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Linking biodiversity to ecosystem function: implications for conservation ecology

Abstract We evaluate the empirical and theoretical support for the hypothesis that a large proportion of native species richness is required to maximize ecosystem stability and sustain function. This assessment is important for conservation strategies because sustenance of ecosystem functions has been used as an argument for the conservation of species. If ecosystem functions are sustained at relatively low species richness, then arguing for the conservation of ecosystem function, no matter how important in its own right, does not strongly argue for the conservation of species. Additionally, for this to be a strong conservation argument the link between species diversity and ecosystem functions of value to the human community must be clear. We review the empirical literature to quantify the support for two hypotheses: (1) species richness is positively correlated with ecosystem function, and (2) ecosystem functions do not saturate at low species richness relative to the observed or experimental diversity. Few empirical studies demonstrate improved function at high levels of species richness. Second, we analyze recent theoretical models in order to estimate the level of species richness required to maintain ecosystem function. Again we find that, within a single trophic level, most mathematical models predict saturation of ecosystem function at a low proportion of local species richness. We also analyze a theoretical model linking species number to ecosystem stability. This model predicts that species richness beyond the first few species does not typically increase ecosystem stability. One reason that high species richness may not contribute significantly to function or stability is that most communities are characterized by strong dominance such that a few species provide the vast majority of the community biomass. Rapid turnover of species may rescue the concept that diversity leads to maximum function and stability. The role of turnover in ecosystem function and stability has not been investigated. Despite the recent rush to embrace the linkage between biodiversity and ecosystem function, we find little support for the hypothesis that there is a strong dependence of ecosystem function on the full complement of diversity within sites. Given this observation, the conservation community should take a cautious view of endorsing this linkage as a model to promote conservation goals.

Key words Species richness · Ecosystem function · Observations · Conservation · Biodiversity

Introduction

Investigation of a link between species richness and ecosystem function has recently intensified. As an example of this trend, a search of *Current Contents* (Institute for Scientific Information Inc.), *Biosis* (Biological Abstracts Inc.) and *Bio85* (Biological Abstracts Inc.) found no citations combining the subject words "biodiversity" and "ecosystem function" between 1985 and 1990, 18 citations between 1991 and 1994, and 76 citations between 1995 and 1998. Despite a growing literature of conceptual theory, quantitative modeling, experimental tests and field observations, debate on this topic only seems to be deepening (Grime 1997). Recent articles assert that a relationship exists between species richness and ecosystem function and that this relationship can be used to argue for the conservation of biodiversity (e.g., Chapin et al. 1997, 1998; Tilman 1997; Edwards and Abivardi 1998). These arguments state that as a society we are interested in maintaining the products of ecosystem functions (e.g. clean air, clean water, soil fertility), sometimes called ecosystem services (e.g., Daily 1997), and maintenance of these functions may depend on maintaining high levels of biodiversity.

In order to use a functional relationship between ecosystem function and diversity as a foundation for advocating for the conservation of biodiversity two criteria

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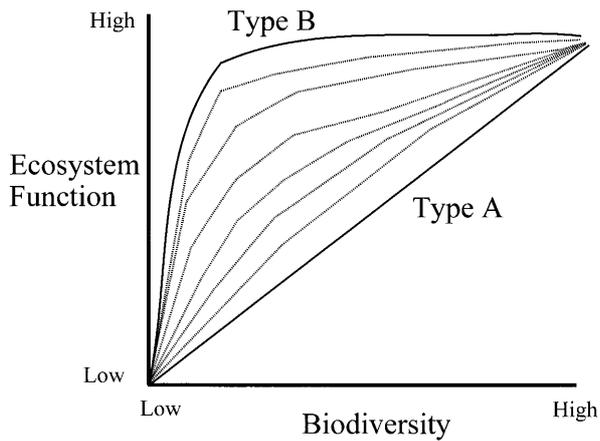
Fig. 1 Hypothetical relationships between biodiversity and ecosystem function where a positive correlation between the two exists. A *type A* relationship is described by a linear, or nearly so, dependence of function on diversity such that even the relatively rare species within an ecosystem contribute to an ecosystem function. A *type B* relationship is one where ecosystem function is effectively maximized by a relatively low proportion of total diversity and that most rare species do not materially contribute to the maintenance of a function. The lack of participation may be a result of a species being redundant or because it is simply too uncommon to have any effect on net function. The *interrupted lines* represent numerous functional relationships that are intermediate between type A and type B extremes

must be met. First, the maintenance of ecosystem processes must depend on a very broad array of species such that conservation of function embraces conservation of most or all diversity within the system. Second, ecosystem function, or the products of that function, ought to depend on native species. If exotic species that dominate ecosystems are redundant to those that they displace (e.g., Stromberg 1998), then conservation of function can be maintained by the conservation of non-native diversity. This would not provide strong support for the conservation of native species diversity.

Several recent articles review the linkage between biodiversity and ecosystem functions (e.g., Chapin et al. 1997, 1998; Johnson et al. 1996; Grime 1997). Our paper differs in two ways. First, we address a broad range of evidence linking species diversity to ecosystem function including observational, experimental and theoretical studies. Second, we approach the subject from the perspective of using the diversity-ecosystem function linkage explicitly as an argument for the conservation of biological diversity.

A variety of relationships between diversity and ecosystem function are possible (e.g., Ehrlich and Ehrlich 1981; Walker 1992; Lawton and Brown 1993; Carpenter 1996; Naeem 1998). Nonetheless, two types of observed responses can be used to evaluate the conservation argument (Fig. 1). A linear response of increasing function with increasing diversity indicates that all species, even rare ones, are required to maintain healthy levels of ecosystem function (Fig. 1, line A). A type A response curve would generally argue for the conservation of the full complement of native species. In contrast, a strongly curvilinear response represents a saturation of function at low levels of species richness relative to the site or the

experiment, despite a generally positive relationship between species richness and function (Fig. 1, line B). Type B response curves suggest that ecosystems can lose much of their diversity without consequence to function. Actual responses may either show no relationship between species number and ecosystem function or vary between type A and B response extremes. In this review, we evaluate where the majority of empirical and theoretical evidence lies in relation to these response curves.

One can argue that at some high level of richness ecosystem functions must saturate and demonstrate a type B function. In fact, a recent survey of ecosystem ecologists suggests that this is the expected relationship between diversity and function (Schläpfer et al. 1999). The critical argument is whether ecosystem function is maximized at a level of species richness considerably below the species richness observed within any chosen community or experimental system. We consider a relationship a type B response when saturation of function is achieved at levels of diversity well below (less than ~50%) local diversity. We also treat stability as an important but distinct type of ecosystem function. Stability of ecosystem function provides a measure of assurance of function and is an important attribute of ecosystems.

The dependence of ecosystem function on biodiversity

Observational studies

Efforts to understand how diversity correlates with ecosystem function appear to be derived from observations of a positive relationship between these variables (Table 1). Some functions found to be positively correlated with diversity include nutrient retention (Finlay et al. 1997), "exergy" (Marques et al. 1997), and biomass (Cuevas et al. 1991; Kutiel and Danin 1987). McNaughton (1977) perturbed plots in grasslands and observed a linear relationship between increasing diversity and a decreasing coefficient of variation for biomass. Frank and McNaughton (1991) found that diversity was positively related to resistance to change in species composition during a drought.

The observation of a positive link between diversity and function, however, is neither simple nor universal. Several researchers find that the relationship between diversity and function is variable through time and space (e.g., Mellinger and McNaughton 1975; Rusch and Oesterheld 1997), negative (Wardle et al. 1997), or nonexistent (Bulla 1996). Rusch and Oesterheld (1997) conclude that diversity and richness are not good predictors of primary productivity and that the identities of the dominant plant species are more important. Other studies present a more complicated picture of the relationship. For example, Kutiel and Danin (1987), in a study designed to investigate the effects of abiotic factors on plant diversity, found that ecosystem functions are low at both extremes of diversity. Although most observational

Table 1 Studies that investigate the hypothesis that there is a positive relationship between biodiversity (species richness) and ecosystem function. Studies are classified into groups basesd on whether the study used observations or experiments to investigate this relationship. Tests of this relationship are categorized by whether it was function or the stability of that function that was assessed. Direction and shape of the response are recorded when possible to discern from the literature

Authors	Ecosystem function	Relationship supports the hypothesis[a]	Type of response curve[b]
Observational studies			
Measures of ecosystem function			
Bulla 1996	Productivity	NO (0)	None
Cuevas et al. 1991	Root biomass	YES (+)	
Cuevas et al. 1991	Above ground productivity	NO (–)	
Finlay et al. 1997	Nutrient cycling	unclear	
Kutiel and Danin 1987	Field water capacity	YES (+)	Possibly A
Kutiel and Danin 1987	Biomass	YES (+)	Possibly A
Marques et al. 1997	Exergy	YES (+)	
Wardle et al. 1997	Biomass	YES (–)	
Wardle et al. 1997	Nitrogen retention (loss)	YES (+)	
Wardle et al. 1997	Respiration	YES (–)	
Measures of resistance			
Frank and McNaughton 1991	Community species composition	YES (+)	Unclear[c]
Measures of variability			
McNaughton 1977	Biomass	YES (+)	A
Experimental studies			
Measures of ecosystem function			
van der Heijden et al. 1998	Plant shoot biomass	Yes(+)	B
van der Heijden et al. 1998	Plant root biomass	Yes (+)	A
Hooper and Vitousek 1997	Above ground biomass	YES (+)	B
Hooper and Vitousek 1997	Nitrogen use	YES (–)	B
McGrady-Steed et al. 1997	Decomposition rates	YES (+)	B
McGrady-Steed et al. 1997	Invasion susceptibility	YES (+)	B
McGrady-Steed et al. 1997	CO_2 flux	YES (+)	A
Naeem et al. 1994	Nitrogen, potassium and phosphorus retention	NO (0)	None
Naeem et al. 1994	Percent cover	YES (+)	
Naeem et al. 1994	Transmittance (as a measure of productivity)	YES (–)	
Naeem et al. 1994	CO_2 flux	YES (+)	
Naeem et al. 1995	Nitrogen retention	NO (0)	
Naeem et al. 1995	Potassium retention	YES (+)	
Naeem et al. 1995	Biomass	YES (+)	A
Naeem et al. 1995	Percent cover	YES (+)	
Symstad et al. 1998	Biomass	YES (+)	B
Symstad et al. 1998	Nitrogen retention	YES (+)	B
Tilman et al. 1996	Extractable nitrogen	YES (–)	B
Tilman et al. 1996	Total cover	YES (+)	B
Tilman et al. 1997a	Biomass	YES (+)	B
Measures of variability			
McGrady-Steed et al. 1997	CO_2 flux	YES (–)	A
Naeem et al. 1995	Biomass	YES (–)	A
Naeem and Li 1997	Biomass	YES (–)	A
Naeem and Li 1997	Species density	YES (–)	A
Tilman 1996	Biomass	YES (–)	A
Measures of resistance or resilience			
Tilman 1996	Relative yearly biomass	YES (+)	B
Tilman and Downing 1994	Biomass	YES (+)	B
Van Voris et al. 1980	Nutrient retention	Unclear	

[a] Direction of the relationship indicated in parentheses

[b] Blank cells indicate that the nature of the relationship could not be evaluated because: (1) differences in diversity were not presented directly in relation to function (Van Voris et al. 1980; Wardle et al. 1997); (2) the diversity measurement was confounded (Marques et al. 1997); (3) the data were not presented graphically (Finlay et al. 1997); or (4) a small (<4) number of diversity classes were used prohibiting any reasonable curve fit (Cuevas et al. 1991; Naeem et al. 1994, 1995)

[c] Diversity and resistance (R) were presented log-transformed, and appear as a type A response. Untransformed resistance data, along with untransformed species richness data, allow assessment of curve shape

studies support the general contention that function and stability increase with increasing diversity, a type A response curve is rarely discernible in the published literature (Table 1).

Experimental studies

Several experimental systems have been used to examine the functional relationship between species richness and a ecosystem function (Table 1). One type of experiment manipulates species richness within semi-natural communities (e.g., Tilman et al. 1996, 1997a; Hooper and Vitousek 1997, 1998; van der Heijden et al. 1998; Hooper 1998). Other investigators have relied upon artificial communities within controlled environments (Van Voris et al. 1980; Naeem et al. 1994, 1995; Naeem and Li 1997; McGrady-Steed et al. 1997; Symstad et al. 1998). Several of these experiments have been criticized for a host of problems. Huston (1997) notes that past studies may have confounded hidden treatments within the experimental design that make the conclusions suspect. For example, weeding plots to maintain diversity may have additional effects on treatments. Beck (1998) asserts that researchers have inappropriately confused species richness with diversity, and make extrapolations to entire ecosystems based on the responses of single trophic levels. Hodgson et al. (1998) criticize controlled-environment experiments (Naeem et al. 1994, 1995) as focusing on effects of adding species to depauperate weedy systems that do not reflect natural communities. They also suggest that the results of such studies are largely driven by changes in functional diversity of adding species to the system and not the species themselves.

Several significant field experiments have failed to find a strong positive relationship between species richness and ecosystem function. For example, species richness failed to appear as a significant variable in multiple regressions for a variety of ecosystem functions (productivity, light penetration, soil nitrogen, and plant nitrogen) in field experiments at Cedar Creek (Table 1 in Tilman et al. 1997a). Hooper (1998) and Hooper and Vitousek (1997, 1998) varied the number of functional groups in order to examine ecosystem function in serpentine grasslands of California. These researchers found that average biomass did not vary with the number of plant functional groups, although the variance around average biomass decreased with increasing diversity (Fig. 2 in Hooper 1998).

A variety of greenhouse and microcosm studies show similarly equivocal support for the hypothesis that high species richness is required to sustain ecosystem function. Symstad et al. (1998) varied species richness to determine effects on biomass and nutrient retention (ecosystem functions) in a greenhouse experiment. They observed no variation in N retention across diversity gradients from one to ten species (Fig. 1 in Symstad et al. 1998). In a second experiment, differences in biomass production and nutrient retention across a species richness gradient were only observed in plots with high le-

gume diversity. These plots were dominated by a single species that constituted 82% of the average total biomass in plots in which it was found (Fig. 2 in Symstad et al. 1998). Thus, the positive result supporting the importance of species richness appears to be the result of this single dominant species. Naeem et al. (1994, 1995) found that species richness within trophic levels had no effect on nitrogen or phosphorus retention in a microcosm experiment (Fig. 10 in Naeem et al. 1995). Van Voris et al. (1980) used complex indices to estimate functional complexity and ecosystem stability in 11 microcosms constructed by extracting cylindrical cores of topsoil with plants from old fields. These investigators, despite observing a lack of correlation between complexity and stability indices, conclude that their data support the hypothesis that diversity might enhance stability.

Even in studies that demonstrate a relationship between ecosystem function and species richness, these effects often follow a type B response curve (i.e., function saturates at low species richness relative to the experiment). Tilman (1996), who measured ecosystem stability as the ratio of total plant biomass during the drought season to predrought biomass, observed that primary productivity was fully stabilized at approximately 25% of the richness observed in his species-rich plots (Fig. 5 in Tilman 1996). Tilman et al. (1996, 1997a) report the results of a field manipulation of species richness in plots and found that nutrient retention was equivalent in all plots with upwards of five species (Fig. 1c,d in Tilman et al. 1996). This result suggests that nutrient retention is maximized at just 20% of the maximum species richness of the experiment. Similarly, total plot biomass was maximized in plots containing 3 species, out of a range of up to 30 species (Fig. 1a in Tilman et al. 1997a). Symstad et al. (1998) found biomass production saturated with three species, just 30% of maximum plot species richness (Fig. 1 in Symstad et al. 1998). Hooper and Vitousek (1998) found that total resource use (nitrogen, phosphorus and soil moisture) was slightly lower in single group plots than multiple group plots, but plots containing from two to four functional groups were indistinguishable (Fig. 5 in Hooper and Vitousek 1998). A study using aquatic microbial communities showed that decomposition rates were effectively stabilized at about 50% of the total species richness of the experimental system and that susceptibility to invasion was minimized at very low diversity (Fig. 3 in McGrady-Steed et al. 1997). Naeem et al. (1995) found that mean plot biomass increased linearly with the log of species richness (type A), but the data are better described as a type B curve on a linear scale (Fig. 13 in Naeem et al. 1995).

Van der Heijden et al. (1998) experimentally manipulated arbuscular mycorrhizal species richness in field macrocosms simulating North American old field plant communities. They found that plant shoot and root biomass both increased significantly with mycorrhizal diversity, with plant shoot biomass saturating at approximately half of the experimental fungal diversity (type B) and plant root biomass being highest at the highest level of experimental fungal diversity (type A).

In the studies that we reviewed there were 20 possible tests of the relationship between diversity and function. Although 19 (95%) tests support a positive relationship between ecosystem function and diversity, 3 results were of the type A shape, 10 were type B and the remaining 6 were not presented in a manner that allowed evaluation (Table 1).

In contrast, the contention that some aspects of stability (decreased variability or increased resistance or resilience) of ecosystem function increases with species richness is supported by seven of eight experimental studies (Table 1). Among these seven studies that support the hypothesis of increasing stability with increasing species richness, five could be classified as type A response curves. Tilman (1996) examined the relationship between species richness and the coefficient of variation for community biomass and found a linear reduction in variability with increasing diversity (Fig. 6 in Tilman 1996). In some cases the coefficient of variation was reduced by 50% in high species richness plots with no apparent saturation of the effect.

Microcosm studies similarly demonstrate a consistent pattern of reduced variance in indices of ecosystem function among high diversity replicate plots in comparison to low diversity replicates (Fig. 13 in Naeem et al. 1995, Fig. 2b in McGrady-Steed et al. 1997, Fig. 2 in Naeem and Li 1997). These authors, in general, conclude that more diverse microcosms exhibit lower variability (are more predictable), and that low variability is a valuable ecosystem attribute. In some studies (e.g., Tilman 1996), the coefficient of variation is measured through time and represents some response of the system to environmental fluctuation. This may present the strongest evidence of an increase in stability with diversity. Other studies (e.g., Naeem et al. 1995) report reduced sample variation of higher diversity plots in controlled constant environments over a short period of time, although it is less clear how this reduced variation relates to ecosystem stability.

To summarize, three experiments (biomass, Naeem et al. 1995; CO_2 flux, McGrady-Steed et al. 1997; root biomass, van der Heijden et al. 1998) found a linear (type A) response of ecosystem function to species richness. In addition, a linear response of some components of stability (i.e., decreased sample variance or resistance) with increasing species richness was found in most of the tests examined (Table 1). These results provide only weak support for the contention that conserving the full suite of species within communities is important for retaining ecosystem function, per se, but stronger support for the argument that high species richness stabilizes ecosystems.

In addition to the previously mentioned constraints to interpreting the results of these experiments (e.g., Huston 1997; Beck 1998; Hodgson et al. 1998) is that, in general, they are conducted in simple systems with a single trophic level (vascular plants) and low maximum species richness relative to natural communities. Finally, the distribution of abundance among species used in experimental systems is typically more equitable than in naturally occurring communities. Most natural communities of plants show strong dominance by a few very common species, with the rest of the species at low abundance (e.g., Whittaker 1975; Ricklefs 1990). In contrast, most experiments begin with equal abundance or equal biomass of species. Artificially increasing the abundance of rare species by planting equal quantities inflates the impact of species richness on ecosystem attributes. It is likely that over time these experimental systems would eventually establish a dominance diversity relationship much like natural communities in which a few species dominate over others. Nonetheless, the failure of authors to establish that the dominance relationship of an experimental community is similar to that of natural communities compromises the interpretation of the results and limits interpretation.

Theory

Several researchers have used general ecological models to draw a relationship between diversity and ecosystem function. For example, Tilman et al. (1997b) model the relationship between species richness and ecosystem function, while Doak et al. (1998) and Tilman et al. (1998) model ecosystem stability.

Tilman et al. (1997b) used resource competition models (e.g., Tilman 1982) to predict the response of resource utilization to increasing diversity. They found that competition for both one and two resources predicted an asymptotic relationship whereby complete resource utilization, is reached at low (<30% of the maximum) levels of species richness (Figs. 1, 2 in Tilman et al. 1997b). Another attempt to relate species richness to ecosystem function used a generalized niche model in which species with a constant niche dimension, specified by the radius of a circle (r), were allowed to randomly colonize a hypothetical two-dimensional (a, b) niche space (Tilman et al. 1997b). Species abundance was proportional to the habitat space occupied such that a colonizer that overlapped in niche space with an occupying species had its abundance reduced by the amount of habitat overlap. The average proportion of the total niche space occupied by a given number of species across repeated simulations reflected the proportion of resources used, which was treated as a proxy for ecosystem function (Fig. 3b in Tilman et al. 1997b). Thus, empty niche space represented unexploited resources and diminished ecosystem function relative to the potential maximum.

The species richness at which resource use is effectively saturated (addition of more species results in trivial increases in the total niche space occupied) depends on model conditions. The radius of a species niche dimension (r) relative to the dimension of the entire niche space ($a \times b$) has a particularly large impact on the outcome of the model. We analyzed the predicted relationship between species number and function by varying the size of the environment space (a, b) relative to niche size (r=1) using Eq. 5 from Tilman et al. (1997b, p. 1860). If the habitat space is small, then only a few species saturate the habitat. Conversely, if the habitat is
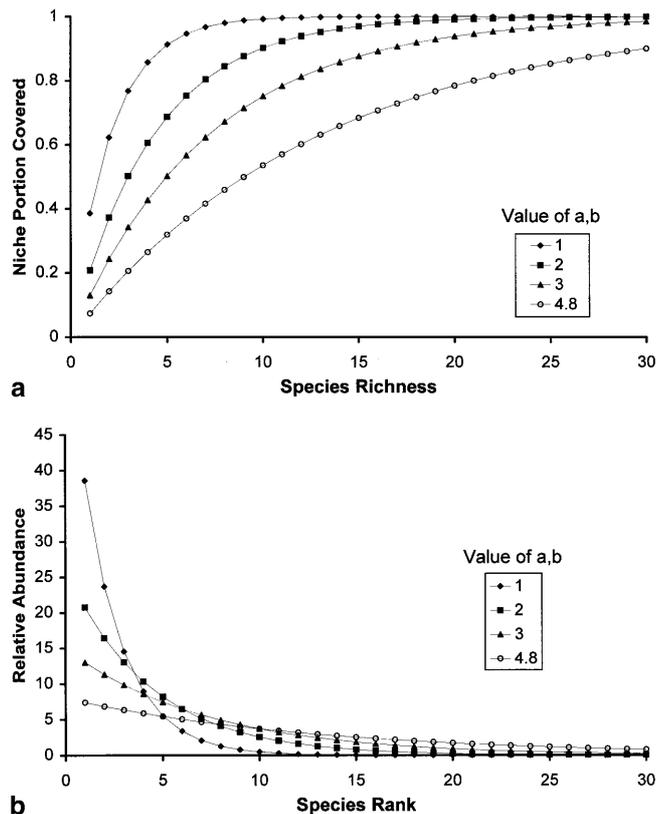
Fig. 2A,B Variations on the generalized niche model of Tilman (1996) of species richness versus ecosystem function. Tilman's original model used the equation $P_{(N)}=1-(1-\{\pi/[ab+2(a+b)+\pi]\})^N$ where N is the number of species, and a and b are the dimensions of the niche space relative to a circle with radius=1, and $P_{(N)}$ is the proportion of environmental conditions covered by species, or the proportion of potential resources utilized. **A** The relationship between species richness and habitat utilization across variation in habitat size such that habitat space is relatively large ($a=b=4.8$) to small ($a=b=1$). Tilman (1996) used values of a and b of approximately 4.8. **B** Dominance curves of the relative abundance of species plotted by species rank for the various values of a and b used above. Abundances were calculated as the amount of habitat space occupied by n species relative to that occupied by $n-1$ species as per the aforementioned equation. Since most natural communities show strong dominance (i.e., $a=1$ to 3), we take this to be a more realistic model response for ecosystem function in **A** than that presented by Tilman (1996)

large, many species coexist with less overlap (Fig. 2A). The saturation of ecosystem function is dependent on far fewer species when using environments that are small relative to niche size (Fig. 2A).

To explore model behavior, we examined dominance-diversity curves that result from different habitat sizes (values of a, b; Fig. 2B) relative to a constant niche size ($r=1$). We find that Tilman et al. (1997b) used an environment space that is large relative to niche size, resulting in weak dominance relationships among species (Fig. 2B). Further, curves based on larger niche sizes relative to environment space (e.g., $a/b<2$) result in dominance-diversity curves that are far more similar to those predicted by basic ecological models of niche partitioning (e.g., Ricklefs 1990, pp. 715–719) and from empirical studies

(Whittaker 1975, pp. 87–94). Our results suggest that a habitat size (e.g., $a=2$, $b=2$) that results in realistic dominance relationships among species within a community predicts a type B response curve of ecosystem function to increasing species richness (Fig. 2A). Thus, niche models suggest a saturation of ecosystem function at relatively low species number in communities with natural dominance-diversity structures. This result also supports our previous contention that experiments using an artificially equitable abundance of species inflate the impact of species richness on ecosystem function.

In a similar vein, two recent articles debate the degree to which diversity confers stability in ecosystem function (Doak et al. 1998; Tilman et al. 1998). Doak et al. (1998) describe factors that make the stability of ecosystem function an inevitable outcome of diversity in what Tilman et al. (1998) call the "portfolio effect". The portfolio effect is a simple concept. As in a mutual fund, the more species (or stocks) in an ecosystem (investment portfolio) the more the fluctuations in function (value) will be buffered as a result of variable responses of the constituent species (stocks). Doak et al. (1998, Fig. 2a) show that, as long as not all species are responding in the same direction and at the same magnitude (a positive correlation of 1.0), the ecosystem effects will be buffered with increasing diversity. The lower the correlation among species, the stronger the stabilizing effect. Doak et al. (1998, Fig. 1) also predict that the ability of species to stabilize ecosystem function is diminished when species are not equally abundant. This result is described well by the stock market analogy. The ability of a diverse portfolio to stabilize stock market fluctuations is diminished by increasing the representation of just one or few stocks. Thus, natural systems with strong dominance of a few species will have a limited capacity to buffer against variation unless there is rapid turnover of dominants.

Tilman et al. (1998) describe another reason why diversity may not inherently stabilize ecosystem function. We expect variance in abundance to increase with mean abundance. Doak et al. (1998) assume that variance scales with the square of the mean. This is an important attribute because Tilman et al. (1998, Fig. 2) show that increasing diversity will be less effective at stabilizing ecosystem function as the scaling of the variance relative to the mean decreases. Tilman et al. (1998) identify a scaling factor z, then state that the empirical estimate for this scaling factor for the Cedar Creek experiment is approximately 1.3, as opposed to the scaling factor of 2 used by Doak et al. (1998).

The models presented by Doak et al. (1998) and Tilman et al. (1998) are important because they link species richness to stability in ecosystems. These models are troubling with respect to the conservation argument, however, when one considers the magnitude of the stabilizing effect predicted in light of the three dampening factors described above. We re-analyzed the Doak et al. (1988) portfolio effect model with three modifications. First, we use the estimate of the scaling of the coefficient
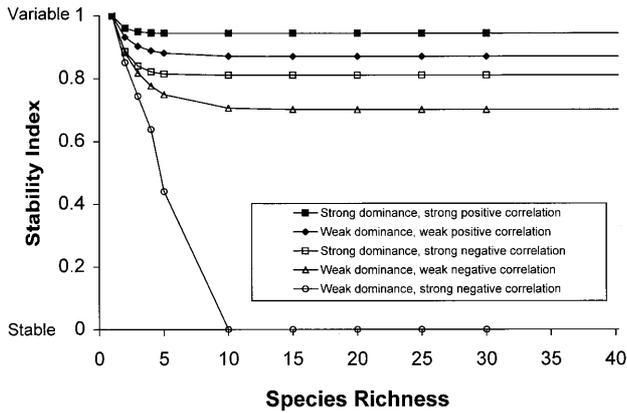
Fig. 3 Model predictions of the effect of species richness on stability where the stability index is defined as the coefficient of variation in an ecosystem function such as community biomass relative to the coefficient of variation observed for a community with a single species. This figure is a modification of Doak et al. (1998, Figs. 1, 2) where variance in the abundance of each species is increased by a exponential factor of 1.3, as Tilman et al. 1998 empirically observe for Cedar Creek data. Further we treat only the conditions where dominance is moderate (a=1) or weak (a=0.5) and correlations among species in their response to environmental variation is moderate (+0.4 or –0.4) or weak (+0.2 or –0.2) using Eq. 6 of Doak et al. (1998): $CV_{(function)} = CVs\{[(1-e^{-a})/(1+e^{-a})] \times [(1+e^{-ak}-2r)/(1-e^{-ak})]+[2r/(1-e^{-ak})]\} 1/z$ where k is the species number, r is the correlation in species abundance, and a is a measure of dominance

of variation as 1.3 from Tilman et al. (1998). Second, we use realistic distributions of species abundance. Third, we vary estimates of correlations between species responses.

Our portfolio effect model shows two important results (Fig. 3). First, the number of species required to reach an asymptote minimizing the coefficient of variation in the system is remarkably low; species are important, but not beyond the five most abundant species. Second, the degree to which the coefficient of variation in diverse communities is reduced over that of a community with just a single primary producer is, in most cases, small (Fig. 3).

This is not to suggest that these models show that increasing species richness never helps to stabilize ecosystem functions. High species richness can, in some cases, reduce the coefficient of variation in ecosystem function and by a large amount. For stabilization of ecosystem function to occur, two conditions must be simultaneously met: inequitability in species abundances must be low and correlations in the responses of species must be large and negative (Fig. 3). By low inequitability of species abundances, we mean that the distribution of abundance must be more equitable than that predicted by any of the niche models (Ricklefs 1990) and lower than is commonly observed in either plant or animal data sets (Whittaker 1975). It also seems likely that correlations among species responses are not frequently strongly negative across entire communities. In fact, it is more likely that species respond generally in the same direction to external environmental perturbations. For example, a

drought may cause an increase in the relative biomass of some species, but an overall decrease in the total biomass for most species (Weaver and Albertson 1956; Albertson and Tomanek 1965; Biondini and Manske 1996).

Theory suggests that the effect of diversity within a trophic level on resistance in real communities should be low. This theory may be overly simple in two ways. First, the model has assumed no species turnover with respect to abundance. If rare and common species frequently change roles with respect to their abundances within communities, then rare species may have a larger effect on stability and function that these models suggest. The rapidity with which species change in abundance with changing environmental conditions has not been discussed in the studies we evaluated. Second, the stability and function of ecosystems may be more dependent upon a broad array of local diversity once additional trophic levels are included. Again, this has not been specifically addressed in this literature.

Discussion and conclusion

We have outlined some basic problems with positing a linkage between species and ecosystem function. Solid evidence in support of a linear dependence of ecosystem function on diversity such that even the rare species contribute to function is practically non-existent. Observational data, while frequently demonstrating positive correlations between diversity and function, are highly equivocal regarding the shape of this relationship. Experimental evidence, as well as theory, suggests that the link between species diversity and function is principally not type A, where function is maximized by a high proportion of local species richness. Although 19 of 20 experimental tests identified a generally positive relationship between species number and ecosystem function, only 3 identified a type A response curve (Table 1). Observations and experimental evidence support the contention that system variability, a component of stability, responds linearly with species richness in 50% of cases examined (Table 1). Constraints of experimental design using unnaturally equitable distributions of abundance make this support suspect. Further, theory does not support this contention.

There are two additional conceptual problems with using the connection between diversity and ecosystem function as a conservation argument. First, the argument that species must be conserved in order to preserve ecosystem function implies consensus on which functions are valued and knowledge of how these functions relate to species richness. However, many ecosystem functions considered important as measured by monetary value (Costanza et al. 1997) or expert opinion (Schläpfer et al. 1999) appear to be extremely difficult to study experimentally (e.g., climate regulation, water cycling and purification). This fact limits the application of this argument for the conservation of species diversity. It remains

a challenge to develop an explicit link between the ecosystem functions that are measured and used in experiments (e.g., primary productivity) and the products of those ecosystem functions (e.g., clean air and water) that are valued by society.

A second conceptual issue concerns the use of functional groups. Functional groups are used to reduce system complexity by aggregating species by some shared role they play in a particular ecosystem function (e.g., guilds, Simberloff and Dayan 1991). In practice, functional groups are often created using trophic status (e.g., Naeem and Li 1997) or life history traits as surrogates for functional attributes (Hooper and Vitousek 1997, 1998). This is done under the assumption that similar species share functional traits. While the efficacy of this approach is obvious, this simplification constrains the conclusions. The unknown diversity within the group prohibits an assessment of the effect of species diversity within the functional group on ecosystem processes. Further, this lumping procedure masks individual population fluctuations, particularly of rare species that may be prone to extinction. Finally, conservationists ought to be concerned that functional redundancy may be achieved by replacing a native species with a non-native. Stromberg (1998) argues that saltcedar (*Tamarix chinensis*) is functionally redundant with Fremont cottonwood (*Populus fremontii*) for many key attributes in riparian zones on the American Southwest.

We suggest four ways to improve research to evaluate the role of species in ecosystem function for the purpose of conservation. First, studies linking diversity to ecosystem functions should focus on functions of practical concern, or at least the linkage to a function of practical concern must be explicit. Second, empirical results must discuss the distribution of abundance among species within the experimental system and relate this to real ecosystems. Third, a critical attribute in linking ecosystem function and stability may be the rate of species turnover within a community. An unrealistic distribution of abundance in an experimental system is likely less of a problem in a multi-year study of an annual system where there can be a rapid transition among rare and common species under environmental perturbation. The rate of change in species abundance ought to be included in the analysis as a response variable of interest. Finally, consideration of additional trophic levels may enhance our ability to demonstrate the linkage between ecosystem attributes and a large suite of local diversity. Recent theoretical research has developed the linkage between intertrophic interactions and stability in a compelling manner (e.g., McCann et al. 1998; Huxel and McCann 1998). Perhaps as a response to the emphasis placed on plants in most of the theoretical and experimental work on biodiversity and ecosystem function, many recent papers focus attention on the vital ecosystem effects of other groups of organisms such as ants (Folgarait 1998), aquatic fungi (Hyde et al. 1998; Wong et al. 1998) Collembola (Rusek 1998) and protozoa (Finlay and Esteban 1998). More attention to other suites of species would allow a broader discussion of the role of diversity in ecosystem function.

Conservation biology has been called a "crisis discipline" (Soulé 1986), requiring timely answers to complex problems. The complexity of the linkage between ecosystem function and species richness (often inappropriately equated with biodiversity) limits our ability to make precise predictions concerning this relationship. The importance of specifying the relationship between ecosystem function and species richness has resulted in recent research activity on this topic. Conservation biology has been characterized by enthusiastic support for key ideas (e.g., island biogeography, keystone species, metapopulation dynamics) presented in abstract form. Once empirically tested, these key ideas often fail to meet expectations as a conservation framework. The biodiversity-ecosystem function linkage appears to be another concept for which enthusiasm outweighs supportive evidence. Experimental tests of the interplay between biodiversity and ecosystem function have required a great investment of research effort, yet the results remain equivocal. Conservationists must temper enthusiasm for the claim that species richness supports ecosystem function lest our arguments, along with supporting data, force us to adopt the position that we could make a list of ten integral species for a given ecosystem and dispense with the remaining diversity.

The one area where the science seems to support the contention that the full complement of diversity is required for stable and sustainable ecosystem functions is in the realm of reducing system variability. This area requires additional work to both clarify the relationship as well as justify the notion that decreasing system variability is an important conservation attribute.

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