

Biodiversity and Ecosystem Functioning

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Annu. Rev. Ecol. Evol. Syst. 2014. 45:471–93

First published online as a Review in Advance on October 1, 2014

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-120213-091917

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Keywords

biodiversity, ecosystem functioning, stability, productivity, invasibility, complementarity, niche differentiation, coexistence

Abstract

Species diversity is a major determinant of ecosystem productivity, stability, invasibility, and nutrient dynamics. Hundreds of studies spanning terrestrial, aquatic, and marine ecosystems show that high-diversity mixtures are approximately twice as productive as monocultures of the same species and that this difference increases through time. These impacts of higher diversity have multiple causes, including interspecific complementarity, greater use of limiting resources, decreased herbivory and disease, and nutrient-cycling feedbacks that increase nutrient stores and supply rates over the long term. These experimentally observed effects of diversity are consistent with predictions based on a variety of theories that share a common feature: All have trade-off-based mechanisms that allow long-term coexistence of many different competing species. Diversity loss has an effect as great as, or greater than, the effects of herbivory, fire, drought, nitrogen addition, elevated CO₂, and other drivers of environmental change. The preservation, conservation, and restoration of biodiversity should be a high global priority.

1. INTRODUCTION

Biodiversity is now known to be a major determinant, perhaps the major determinant, of community and ecosystem dynamics and functioning. This discovery, which required two decades of research by hundreds of ecologists from around the world, represents a major reversal from the paradigm of the 1970s through the 1990s. In many ways, the hundreds of experiments, the numerous theoretical explorations, and the observational studies that led to this paradigm shift mark a maturation of the standards of evidence for resolving debates in ecology. Unlike some earlier ecological debates that arose when a paradigm was challenged, the biodiversity and ecosystem functioning debate was resolved not via rhetoric but by successive rounds of publication of new data and theory.

On the basis of natural history observations and qualitative comparisons across habitats, Elton (1958) proposed that greater diversity led to greater ecosystem stability, greater resistance to invasion by exotic species, and lower disease incidence. His ideas were widely accepted but put aside in the 1970s as ecology transitioned toward being a more mechanistic, quantitative, experimental, and theoretical discipline. May (1973), building on the work of Gardner & Ashby (1970), led this transition by presenting numerous lines of mathematical theory showing that stability, as defined by the dominant eigenvalue of the Jacobian matrix for a differential equation model of multispecies interactions, was lower when models had more interacting species. The theoretical demonstration that individual species were less stable at higher biodiversity levels sparked debate about the effects of diversity on the stability of natural ecosystems. A review of the literature (Goodman 1975) found little quantitative evidence for the diversity-stability hypothesis and concluded that there was no evidence of a link between diversity and stability. McNaughton (1977) defended the validity of the diversity-stability hypothesis and asserted that empirical evidence, not theory, should be the arbiter of ideas in ecology. However, the rigor of May's theory outweighed the scant evidence then available. For the second printing of his book, May (1974) added an alternative resolution to the debate—that ecosystem properties could be more stable at higher diversity even as population stability was lower. This possibility, however, was generally overlooked for two decades.

Ecology's focus then shifted to (*a*) using field experiments and theory to study interactions among a few species and (*b*) examining the effects of the traits of individual species on ecosystem processes. Inspired by Hutchinson (1959), researchers began to focus on the causes of high diversity, rather than its effects, as they pursued the question of why so many competing species coexisted in nature. A few researchers, notably Pimm (1979, 1984), Vandermeer (1981), Ehrlich & Ehrlich (1981), and McNaughton (1985), continued to pursue the effects of diversity on ecosystems, but the Eltonian diversity paradigm had, for the moment, been replaced by an individualistic paradigm—that interspecific interactions among a few dominant species determined community and ecosystem processes and dynamics.

2. A REAWAKENING

As concerns about habitat destruction and the potential impacts of the loss of biodiversity mounted (Ehrlich & Ehrlich 1981; Myers 1990; Wilson 1988, 1989), assertions that biodiversity loss could impact ecosystem functioning led to a conference in Germany and a book edited by Schulze & Mooney (1993). Notable chapters by Swift & Anderson (1993), Vitousek & Hooper (1993), and McNaughton (1993), among others, presented plausible cases for the hypothesis that greater diversity could lead to greater primary productivity, more efficient use of limiting resources, and

greater ecosystem stability. These possibilities raised four critical questions, the evidence for which we review in this article:

1. Are diversity effects real—that is, can they be documented in well-designed experiments?
2. What underlying processes and mechanisms could cause changes in diversity to impact ecosystem functioning?
3. How general are diversity effects?
4. How important are diversity effects—that is, how large are they relative to effects of other factors?

In 1994, two papers presented evidence supporting the emerging biodiversity and ecosystem functioning hypotheses. The first paper (Tilman & Downing 1994) was based on >200 grassland plots that differed in diversity and composition because of different rates of nitrogen addition, among other reasons. Annual data from before and during a major drought showed that the primary productivity of plots containing more plant species was more resistant to drought (and thus more stable) and that this apparent effect of biodiversity on stability remained highly significant even after the paper's authors statistically controlled for many potentially confounding variables, including rates of nitrogen addition and species composition (**Figure 1a**) (Tilman & Downing 1994). Next, a study of experimentally assembled laboratory foodwebs showed that more diverse foodwebs had, among other ecosystem properties, greater primary productivity (**Figure 1b**) (Naeem et al. 1994). A related greenhouse experiment found that primary productivity was greater in pots planted with more species (**Figure 1c**) (Naeem et al. 1995).

3. THE ADVENT OF BIODIVERSITY FIELD EXPERIMENTS

Field experiments have become a major arbiter of alternative ecological ideas, concepts, and theories, as well as a major generator of new ideas and concepts. The first results of a replicated field experiment that manipulated plant species numbers appeared in 1996 (Tilman et al. 1996). This small biodiversity experiment (termed small because each plot was 3×3 m) at Cedar Creek Ecosystem Science Reserve in Minnesota had several levels of plant diversity and many replicate plots at each level. The species composition of each plot was randomly determined to avoid biases that could be caused by traits of particular species. High replication and randomized species compositions allow statistical tests for effects of diversity and simultaneously allow tests for effects of functional group or species composition within limits set by the collinearity of these variables.

In the second year of the experiment (1995), primary productivity, as estimated by total plant cover, increased with plant species numbers (**Figure 1d**). In this nitrogen-limited ecosystem, nitrate is the form of nitrogen readily taken up by plants and for which they compete. Plants drew soil nitrate down to lower concentrations at higher diversity (**Figure 1d**), and less nitrate leached from the rooting zone at higher diversity. A related survey of 120 plots (each 1×1 m) in nearby native grasslands showed that total plant abundance, similarly estimated, increased with plant species numbers and that soil nitrate concentrations decreased (Tilman et al. 1996).

Two additional biodiversity field experiments highlighted the effects of plant functional diversity and functional group composition on ecosystem functioning. An experiment in a California serpentine grassland found that plant functional group composition (i.e., which plant functional groups were present in each plot) was generally a more important determinant of primary productivity and soil nitrate than was the number of functional groups (**Figure 1g**) (Hooper & Vitousek 1997). A second Cedar Creek study, the big biodiversity experiment (termed big because each plot was 9×9 m), found that primary productivity and the amount of nitrate left unconsumed in

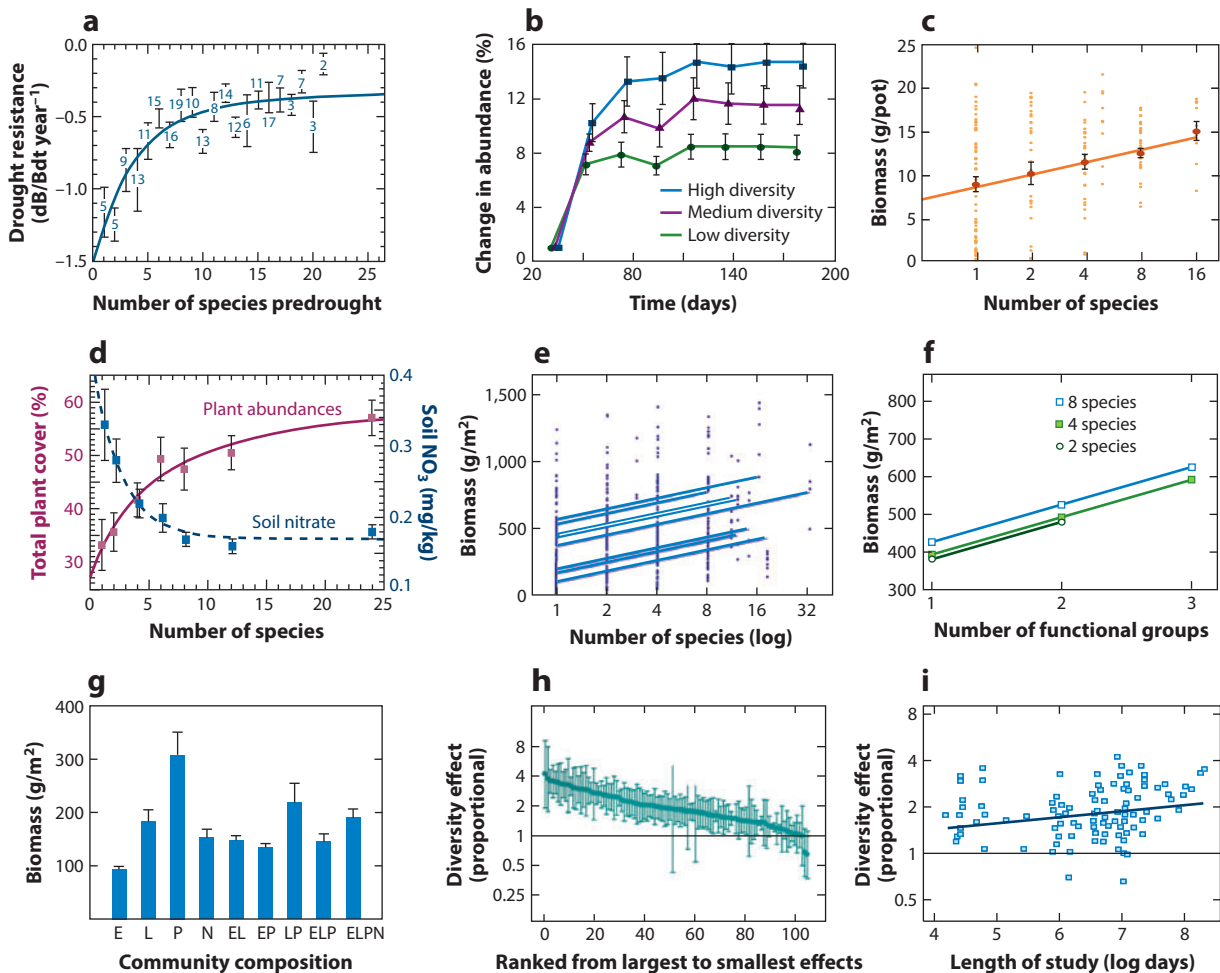


Figure 1

Relationships among species richness, functional composition, and ecosystem function. Increasing species number (*a*) increases drought resistance; high resistance is associated with a low rate of biomass decline during drought (Tilman & Downing 1994). Increasing species number also (*b*) increases vegetation cover (Naeem et al. 1994) and (*c*) increases biomass in a greenhouse experiment (Naeem et al. 1995). (*d*) Plant abundances (summed percent covers, *solid line*) increase, whereas soil nitrate (*dashed line*) decreases (more is taken up by plants) with increasing plant species numbers (Tilman et al. 1996). Aboveground biomass increases with both (*e*) the number of species and (*f*) the number of functional groups (Hector et al. 1999). (*g*) Aboveground biomass depends on plant community composition (Hooper & Vitousek 1997). Abbreviations: E, early-season annuals; L, late-season annuals; P, perennial bunchgrasses; N, nitrogen fixers. (*h,i*) Diversity effect is plant productivity at high diversity divided by that of monocultures for ~100 experiments, with diversity effects (*h*) ranked from largest to smallest effects and (*i*) graphed against length of study (ln of number of days, where “7” = 3 years) (Cardinale et al. 2007). Error bars indicate 1 SEM (standard error of the mean). Figure panels adapted from cited sources with permission.

the soil were simultaneously highly dependent on both functional diversity and functional composition (Tilman et al. 1997a). These variables were similarly dependent on plant species number, thus suggesting that functional differences among plant species were a likely reason that plant diversity increased primary productivity and decreased soil nitrate. The number of species within

a functional group was also a significant determinant of productivity, and there was a significant positive interaction between C4 grasses and legumes.

The trans-European BIODDEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems) biodiversity experiment imposed similar biodiversity treatments across eight sites ranging from Sweden to Portugal to Greece, thus giving the study's authors the power to make broad inferences about the generality of diversity and ecosystem functioning in European grasslands (Hector et al. 1999). Across all eight sites, the dependence of primary productivity on plant species number was described by log-linear relationships, with productivity thus being an increasing but decelerating function of plant species numbers (**Figure 1e**). Moreover, at each level of plant species number, productivity was an increasing linear function of the number of functional groups (**Figure 1f**).

4. CAUSES OF BIODIVERSITY EFFECTS: CONCEPTS, THEORY, AND DEBATE

These studies were generally interpreted by their authors as suggesting that diversity effects arose because greater species numbers led to greater trait diversity, which was the hypothesized direct cause of the observed responses. Alternative explanations offered soon thereafter initiated a prolonged debate (Aarssen 1997, Doak et al. 1998, Grime 1998, Huston 1997, Huston et al. 2000, Wardle et al. 1997).

Huston (1997) suggested that biodiversity was not the actual cause of greater stability in high-diversity plots following drought (Tilman 1996, Tilman & Downing 1994), nor of greater productivity in the foodweb experiment (Naeem et al. 1994, 1995), nor of greater productivity and greater use of soil nitrate in the Cedar Creek biodiversity experiments (Tilman et al. 1996). Rather, Huston proposed that the results were caused by "hidden treatments" that correlated with biodiversity: impacts of nitrogen fertilization on species composition and water limitation in the stability study; nonrandom or replicated species composition in the foodweb experiment; and a "selection effect," also proposed by Aarssen (1997), for the Cedar Creek biodiversity experiments. This selection effect was hypothesized to result from differences in the fundamental productivities of species, as revealed in monocultures, and from the greater likelihood that a more productive species would be present ("selected") at higher diversity.

Using data from an observational study on small islands, Wardle et al. (1997) suggested that environmental factors were a more important correlate of ecosystem processes than was plant diversity, and they used these findings to critique experimental results. Doak et al. (1998) proposed that the reported effects of plant diversity on the stability of primary productivity (Tilman & Downing 1994) could be due to statistical averaging rather than interspecific niche complementarity. Finally, Grime (1998) argued that species' effects on ecosystem processes were simply proportional to species' productivities. The resultant dialogue helped clarify ways to distinguish selection from niche complementarity; the causes of overyielding; the causes of diversity-stability relationships; and the roles of species number, evenness, phylogenetic diversity, and functional trait diversity.

Just as experiments are a major arbiter of the predictions of different theories, mathematical theory has become an arbiter of the logical strength of alternative ideas and concepts. Indeed, it seems that ecologists treat unexpected observations or experimental results for which there is no rigorous logical explanation with the same skepticism that they apply to theory that lacks an empirical basis. We take particular note when theoretical predictions, experimental results, and observations all concur.

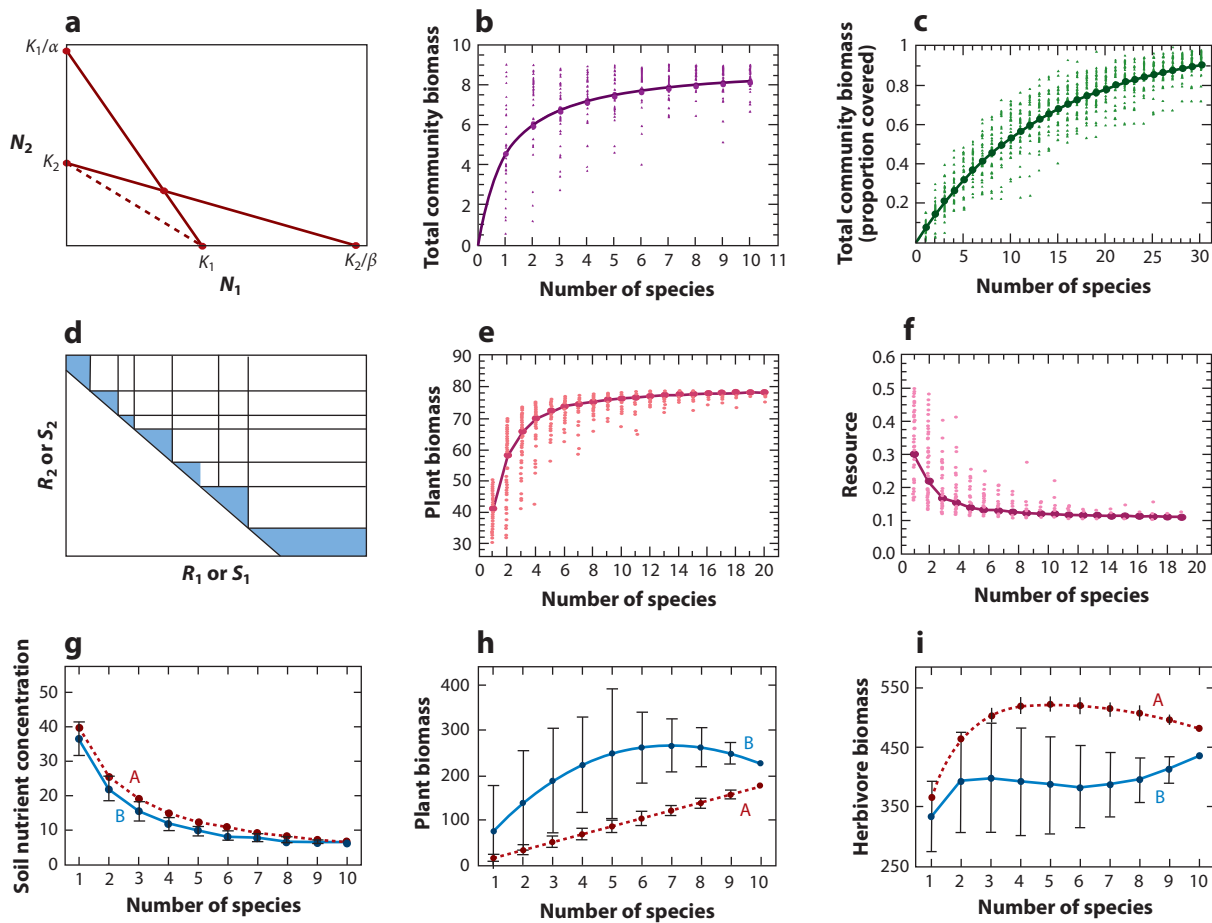


Figure 2

Theoretical considerations of biodiversity and ecosystem functioning. (a) Species coexistence and overyielding for the Lotka-Volterra competition model, with N_1 and N_2 representing abundances of species 1 and 2. The two-species equilibrium point is outside the dashed line, resulting in overyielding. (b) A model of selection effects predicts a flat upper bound for dependence of community biomass on species numbers (Tilman et al. 1997b). (c) A model of niche differentiation and coexistence predicts an increasing upper bound, characteristic of complementarity effects (Tilman et al. 1997b). (d) Competition between multiple species for two limited resources. Unused resources are indicated by the shaded areas (Tilman et al. 1997b). (e-f) This model predicts (e) increasing productivity and increasing upper and lower bounds of productivity, and (f) greater resource use; thus, lower concentrations are left over (shown) at higher species numbers (Tilman et al. 1997b). (g-i) Model of Thébault & Loreau (2003) shows how increasing plant species numbers affect a food chain, including (g) concentrations of unused soil nutrients, (h) plant community biomass, and (i) herbivore community biomass. Line A represents food chains containing a single resource, variable numbers of plant species, and one herbivore species for each plant species; line B represents similar chains, but with one herbivore-resistant plant species and one fewer herbivore species.

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4.1. Diversity-Productivity Theory

Classic models of coexistence of two competing species predict that coexistence can lead to overyielding (Harper 1977, Vandermeer 1981). A simple example can be seen in a phase plane graph of stable Lotka-Volterra competitive coexistence (Figure 2a), which requires that each species inhibit itself more than it inhibits the other species, as indicated by $K_1 < K_2/B$ and $K_2 < K_1/a$. The line from K_1 to K_2 shows linear combinations of the abundances of these

two species set by their carrying capacities. The two-species equilibrium point (where the two isoclines cross) is outside this line; for cases like that shown, species 1 and 2 have greater summed abundances than either could achieve on its own; thus, they overyield when they coexist.

The concepts and ideas proposed both by the authors of observational and experimental studies and by their critics were soon formalized into mathematical theories. A model of the equilibrium outcome of competition among any number of species for a single limiting resource (**Figure 2b**) (Tilman et al. 1997b), which was proposed as a simple model of the effects of diversity, also meets the assumptions that Huston (1997) and Aarssen (1997) said led to an artifactual effect of diversity on productivity. That model provides a diagnostic signature for selection effects. It predicts that primary productivity would be an increasing function of species numbers; that a single species would displace all other species from each plot; and that the upper bound of variation would be flat, meaning that the productivity of the highest diversity plots would be no greater than the productivity of the single best species in monoculture. The lower bound of the variation would be an increasing function of diversity (**Figure 2b**). The flat upper bound and lack of long-term multispecies coexistence result from a selection effect.

In contrast, niche trade-off models of competition and coexistence make a markedly different prediction. In such models, both the upper and lower bounds of variation in productivity are predicted to increase with diversity (**Figure 2c**) (Tilman et al. 1997b). The increasing upper bound means that, given sufficient replication, some combinations of a given number of coexisting species are more productive than any possible species combination of lower diversity. Thus, overyielding that results from niche differentiation and multispecies coexistence has, as its signature, an increasing upper bound (**Figure 2c,e**).

Such models of interspecific competition among stably coexisting species predict that community productivity increases with increasing diversity while levels of unconsumed resources decline. This scenario is predicted by five models: (*a*) a model of competition for two essential resources (**Figure 2d-f**) (Tilman et al. 1997b), (*b*) a model of competition for a single limiting resource in a spatially structured ecosystem model (Loreau 1998), (*c*) a model of competition for a single resource along a fluctuating temperature gradient (Lehman & Tilman 2000), (*d*) a model of competition in a two-dimensional niche space (Tilman et al. 1997b), and (*e*) a modified broken-stick model (Lehman & Tilman 2000). However, Loreau (1998) found that the local effects of plant diversity on ecosystem processes could be masked by spatial heterogeneity in environmental conditions, potentially making it difficult for observational studies to detect the effects of plant diversity on ecosystem processes. The similarity of the predictions based on these five models suggests that the same processes and mechanisms that allow stable coexistence of competing species may also cause community productivity and resource use to increase with diversity.

Later theoretical studies considered models with greater trophic complexity (e.g., limiting plant resources, plant species, herbivore species), finding that plant biomass does not always increase with increasing plant diversity (**Figure 2g-i**) (Thébaud & Loreau 2003). For example, increases in diversity within both plant and herbivore trophic levels often, but not always, lead to greater plant biomass. Increasing the diversity of herbivores (consumers) may decrease plant biomass (their resources), in a manner similar to the way in which increasing the diversity of plants may decrease their resources, i.e., soil nutrient concentrations (Thébaud & Loreau 2003). Analysis of a simple linear food chain revealed that the equilibrium abundance of any particular trophic level converged on an intermediate value as the number of trophic levels increased (Loreau 2010).

4.2. Diversity-Stability Theory

Numerous theoretical analyses of the effects of the number of competing species in a community on the stability of individual species and on the stability of the summed abundances of all species

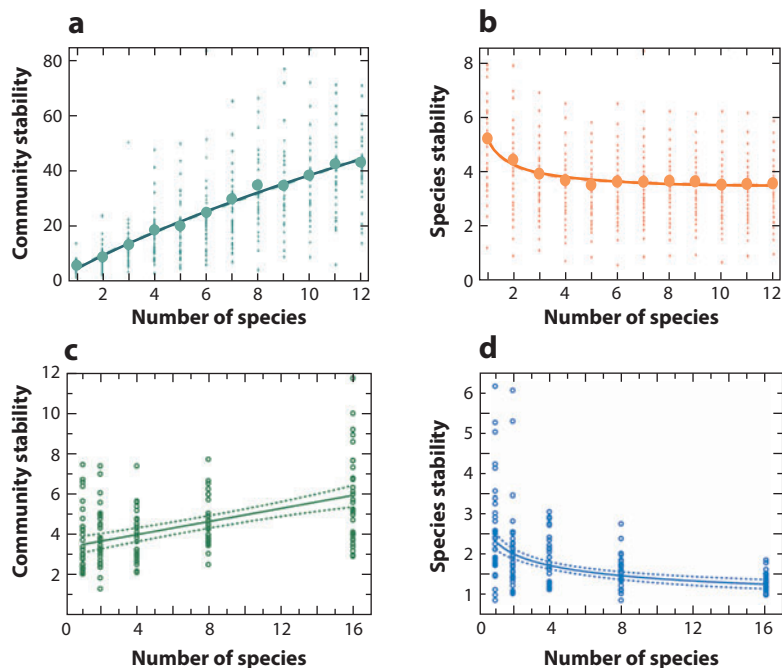


Figure 3

Diversity and stability of communities and species. (*a,b*) Predictions based on a model of resource competition in a temporally fluctuating environment, showing dependence of (*a*) community temporal stability and (*b*) species temporal stability on species number. Large dots represent the means of 100 simulations (which are represented by small dots) (Lehman & Tilman 2000). (*c,d*) Observed temporal stability of (*c*) primary productivity (summed productivities of all plant species) and (*d*) species across 10 years in the Cedar Creek big biodiversity experiment. Lines represent regression fits and 95% confidence intervals (Tilman et al. 2006b). In all cases, stability is calculated as the mean abundance of a community or of each species divided by its temporal standard deviation. Figure panels adapted from cited sources with permission.

(community stability) have generated similar predictions. As found by Robert May (1973, 1974) for Lotka-Volterra models of competing yet coexisting species, and as found more recently in several other models of competition (Lehman & Tilman 2000, Tilman 1999), species stability is a decreasing function of species diversity. However, community stability, measured as total community biomass divided by its temporal standard deviation, is an increasing function of the number of species in these and other models (Figure 3*a,b*) (Lehman & Tilman 2000, May 1974, Tilman 1999, Yachi & Loreau 1999). In addition, Ives et al. (1999) found that, in most cases, increases in diversity increased community stability in their model mainly because of statistical averaging (Doak et al. 1998, Tilman et al. 1998), which results in lower community variance when species respond differently to environmental fluctuation. In Yachi & Loreau's (1999) stochastic population model, as in other models, community variability (standard deviation) declined with diversity, and community biomass increased, causing community stability to be greater at higher diversity. Their notion of biodiversity as "insurance" against temporal fluctuations was later extended to consider biodiversity as spatial insurance in heterogeneous landscapes (Loreau et al. 2003). These models, though emphasizing different processes, make a similar prediction—that community stability is an increasing function of the number of species.

4.3. Diversity-Invasion Theory

On the basis of comparisons of mainland and island communities and other observational data, Elton (1958) proposed that more diverse communities were more difficult to invade and thus resistant to invasion. Many of the models of diversity-productivity-stability can apply to invasions. For instance, the model of resource competition along a temperature gradient (Lehman & Tilman 2000) was used to predict, via stochastic simulations, that the probability of invasion by a novel species would decline sharply with increasing numbers of resident species (Tilman 2004). This decreased probability had a simple underlying mechanism. Invaders must survive and grow on whatever levels of resources are left unconsumed by the established species. Because the levels of unconsumed resources decline as diversity increases in models of consumer-resource interactions (**Figure 2f-g**) (Lehman & Tilman 2000, Thébault & Loreau 2003, Tilman et al. 1997b), invader success declines with diversity.

5. TESTS OF CAUSALITY: THE INTERPLAY OF THEORY AND EXPERIMENTS

5.1. Diversity-Productivity

By 2006, the preponderance of evidence from more than 100 biodiversity experiments had shown that species diversity had a repeatable and consistent effect on productivity (Cardinale et al. 2006, Hooper et al. 2005, Loreau et al. 2001, Tilman et al. 2001). Most of these studies manipulated the number of herbaceous plant species; similar results were observed in other types of ecosystems (for example, results reported in Bell et al. 2005, Stachowicz et al. 1999, and Van der Heijden et al. 1998). Other questions remained incompletely answered. Were selection effects more or less important than niche complementarity? What trait differences mattered? Can the number of species alone summarize these differences, or is added information provided by functional classifications or phylogenetic relatedness? Does it matter whether a set of species coevolved in the same biome or whether some were exotics? Might species evenness matter as much as species richness?

Huston (1997) cited, as support for the selection hypothesis, the results of a plant biodiversity greenhouse experiment (**Figure 1c**). In that experiment, monocultures of 24 plant species differed greatly in productivity. Of particular note is that none of the higher-diversity mixtures of plant species had greater productivity than the best single species in monoculture. Rather, the mean productivity increased with diversity because higher-diversity mixtures had a higher lower bound on their productivity. Thus, as Huston asserted, the results of that greenhouse experiment could be interpreted as selection effects. Both the small and big Cedar Creek biodiversity experiments, during their first few years, had an upper bound of the diversity-productivity relationship that seemed fairly flat (Tilman 2001, Tilman et al. 2001), which as Huston (1997) and Aarssen (1997) suggested would be consistent with selection effects.

However, the frequency of occurrence of transgressive overyielding (i.e., polycultures that outyielded the most productive monoculture) increased as experiments progressed (**Figure 1d**) (Cardinale et al. 2007). For instance, by 1998, the fourth year of the two Cedar Creek experiments, the upper bounds of productivity-versus-diversity graphs were generally increasing for both experiments (Tilman 2001, Tilman et al. 2001). This trend has strengthened through time for the big biodiversity experiment (still under way in 2014, its twentieth year). For 2011, 2012, and 2013 (**Figure 4f**), 34, 35, and 32 plots, respectively, of the 35 plots planted to 16 species had aboveground plant biomass greater than the single most productive monoculture species.

Huston et al. (2000) suggested that overyielding did not come from diversity per se but rather explicitly required the presence of nitrogen-fixing legumes. Two grassland biodiversity experiments tested this hypothesis by not including any legumes. Both found that mixtures with more species of grasses and forbs were more productive than their respective monocultures (Van Ruijven & Berendse 2003, Wilsey & Polley 2004) and that the effect size of diversity was as large as that observed in grass-legume mixtures.

Transgressive overyielding tests have been informative and useful (Cardinale et al. 2006) but may have limited power to detect some cases of transgressive overyielding (Schmid et al. 2008). Loreau & Hector (2001) developed an alternative approach, an additive partition that teases apart how much community-level overyielding is due either to complementarity or to increasing dominance by productive species. They found stronger evidence for complementarity than for selection effects in the BIODEPTH experiments (Loreau & Hector 2001), as did Fargione et al. (2007) for the Cedar Creek data, and as did meta-analyses of many biodiversity experiments, especially in longer-term experiments (Cardinale et al. 2007, 2011).

5.1.1. Are the effects of diversity general? Two approaches, multisite experiments and meta-analyses, both of which are relatively new to ecology, have allowed broader inferences of the effects of biodiversity on ecosystem processes to be drawn. The BIODEPTH network found that the same quantitative relationship could describe the dependence of productivity on plant species numbers across 8 sites in Europe (**Figure 1e**) and showed that productivity significantly increased with plant species richness at 7 of the 8 sites (Hector et al. 1999, Spehn et al. 2005). The Agrobiodiversity network (Finn et al. 2013, Kirwan et al. 2007) included 31 sites (30 in Europe and 1 in Canada). Productivity was significantly greater in mixtures of 4 species than in monocultures at all 31 sites, including 680 out of 682 species mixtures (Finn et al. 2013).

Meta-analyses, which synthesize the results of numerous experiments, have provided important tests of the breadth of applicability, generality, and magnitude of the effects of diversity (Balvanera et al. 2006; Cardinale et al. 2006, 2011, 2012; Gross et al. 2014; Stachowicz et al. 2007; Worm et al. 2006). For instance, a meta-analysis by Cardinale et al. (2007) found, as in the initial field experiments, that productivity was an increasing function of the number of species (**Figure 1b**) (Cardinale et al. 2007); that high-diversity treatments had, on average, approximately double the productivity of monocultures (**Figure 1b-i**); and that resource use was higher (levels of unconsumed resources were lower) at higher diversity. Importantly, they also found that such biodiversity effects occurred across terrestrial, freshwater, and marine ecosystems, greatly increasing the breadth of inference (Balvanera et al. 2006; Cardinale et al. 2006, 2011; Stachowicz et al. 2007; Worm et al. 2006).

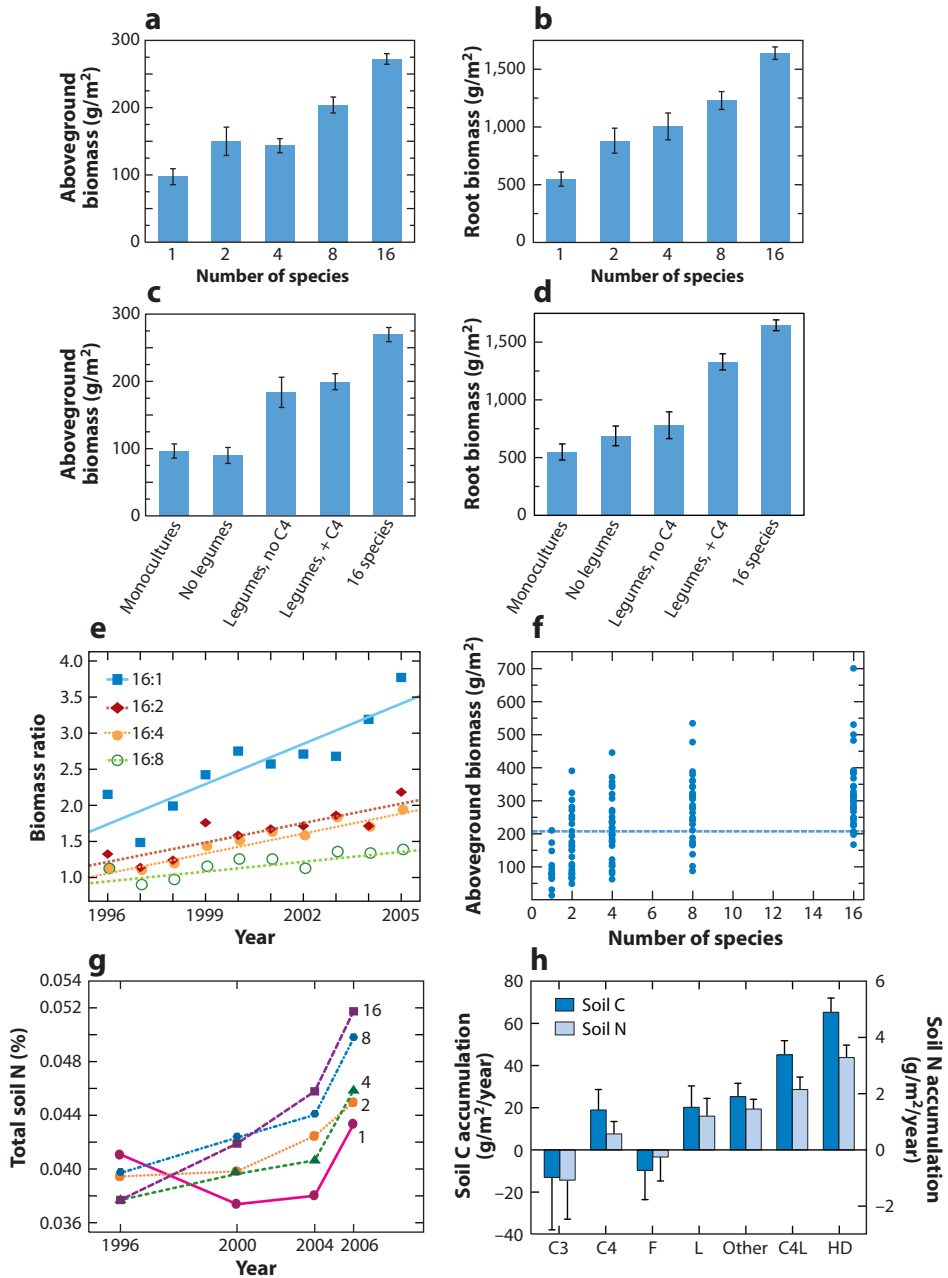
Consensus papers have provided a forum for reasoned discussion among scholars with differing views, encouraged a search for areas of agreement, and clarified areas in need of further exploration. Two consensus reviews (Hooper et al. 2005, Loreau et al. 2001) intentionally brought together investigators with diverging perspectives to find common ground. By 2001, there was consensus that many species were needed to maintain the stability of ecosystem functioning in changing environments (Loreau et al. 2001). By 2005, there was consensus that functional complementarity associated with higher diversity led to increased productivity and nutrient retention at higher diversity; that some ecosystem processes can be initially insensitive to species loss due to functional redundancy or relatively weak biotic effects; and that even relatively rare species can strongly influence ecosystem functioning (Hooper et al. 2005). Comprehensive reviews have also been provided in several books (Kinzig et al. 2002, Loreau et al. 2002, Naeem et al. 2009, Schulze & Mooney 1993).

5.1.2. Nonrandom species loss. Most biodiversity experiments have been designed to determine the consequences of random gains or losses of species, which has allowed these experiments to tease apart the effects of species number and composition (see Section 4). However, species losses are rarely random in nature. One study imposed preferential loss of rare species and found that it did not significantly alter productivity in the short term (Smith & Knapp 2003). In contrast, another study found that realistic losses of plant species (mimicking those observed nearby, including losses of some rare species) affected invasion resistance at least as much as random species losses did (Zavaleta & Hulvey 2004). Experimental fragmentation, another form of nonrandom community change, reduced the diversity and community biomass of arthropods in microcosm fragments (Gonzalez & Chaneton 2002). Furthermore, nutrient-induced losses of plant species, including initially dominant plant species, impacted productivity twice as much per lost species as did random species losses in a nearby biodiversity experiment (Isbell et al. 2013). More studies are needed to infer underlying causes of these results, but it is clear that realistic species losses can impact ecosystem functioning both more or less than the random species losses imposed in most experiments and assumed in most theory.

5.1.3. Short- versus long-term experiments. Within natural ecosystems, interactions among species and various community and ecosystem feedback effects have been occurring for long periods of time. Even small feedback effects can have great long-term importance if effects accumulate, as might happen for effects of composition and diversity on foodweb structure, of pathogens on their hosts, and of productivity and species composition on decomposition, biogeochemistry, and nutrient cycling. In contrast, most biodiversity experiments, which provide the preponderance of evidence for meta-analyses, have lasted only one to three years (Cardinale et al. 2006). Cardinale et al. (2007) found that analyses that included the duration of experiments showed that diversity effects on both productivity and transgressive overyielding became significantly stronger through time (**Figure 1i**). Similarly, the shape of the dependence of ecosystem functioning on biodiversity may change as biodiversity experiments mature (Reich et al. 2012). A quickly saturating curve, as observed in short-term experiments (Cardinale et al. 2011), would be interpreted as meaning that many species could be lost from diverse communities with relatively little change in ecosystem functioning. However, as biodiversity experiments mature, this relationship becomes both steeper and more linear (Reich et al. 2012). Such long-term results likely apply to mature natural ecosystems, suggesting that species loss may have a larger impact on natural ecosystems than the short-term experiments imply. In addition, the more linear curve means that the first few species lost from a diverse ecosystem have an impact per species about as great as would the loss of any subsequent species.

The results of the longest-running plant species diversity experiment, the big biodiversity experiment at Cedar Creek, illustrate the diversity-dependent, cumulative impacts of nutrient cycling, changes in foodweb structure, and other feedback effects on ecosystem functioning. By 2006, the thirteenth year of the experiment, aboveground biomass production and total root biomass of 16-species plots were approximately 200% greater than in monocultures (**Figure 4a,b**) (Mueller et al. 2013). A legume \times C4 grass interaction played a significant part in this, as did the number of plant species (**Figure 4c,d**) (Mueller et al. 2013). Moreover, the effect of diversity became progressively larger through time (**Figure 4e**) as measured by the ratio of the aboveground productivity of the 16-species treatment to that of the monocultures and to that of each of the other lower-diversity treatments. The first time the experiment was sampled (its third year), the 16-species plots were \sim 70% more productive than the monocultures. By the thirteenth year, they were $>$ 200% more productive (**Figure 4e**) (Tilman et al. 2006a). Monoculture productivity had no significant temporal trend, whereas productivity of higher-diversity treatments

increased through time (**Figure 4e**). The response of aboveground biomass to plant diversity in 2013 reveals strong complementarity and transgressive overyielding (**Figure 4f**). A portion of this overyielding results from diversity-dependent cumulative increases in soil fertility. In particular, a feedback effect of the elevated root mass of higher-diversity plots (**Figure 4b**) caused total soil nitrogen to increase through time at higher diversity (**Figure 4g**) (Fornara & Tilman 2008). Most soil nitrogen is in organic forms that are unavailable to plants but that are slowly converted



to nitrate by soil microbial processes. Soil organic carbon also increased (**Figure 4b**; annual rates shown, based on years 1–13), which contributes to soil fertility. Rates of increase depended on both functional group compositions and plant species number (**Figure 4b**). In addition, plant roots went deeper and occupied a greater soil volume in higher-diversity plots, providing access to a greater pool of soil nutrients (Mueller et al. 2013). Finally, higher-diversity treatments had lower incidence of foliar fungal diseases (Mitchell et al. 2002) and had predator-dominated foodwebs with lower abundances of herbivorous insects (Haddad et al. 2009). Mueller et al. (2013) found that plot productivity in 2006 was significantly and positively dependent on initial (1994) total soil nitrogen, on the change in total soil nitrogen from 1994 to 2006, on the change in the total nitrogen stores of roots from 1995 to 2006, on net soil nitrogen mineralization, on the proportion of deep roots (which increased with diversity), on the presence of legumes, and on the number of planted species. Thus, a suite of variables that slowly changed in response to higher diversity, and thus that were missed in short-term experiments, caused the diversity effect size to almost triple from its initial response to its thirteenth field season. We suggest that such feedback effects are common in natural ecosystems but are missed in short-term biodiversity experiments.

5.1.4. Different metrics of diversity. There are many possible metrics of diversity in addition to the number of species, including evenness, phylogenetic diversity, and various measures of functional diversity. Common diversity indices have richness (number of species) and evenness (equity of species abundances) components. Experimental manipulation of evenness tends to have either positive or neutral effects on biomass production and associated ecosystem-level responses (Hillebrand et al. 2008, Kirwan et al. 2007, Wilsey & Polley 2004, Wilsey & Potvin 2000, Wittebolle et al. 2009). The number of functional groups in a system, which is termed functional diversity, is strongly related to many aspects of ecosystem functioning (Fornara & Tilman 2008; Hooper & Vitousek 1997; Reich et al. 2004; Tilman et al. 1997a, 2001). Nested measures, such as the number of species within each functional group, have proven insightful (Reich et al. 2004). Functional trait or phylogenetic distance indices can also be strong correlates of responses (Cadotte et al. 2008, Flynn et al. 2011). Furthermore, combinations of native species that have a coevolutionary history of interaction have been observed to exhibit greater complementarity than combinations of exotic species with briefer histories of interaction (Isbell & Wilsey 2011, Wilsey et al. 2009). It seems unlikely that any one diversity metric will be consistently superior to all others; rather, there will likely be taxa and questions for which each may provide more insight.

Figure 4

Case study of the big Cedar Creek biodiversity experiment. (*a,c*) Aboveground and (*b,d*) root biomass responses in 2006, the thirteenth year of the experiment, as dependent on (*a,b*) number of plant species and (*c,d*) functional composition (Mueller et al. 2013). (*c,d*) Monocultures; mixtures of 2, 4, or 8 species without legumes (No legumes), with legumes but without C4 grasses (Legumes, no C4), and with both legumes and C4 grasses (Legumes, + C4); and 16-species mixtures. (*e*) Temporal trends in the ratio of mean aboveground biomass in 16-species mixtures to less diverse plots (Tilman et al. 2006a). (*f*) Aboveground biomass of each plot in 2013; nearly all 16-species plots were more productive than the single best species in monoculture (whose biomass is indicated by the *horizontal dashed line*). (*g*) Temporal trends in soil nitrogen content by number of species (1, 2, 4, 8, or 16 species) during the first decade (Fornara & Tilman 2008). (*h*) Response of soil carbon and nitrogen annual sequestration rates to species composition. Monocultures of C3 grasses (C3), C4 grasses (C4), forbs (F), and legumes (L); mixtures of 2, 4, or 8 species that included either at least one C4 grass and at least one legume (C4L) or neither (Other); and 16-species high-diversity mixtures (HD) (Fornara & Tilman 2008). Error bars indicate 1 SEM. Figure panels adapted from cited sources with permission.

5.2. Tests of Diversity-Stability Relationships

A variety of observational data sets have been used to test the diversity-stability hypothesis. The early analyses by McNaughton (1977, 1993) and Frank & McNaughton (1991) generally supported this hypothesis, as have more recent analyses based on larger data sets such as those for Minnesota grasslands and drought (Tilman & Downing 1994), grasslands and nondrought climate variations (Tilman 1996), Mongolian grasslands (Bai et al. 2004), and a Chinese wetland (Li et al. 2013).

The big Cedar Creek biodiversity experiment allowed a direct test of the effects of plant diversity on both community and species stability. As predicted by theory (**Figure 3a**) (Lehman & Tilman 2000, Loreau 1998, Loreau et al. 2003, Tilman 1999), community temporal stability across a 10-year period was significantly greater at higher plant diversity (**Figure 3c**); this greater stability resulted more from increases in community biomass with diversity than from statistical averaging (Tilman et al. 2006b). Also as predicted by theory (**Figure 3b**), stability of individual species was lower at higher diversity (**Figure 3d**). Data analyses and related theory by de Mazancourt et al. (2013) suggest that biodiversity may stabilize ecosystems through asynchrony in the responses of species to environmental variation and overyielding. An experimental study of genotypic diversity within the seagrass *Zostera* found that greater genetic diversity contributed to its stability and impacted higher trophic levels (Reusch et al. 2005). However, studies of population stability in aquatic foodwebs (Steiner et al. 2005, Vogt et al. 2006) found the opposite, suggesting that the complexity of interactions in foodwebs may lead to diversity-stability relationships different from those predicted by models that assume that competition is the only interaction.

A reanalysis of results of 27 biodiversity experiments showed that community stability of grasslands was greater at higher plant species numbers and that individual species were destabilized by higher diversity (Gross et al. 2014). The underlying cause for the higher community stability at higher diversity was much like that observed at Cedar Creek (Tilman et al. 2006b): The increase in total community biomass with diversity was much greater than the change in community variance, thus causing stability (the ratio of mean community abundance to its temporal standard deviation) to be greater at higher diversity. Compensatory interactions among species also contributed to greater stability at higher diversity (Gross et al. 2014).

5.3. Tests of Diversity-Invasibility

Grassland biodiversity experiments have found strong support for Elton's diversity-invasibility hypothesis. At Cedar Creek, higher-diversity treatments were invaded by many fewer plant species (Knops et al. 1999). Naeem et al. (2000) found that invader success decreased with planted diversity and that this decrease was associated with lower soil nitrate, higher abundances of neighboring plants, and lower light availability. The experimental addition of seeds of numerous species showed that both the number of added species that became established and their summed biomasses were declining functions of the preinvasion number of species (Fargione et al. 2003). Moreover, the total biomass attained by all invaders of a given functional group was most strongly inhibited by the total biomass of all planted species within that same functional group and, in many cases, was not significantly inhibited by other functional groups. This finding suggests that established species exert their greatest competitive inhibition on invaders that are functionally similar to them (Fargione et al. 2003). A similar result was observed in the Jena, Germany, biodiversity experiment, in which invading species tended to be from functional groups not already present, and communities converged on high functional richness (Petermann et al. 2010). In a California grassland experiment in which plant diversity was manipulated to reflect observed patterns of species loss, the productivity of a major invasive species, star thistle, was greatly increased at

lower diversity (Zavaleta & Hulvey 2004). Greater species diversity in marine sessile invertebrate communities was found, in a biodiversity experiment, to inhibit invader success because a major limiting resource, open space, was less available at higher invertebrate diversity (Stachowicz et al. 1999).

However, other studies of invasion suggest that a more complex suite of factors can be involved. An invasion experiment in native Kansas grassland (not a biodiversity experiment) found that removing many rare plant species did not change the invasion success of a legume species and that reducing the biomass of the dominant perennial C4 grasses reduced the invasion success of this legume (Smith et al. 2004). An experiment in a California riparian system found that local diversity inhibited invader success but that on larger scales, the most diverse communities were the most invaded, likely because other factors covaried with diversity (Levine 2000). A similar pattern of greater invasion into regions with greater plant diversity has been seen at larger geographic scales (Stohlgren et al. 1999, 2003). Although these studies do not refute the inhibitory effects of local diversity on invader success, they do suggest that such inhibition is one of many processes that determine rates of invasion into ecosystems.

5.4. Biodiversity and Multifunctionality

As summarized above, biodiversity impacts many different population, community, and ecosystem processes and their dynamics. Analyses of the number of species, along with their identities, involved in each of several different processes have shown that different suites of species tend to influence different processes. Although there is some overlap in the identities of the species, the net effect found by Hector & Bagchi (2007) is that many more species are needed to maintain multiple types of ecosystem processes than are demonstrably linked to any given process (**Figure 5**). Moreover, their results show that this dependence of multifunctionality on high diversity occurs consistently across eight different European sites. Measured levels of multiple ecosystem functions (Maestre et al. 2012) and ecosystem services (Gamfeldt et al. 2013) tend to be higher in communities with more species. Furthermore, more diverse communities tend to reliably provide higher levels of multiple ecosystem functions across years (Zavaleta et al. 2010). Byrnes et al. (2014) provide a useful review of multifunctionality studies.

6. MULTITROPHIC LEVELS AND IMPACTS OF DIVERSITY

The past two decades of biodiversity research have advanced the disciplines of community and ecosystem ecology, but major questions remain unanswered. Despite the insights provided by Hairston et al. (1960) more than a half century ago, the factors controlling the diversity, composition, and dynamics of foodwebs still remain a mystery. The work of Thébaud & Loreau (2003) is demonstrative of the types of mechanistic theory needed to better understand foodwebs (**Figure 2g–i**). Consistent with these theoretical predictions, Duffy (2002) found that experimentally increasing grazer diversity increased grazer biomass but decreased algal biomass. Gamfeldt et al. (2005) factorially manipulated consumer (ciliates) and prey (algae) richness, finding more efficient use of resources (prey) and higher consumer biomass at higher consumer richness. Another study examined effects of natural enemy diversity and host plant diversity on an herbivore (pea aphid) (Aquilino et al. 2005). Greater enemy diversity increased the biocontrol of aphids, whereas greater plant diversity reduced it. Schnitzer et al. (2011) did soil manipulations to test for possible roles that soil pathogens or mutualists might play in a biodiversity experiment and found results suggesting that pathogens have notable effects. Latz et al. (2012) found that greater plant diversity decreased the incidence of soil-borne pathogens by changing the community composition of bacteria that were antagonistic to the pathogens. These findings suggest that additional

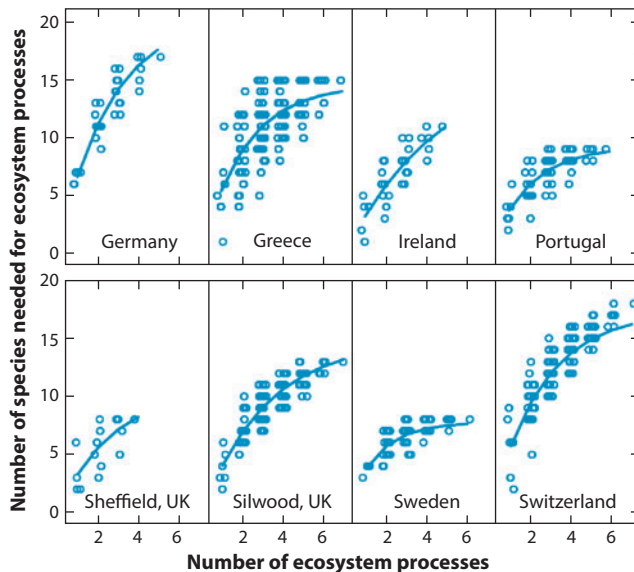


Figure 5

Multifunctionality and diversity. At each of eight European sites, different sets of species were involved in the provisioning of different ecosystem services. Because of this, many more species are needed, in total, to provide many services than are needed to provide a single service. The aggregate numbers of species influencing various numbers of ecosystem processes at each of the eight sites (y axis) depend on the number of ecosystem processes considered (x axis). Points show estimated relationships for plots from experimental manipulations of species number. Lines show predictions from a theoretical model based on the number of species that influence each process and based on the degree of species overlap between functions. Figure adapted from Hector & Bagchi (2007) with permission.

experimental and theoretical studies of the effects of the diversity on multiple trophic levels may be particularly insightful in advancing the understanding of food chain and foodweb functioning.

Another poorly understood aspect of foodweb ecology is how and why changes in the species diversity of one trophic level might cascade to impact higher and lower trophic levels. Plant diversity experiments have allowed analyses of effects of plant diversity on other trophic levels. Scherber et al. (2010) found that most herbivores responded positively to plant diversity and that such effects cascaded through foodwebs. Arthropods in the big Cedar Creek biodiversity experiment were more abundant at higher plant diversity; within that community, foodwebs were more predator-dominated at high plant diversity but more herbivore-dominated at low diversity (Haddad et al. 2009, Siemann et al. 1998). Proulx et al. (2010) found that plant diversity influenced the stability of multiple trophic levels, especially for aboveground organisms. These studies highlight the importance of examining diversity-induced effects on trophic structure.

Consider, also, a marine benthic diversity experiment in which greater primary producer diversity did not impact producer biomass (Bruno et al. 2006). A new experiment that crossed the producer diversity treatment with an herbivore exclusion treatment found that more biomass was produced at high producer richness but was being consumed by herbivores that held biomass at a fairly constant level (Bruno et al. 2008). This finding suggests that plant diversity experiments that have included herbivores may have underestimated the effect of plant diversity on primary productivity by ignoring the amount of primary productivity that was being consumed by a higher trophic level.

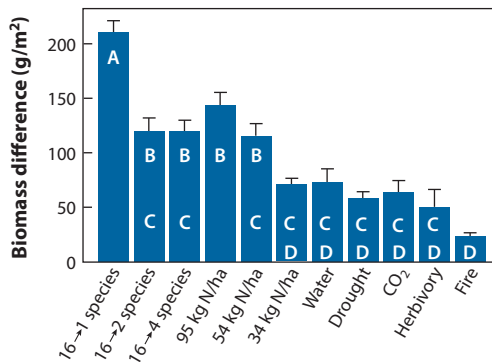


Figure 6

Importance of biodiversity relative to other ecological factors. Differences in biomass production between various treatment and control plots, showing effects of 16-versus-1-, 16-versus-2-, and 16-versus-4-species diversity treatments, as well as of various nitrogen addition rates and other ecological factors. Bars with the same letter are not significantly different at the $p \leq 0.01$ level on the basis of Tukey's contrasts. Figure adapted from Tilman et al. (2012) with permission.

7. HOW IMPORTANT IS BIODIVERSITY?

Many factors can impact the functioning of terrestrial ecosystems, including the availability of water, nitrogen, phosphorus, carbon dioxide and other limiting resources, herbivory, fire, drought, and weather. In 2012, strikingly similar results were obtained by two studies that used different data sets to compare the impacts of plant diversity versus other factors on primary productivity (Hooper et al. 2012, Tilman et al. 2012). In total, these two studies found that decreases in plant biodiversity of the magnitude imposed by human actions had an impact as large as or larger than equally relevant rates of nitrogen deposition, elevated CO₂, fire, herbivory, and drought (**Figure 6**).

These two studies have significant scientific and societal implications. Hooper et al. (2012) concluded that their “analyses clearly show that the ecosystem consequences of local species loss are as quantitatively significant as the direct effects of several global change stressors that have mobilized major international concern and remediation efforts” (p. 105). The other study, by Tilman et al. (2012), stated that “changes in diversity of the magnitude being imposed by human actions can have at least as great of an effect on primary productivity as anthropogenic changes in atmospheric CO₂, the availability of a limiting soil resource, herbivory, fire, and variation in water availability” (p. 10397). It concluded by saying that “contemporary biodiversity declines are among the dominant drivers of changes in ecosystem functioning” (p. 10397). Biodiversity, a factor whose importance was not recognized in the ecology literature 25 years ago, has, through the rigorous efforts of hundreds of scholars, now been shown to be of central ecological and societal importance. The preservation, conservation, and restoration of biodiversity (Rey Benayas et al. 2009) should be a high global priority.

8. FUTURE DIRECTIONS

Research during the past two decades has shown that biodiversity effects on ecosystems are (a) real and large; (b) often caused by complementarity; and (c) occur in many terrestrial, freshwater, and marine ecosystems. These findings, and the research that led to them, have both changed the standards by which ecological research is judged and raised many new questions.

The first question is, How should results of experiments be used to predict the effects of diversity loss or restoration on large habitats? If 12 species are needed to attain a high level of primary productivity in a 10-m² biodiversity plot, how many would be needed in a 10,000-ha grassland? A plausible first approximation may come from application of species-area relationships. If the scaling coefficient were $z = 0.22$, then approximately 400 species would be needed in the 10,000-ha grassland to assure that a typical 10-m² area contained 12 species and thus had the desired level of productivity. The second question relates to natural ecosystems, which can have great trophic complexity: How applicable to these ecosystems are results of theory and biodiversity experiments that are based not on whole foodwebs but on only communities of competing species? A third question, likely of fundamental societal importance, is, How will habitat loss and ecosystem degradation impact the multiple biodiversity-dependent services provided to society by managed and remnant ecosystems? How will ecosystem services depend both on biodiversity and on species compositions, especially in a world where species experience novel climatic conditions to which they are poorly adapted?

Ecology must be a discipline that can explain what structured the natural world in the era before human global dominance of ecosystems and that can predict how anthropogenic forces will change that world. The major and simultaneous advances that have occurred during two intensive decades of investigating biodiversity are a model of the scientific efforts required if society is to gain the knowledge needed to wisely manage a world that humans now dominate through a myriad of often inadvertent actions. And, humanity must also gain the wisdom to do so.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank the National Science Foundation for NSF-LTER Award 1234162 and the Andrew W. Mellon Foundation for supporting our biodiversity research. We thank Kate Thompson, Adam Clark, and Michael Clark for their assistance, comments, and edits. We also thank the many ecologists whose efforts so profoundly advanced our understanding of biodiversity and its impacts.

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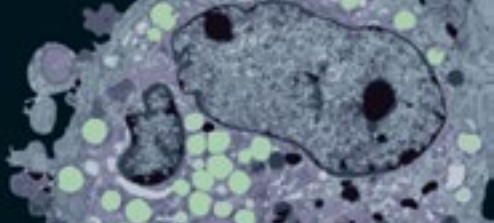
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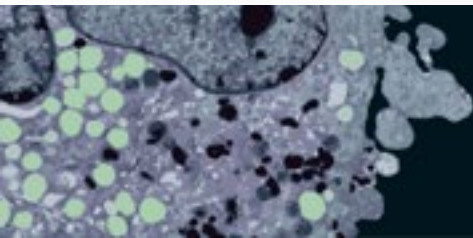
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