These differences in recruitment limitation among functional groups in turn affected ecosystem properties such as aboveground plant

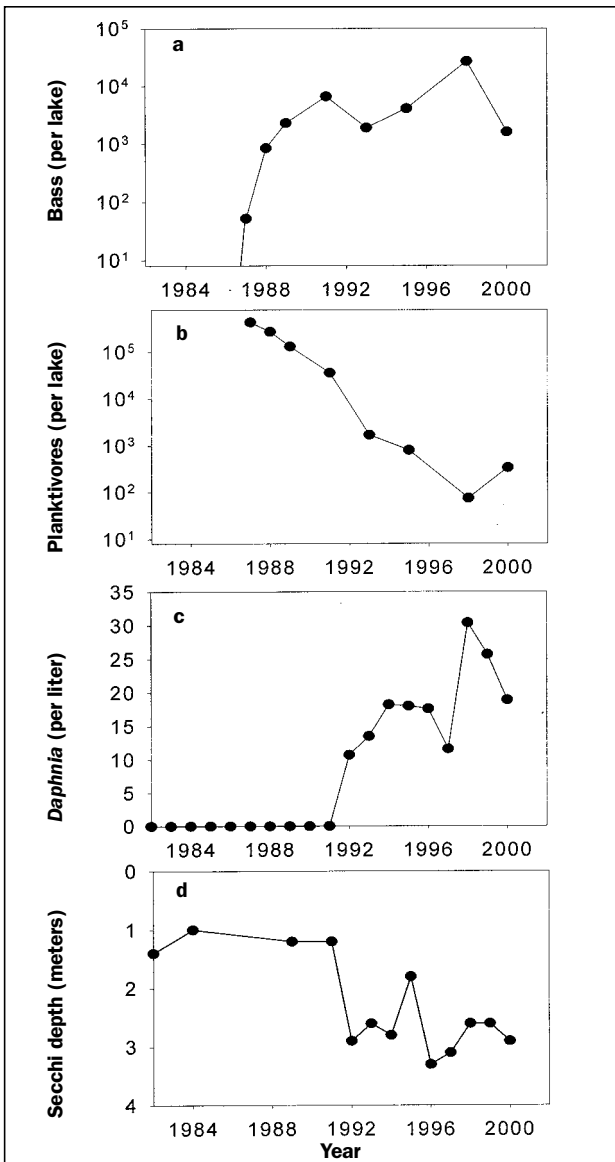


Figure 4. Cascading effects across trophic levels following the reintroduction of a top predator, the largemouth bass (*Micropterus salmoides*), to Wintergreen Lake, MI. Pre-1994 data are from Mittelbach and colleagues (1995).

biomass and soil N-leaching rates (Symstad and Tilman 2001). In this case, even in the treatments that reacted more slowly, compensation had occurred within 5 years of the original removal. In the classic experiments of Brown and colleagues, compensation did not occur until 20 years after a keystone functional group was removed. In 1977 (before the LTER Network existed), fences that excluded different components of the small mammal community were erected around large plots in the Chihuahuan Desert. Long-term study of these plots has shown large effects of kangaroo rats (*Dipodomys* spp.) on numerous aspects of animal and plant community structure (Heske et al. 1993). In addition, energy flow, in terms of seed resources consumed, in plots from which kangaroo rats were excluded was only approximately 33% of that in control plots. This changed in 1996, when a

pocket mouse species (*Chaetodipus baileyi*) with feeding habits similar to those of the kangaroo rats appeared at the site for the first time. By 1999 energy flow in the kangaroo rat-free plots had rebounded to approximately 80% of that in control plots (Ernest and Brown 2001). It remains to be seen, however, whether the new pocket mouse species will have similar effects on the plant and rodent communities.

In some cases, not only is ecosystem response slow to be expressed, but long-term responses may differ qualitatively from initial or transient responses. In 1995 a plant diversity experiment was established in a diverse shrubland at the Jornada Basin LTER site. Treatments included removal of all individuals of particular functional groups (e.g., removal of all shrubs or of all perennial grasses) and reduction of species diversity within functional groups. Erosion of surface sediment was monitored with collection pans on the downslope margin of each plot, because redistribution of surface soil and organic matter is thought to be a critical aspect of ecosystem change in desertified or desertifying systems. Overall sediment erosion rates were much higher in the first 2 years than they were later, probably reflecting the disturbance of the original treatments. More important, the pattern of treatment differences changed over time. In early sample periods, treatments involving removal of shrubs had significantly higher erosion rates. After several years, however, the treatments involving removal of most or all perennial grass cover had the highest erosion rates (figure 5; Huenneke et al. 2000).

Another aspect of short-term versus long-term effects of biodiversity loss demonstrated by these experiments, particularly by the plant removals, is related to diversity within functional groups. Initial classification of functional groups of species in both the Jornada Basin and the Cedar Creek experiments followed conventions of growth form and physiology based on evidence that these traits determine how species affect ecosystem functioning. At Jornada Basin, virtually all shrubs use the C_3 photosynthetic pathway, the important perennial grasses use the C_4 pathway, and the leaf and stem succulents use crassulacean acid metabolism (they close their stomata during the day). Because photosynthetic pathway and growth form are strongly correlated with phenology of resource use, the designation of species into these functional groups seemed straightforward. However, experimental removals of species within functional groups have demonstrated substantial variation among species within these groups. For example, the two most abundant perennial grasses in the Jornada Basin community responded very differently to the removal of shrubs. At Cedar Creek, the dominant C_4 grass (a perennial) failed to colonize open space, whereas subordinate annual C_4 grasses increased slightly in response to removals.

These examples illustrate how species with similar effects on ecosystem functioning (functional effect groups sensu Landsberg 1999) may not respond to a change in the environment in the same way. Conversely, species that respond in the same fashion (functional response groups; Landsberg 1999) often vary in the traits that affect ecosystem function-

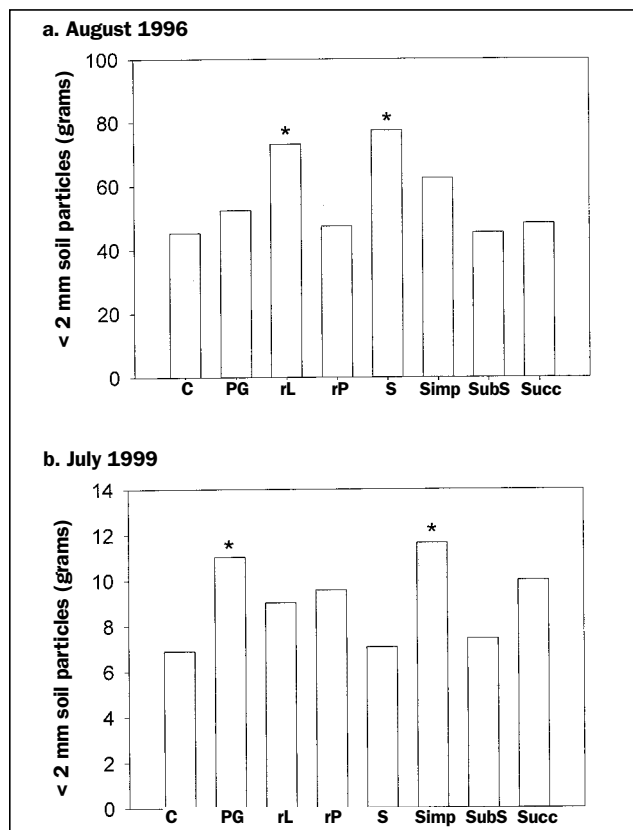


Figure 5. Soil surface erosion, as reflected in accumulation of mineral soil particles less than 2 millimeters (mm) in diameter in collection pans, 1 year (a) and 4 years (b) after removal of plant species or species groups in a desert shrubland of the Jornada Basin LTER site. Treatments: C, control; PG, all perennial grasses removed; rL, removal of dominant species of each functional type, including removal of *Larrea* (creosote bush); rP, removal of dominant species of each functional type, where *Prosopis* (mesquite) was removed rather than *Larrea*; S, all shrubs removed; Simp, simplified, or dominant species of each functional type retained while all subordinate species were removed; SubS, all subshrubs removed; Succ, all stem and leaf succulents removed. An asterisk (*) indicates those treatments in which accumulation was significantly different from that in control plots.

ing (Lavorel and McIntyre 1999). This suggests that short-term effects of diversity loss on ecosystem functioning will be influenced by the functional traits of the organisms lost, whereas long-term effects will depend not only on the functional traits of the remaining organisms but also on their response traits. Depending on how these different factors balance out, the direct, short-term effects may be substantially different from the indirect, long-term effects of diversity loss.

Conclusions

A growing body of literature from LTER and other sites shows strong evidence that various components of biodiversity affect ecosystem functioning in a variety of ecosystems when conditions are highly controlled. The LTER studies we have highlighted illustrate how long-term and cross-scale research

projects are particularly important for addressing temporal and spatial scale issues that are difficult or impossible to address in these highly controlled situations.

Clearly, however, there is still much work to be done in this arena. Among the questions that our examples have raised are these: Given that the coupling between soil community diversity and edaphic or biotic factors varies among ecosystems, what does this imply for the effect of soil flora and fauna composition and richness in productive versus unproductive ecosystems? Are the mechanisms behind observed relationships between productivity and diversity the same as those behind the effects of experimental manipulations of biodiversity on productivity? What are the relative effects of biodiversity loss compared with those of other components of global change (climate change, CO₂ enrichment, habitat fragmentation) on the sustainability of ecosystem functioning? How do community assembly processes influence differences between short-term and long-term, small-scale and large-scale effects of diversity loss?

The time frames at which different mechanisms of biodiversity–functioning relationships and consequences of local diversity loss occur are just now becoming evident as LTER experiments truly become long-term. The spatial scales over which diversity contributes to ecosystem processes need closer examination, but more cross-site comparisons of LTER projects could yield interesting insights. Long-term research such as that conducted at the LTER sites, and the collaboration that is facilitated by the LTER Network, will play an important role in finding the answers to these and other exciting questions.

References cited

- Baggs JE. 1997. The role of *Bouteloua eriopoda* in the community structure and ecosystem function of a semi-arid grassland. Master's thesis. New Mexico State University, Las Cruces.
- Broughton LC, Gross KL. 2000. Patterns of diversity in plant and soil microbial communities along a productivity gradient in a Michigan old-field. *Oecologia* 125: 420–427.
- Buckley DH, Schmidt TM. 2001. The structure of microbial communities in soil and the lasting impact of cultivation. *Microbial Ecology* 42: 11–21.
- Cater TC, Chapin FS III. 2000. Differential effects of competition or micro-environment on boreal tree seedling establishment after fire. *Ecology* 81: 1086–1099.
- Chapin FS III, Shaver GR. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66: 564–576.
- Chapin FS III, et al. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology* 6: S211–S223.
- Chase JM, Leibold MA. 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416: 427–430.
- Courtright EM, Wall DH, Virginia RA. 2001. Determining habitat suitability for soil invertebrates in an extreme environment: The McMurdo Dry Valleys, Antarctica. *Antarctic Science* 13: 9–17.
- Doak DF, Bigger D, Harding EK, Marvier MA, O'Malley RE, Thomson D. 1998. The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist* 151: 264–276.
- Downing AL, Leibold M. 2002. Ecosystem consequences of species richness and composition in pond food webs. *Nature* 416: 837–841.

- Duffy JE, Macdonald KS, Rhode JM, Parker JD. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. *Ecology* 82: 2417–2434.
- Ernest SKM, Brown JH. 2001. Delayed compensation for missing keystone species by colonization. *Science* 292: 101–104.
- Foster DR, Motzkin G. 1998. Ecology and conservation in the cultural landscape of New England: Regional forest dynamics in central New England. *Ecosystems* 1: 96–119.
- Gonzalez G, Seastedt TR. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82: 955–964.
- Gross KL, Willig MR, Gough L, Inouye R, Cox SB. 2000. Patterns of species density and productivity at different scales in herbaceous plant communities. *Oikos* 89: 417–427.
- Hector A, et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123–1127.
- Herman RP, Provencio KR, Herrera-Matos J, Torrez RJ. 1995. Resource islands predict the distribution of heterotrophic bacteria in Chihuahuan Desert soils. *Applied and Environmental Microbiology* 61: 1816–1821.
- Heske EJ, Brown JH, Guo QF. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant-species diversity in the Chihuahuan Desert. *Oecologia* 95: 520–524.
- Hochstrasser T. 2001. Pattern and process at a desert grassland–shrubland ecotone. PhD dissertation. Colorado State University, Fort Collins.
- Hueneke LF, Buonopane M, Bothern L, Herrick JE. 2000. Effects of plant removals on soil surface erosion in a Chihuahuan Desert shrubland. Paper presented at the 85th Annual Meeting of the Ecological Society of America; August 6–10, 2000; Snowbird, UT.
- Huston MA. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449–460.
- Huston MA, McBride A. 2002. Evaluating the relative strengths of biotic versus abiotic controls of ecosystem processes. Pages 47–60 in Loreau M, Naeem S, Inchausti P, eds. *Biodiversity and Ecosystem Functioning—Synthesis and Perspectives*. Oxford (United Kingdom): Oxford University Press.
- Huston MA, et al. 2000. No consistent effect of plant diversity on productivity. *Science* 289: 1225.
- Landsberg J. 1999. Response and effect—different reasons for classifying plant functional types under grazing. Pages 911–915 in Eldridge D, Freudenberger D, eds. *People and Rangelands: Building the Future*. Proceedings of the 6th International Rangeland Congress. Aitkenvale (Australia): International Rangeland Congress.
- Lavorel S, McIntyre S. 1999. Plant functional types: Is the real world too complex? Pages 905–911 in Eldridge D, Freudenberger D, eds. *People and Rangelands: Building the Future*. Proceedings of the 6th International Rangeland Congress. Aitkenvale (Australia): International Rangeland Congress.
- Lehman CL, Tilman D. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156: 534–552.
- Loreau M, et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294: 804–808.
- MacArthur RH. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36: 533–536.
- Mann DH, Plug LJ. 1999. Vegetation and soil development at an upland taiga site, Alaska. *Ecoscience* 6: 272–285.
- Mazumder A, Taylor WD, McQueen DJ, Lean DRS. 1990. Effects of fish and plankton on lake temperature and mixing depth. *Science* 247: 312–315.
- McNaughton SJ. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. *American Naturalist* 111: 515–525.
- Mittelbach GG, Turner AM, Hall DJ, Rettig JE, Osenberg CW. 1995. Perturbation and resilience: A long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76: 2347–2360.
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Naeem S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12: 39–45.
- Perin S, Pick FRA, Lean DRS, Mazumder A. 1996. Effects of planktivorous fish and nutrient additions on primary production of shallow versus deep (stratified) lake enclosures. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1125–1132.
- Peters DPC, Herrick JE. 2002. Modelling vegetation change and land degradation in semiarid and arid ecosystems: An integrated hierarchical approach. *Advances in Environmental Monitoring and Modelling* 1. (26 November 2002; www.kcl.ac.uk/kis/schools/hums/geog/advem/vol1no2/petersfinal.pdf)
- Pfisterer AB, Schmid B. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* 416: 84–86.
- Reich PB, et al. 2001. Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition. *Nature* 410: 809–812.
- Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge (United Kingdom): Cambridge University Press.
- Schindler DW. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57: 25–41.
- Schindler DW, Mills KH, Malley DF, Findlay DL, Shearer JA, Davies JJ, Turner MA, Linsey GA, Cruikshank DR. 1985. Long-term ecosystem stress: The effects of years of experimental acidification on a small lake. *Science* 228: 1395–1401.
- Schindler DE, Carpenter SR, Cole JJ, Kitchell JF, Pace ML. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277: 248–251.
- Symstad AJ, Tilman D. 2001. Diversity loss, recruitment limitation, and ecosystem functioning: Lessons learned from a removal experiment. *Oikos* 92: 424–435.
- Tilman D. 1996. Biodiversity: Population versus ecosystem stability. *Ecology* 77: 350–363.
- . 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80: 1455–1474.
- Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300–1302.
- Tilman D, Reich P, Knops J, Wedin D, Mielke T, Lehman C. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294: 843–845.
- Troumbis AY, Dimitrakopoulos PG, Siamantziouras ASD, Memtsas D. 2000. Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos* 90: 549–559.
- Van Cleve K, Chapin FS III, Dryness CT, Viereck LA. 1991. Element cycling in taiga forest: State-factor control. *BioScience* 41: 78–88.
- van der Heijden MGA, Klironomos JN, Ursic M, Moutoglou P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72.
- Vanni MJ, Layne CD, Arnott SE. 1997. “Top-down” trophic interactions in lakes: Effects of fish on nutrient dynamics. *Ecology* 78: 1–20.
- Viereck LA. 1973. Wildfire in the taiga of Alaska. *Quaternary Research* 3: 465–495.
- Wardle DA. 1999. Is “sampling effect” a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* 87: 403–407.
- . 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton (NJ): Princeton University Press.
- Wardle DA, Huston MA, Grime JP, Berendse F, Garnier E, Lauenroth WK, Setälä H, Wilson SD. 2000. Biodiversity and ecosystem function: An issue in ecology. *Bulletin of the Ecological Society of America* 81: 235–239.
- Wilson KA. 2002. Impacts of the invasive rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. PhD dissertation. University of Wisconsin, Madison.