REVIEW

Biodiversity may regulate the temporal variability of ecological systems

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Abstract

The effect of biodiversity on natural communities has recently emerged as a topic of considerable ecological interest. We review studies that explicitly test whether the number of species in a community (species richness) regulates the temporal variability of aggregate community (total biomass, productivity, nutrient cycling) and population (density, biomass) properties. Theoretical studies predict that community variability should decline with increasing species richness, while population variability should increase. Many, but not all, empirical studies support these expectations. However, a closer look reveals that several empirical studies have either imperfect experimental designs or biased methods of calculating variability. Furthermore, most theoretical studies rely on highly unrealistic assumptions. We conclude that evidence to support the claim that biodiversity regulates temporal variability is accumulating, but not unequivocal. More research, in a broader array of ecosystem types and with careful attention to methodological considerations, is needed before we can make definitive statements regarding richness-variability relationships.

INTRODUCTION

Temporal variability is a fundamental property of ecological systems. Populations and communities fluctuate through time, and ecologists have devoted considerable attention to understanding the causes and consequences of this variability. Along the way, we have learned that variability contains information that can be of great practical and theoretical value (Micheli *et al.* 1999); for example, increased variability can be an indicator of ecosystem stress (Odum *et al.* 1979; Underwood 1991; Cottingham *et al.* 2000). However, variability can also cloud our perceptions of how nature operates and prevent us from making definitive conclusions about ecological systems. High rates of background variability increase the risk of species extinctions (Pimm 1991), reduce reliability of ecosystem processes (Naeem & Li 1997; Naeem 1998), and reduce our ability to detect (Cyr 1997) and predict (Cottingham *et al.* 2000) change in natural communities. As such, a better understanding of the factors that regulate temporal variability would improve the monitoring and management of endangered species, natural resources, and ecosystem services.

Biodiversity, particularly species richness, has long been thought to influence temporal variability. The idea that communities with many interacting species are less prone to large fluctuations (i.e. are more stable) than communities with fewer species (MacArthur 1955; Elton 1958) spurred a considerable amount of research during the 1960s and 1970s (see reviews by Goodman 1975; King & Pimm 1983; Pimm 1984; Haydon 1994). However, little consensus emerged from this flurry of activity. Although empirical studies tended to support the "complexity-stability" hypothesis (e.g. McNaughton 1977, 1985), theoretical studies indicated that models with more interacting species were less stable than models with fewer interacting species (e.g. May 1972, 1974). Interest in complexity–stability relationships waned during the 1980s, probably due to difficulties in defining complexity and stability (Pimm 1984) and the lack of consistent, conclusive evidence for or against the hypothesis.

Recently, though, ecologists have renewed their interest in the effects of biodiversity on ecosystem processes, including stability and a wide range of ecosystem functions (see reviews by Johnson *et al.* 1996; Chapin *et al.* 1998, 2000; Schläpfer & Schmid 1999; McCann 2000; Schwartz *et al.* 2000). Many of these studies have enjoyed a high profile both in the scientific literature and the public press. As a result, quite a few ecologists have come

to believe that species richness influences ecosystem processes, including temporal variability (Schläpfer *et al.* 1999). In fact, it has been suggested that biodiversity is comparable to disturbance, species composition and climate as a major driver of ecological processes (Tilman 1999).

In this paper, we review the recent theoretical, observational and experimental studies that have explicitly evaluated the relationship between species richness and the temporal variability of population and community metrics. We then critically evaluate the extent to which these studies support the MacArthur–Elton hypothesis that increased biodiversity leads to decreased variability. Recent reviews (e.g. Schwartz *et al.* 2000) indicate that biodiversity and ecosystem function may not be as tightly linked as many ecologists think (Schläpfer & Schmid 1999); we examine whether a similar caveat holds for richness–variability relationships.

RECENT EXPLORATIONS OF RICHNESS-VARIABILITY RELATIONSHIPS

We begin with a review of recent studies that evaluate the relationship between species richness and the temporal variability of two types of ecological variables: (1) population properties that apply to particular species, such as density and biomass and (2) aggregate community properties that are summed over species, such as total biomass, primary production and nutrient retention. We consider population and community variability separately because species richness appears to have contrasting effects on population vs. community properties (May 1974; King & Pimm 1983; Tilman 1996). Specifically, studies that support the hypothesis that more complex communities are less variable tend to focus on aggregate community properties, while studies that reject the hypothesis tend to focus on population properties. Below, we explain how recent theoretical studies account for these differences, and describe the empirical studies that test theoretical expectations.

Variability in aggregate community properties

Variability in aggregate community properties can be calculated using a statistical rule (Box *et al.* 1978; Schulter 1984; Frost *et al.* 1995; Doak *et al.* 1998):

$$\text{var}(B_c) = \text{var}\left(\sum_{i-1}^{N} B_i\right) = \sum_{i=1}^{N} \text{var}(B_i)$$

$$+2\left(\sum_{i=1}^{N}\sum_{j=1}^{i-1} \text{cov}(B_i, B_j)\right) \qquad (1)$$

In this equation, B_i is a property (e.g. biomass or productivity) of an individual species i, B_c is the aggregate community property created by summing that property across all species, N is the number of species, var is variance and cov is covariance. Thus, the variance of the aggregate community property is a function of summed variances and summed covariances. When species vary independently, their covariance is zero and the variance of the community property equals the summed species variances. However, if species do not vary independently, the (nonzero) summed covariances cause overall variability to increase or decrease. In order for there to be a negative relationship between species richness and the variability of an aggregate community property, the summed variances or summed covariances must decrease with increasing species richness (Tilman 1999). Consequently, the factors that change summed variances and summed covariances across richness gradients are a major focus of theoretical explorations of richness-variability relationships.

Theoretical studies

Theoretical studies have established that both statistical and biological mechanisms have the potential to influence richness–variability relationships (Table 1). Statistical averaging and mean–variance rescaling are predominantly statistical mechanisms, while evenness, overyielding, species interactions, and contrasting responses of different species to environmental fluctuations are primarily biological mechanisms. These mechanisms are not necessarily independent of one another, and some have both statistical and biological elements. Below, we briefly review these mechanisms and what is currently known about how each might contribute to the relationship between species richness and the temporal variability of aggregate community properties.

Statistical averaging, also called the portfolio effect, is a key mechanism for generating a negative correlation between the temporal variability of aggregate community properties and increased species richness (Doak *et al.* 1998; Tilman *et al.* 1998; Tilman 1999). Introduced to ecologists by Doak *et al.* (1998), statistical averaging occurs because individual species fluctuate through time. When community properties are calculated by summing across these individual fluctuations, the probability that their fluctuations will average out statistically increases with the number of species being added together (Fig. 1). This averaging reduces variation in the aggregate property relative to variation in the average individual species, and is the same process that causes the standard error of an estimate to decline as sample size increases (Ives *et al.* 2000). Greater asynchrony among species leads to greater dampening of the variability of the aggregate community metric; thus, statistical averaging is due in part to

Table 1 Brief guide to the statistical and biological mechanisms that may influence the relationship between species richness and the variability of aggregate community metrics such as total biomass, primary productivity and nutrient cycling. See text for more complete explanations and references.

Statistical	
Statistical averaging (portfolio effect)	If the temporal fluctuations of species in a community are not perfectly correlated, the variability of an aggregate community metric will be lower than the variability of the individual species due to averaging across species. See Fig. 1.
Mean–variance rescaling	Refers to the way in which variance changes with the mean [Eq. (2)]. If the variance of a population property increases with the mean, as is generally expected, variability of the associated aggregate community property should decline with increasing species richness. See Fig. 2.
Biological	
Evenness	The greater the evenness, the greater the role of each species in decreasing aggregate community variability due to statistical averaging. There is little statistical averaging if a few species dominate. See Fig. 3.
Overyielding	Occurs when an aggregate community property increases with increasing richness, i.e. when mixtures are more productive than monocultures. Broadens the range of scaling coefficients z [Eq. (2)] for which community variability decreases with increasing species richness.
Competition	Should encourage negative covariance and therefore decrease community variability.
Insurance effect	Applies when increased richness leads to larger differences in species' responses to changing environmental conditions, more negative covariance, and thus greater statistical averaging.

biological differences among species. Due to statistical averaging, we expect a negative correlation between community variability and increasing species richness whenever species fluctuations are not perfectly synchronous (Doak *et al.* 1998). Furthermore, because species need not interact with one another for this process to occur (Doak *et al.* 1998; Tilman *et al.* 1998; Tilman 1999), statistical averaging is a useful null model (*sensu* Gotelli & Graves 1996) against which to determine the effects of other potential mechanisms on richness-variability relationships (Doak *et al.* 1998).

Variance–mean rescaling, the degree to which the variance of an aggregate community property changes with the mean, is a second statistical property that may influence richness-variability relationships (Tilman *et al.* 1998; Tilman 1999). Most ecologists are familiar with the general tendency for variance to increase with the mean, which is why ecological data are often log-transformed prior to statistical analysis. This positive relationship between the mean and variance can be described with Taylor's power function (Taylor 1961),

$$s^2 = cm^z \qquad (2)$$

where s^2 is the variance, c is a constant, m is the mean and z is the scaling coefficient, such that larger values of z indicate that the variance increases more rapidly with the mean. Recent work by Tilman and colleagues (Tilman *et al.* 1998;

Tilman 1999) has established that the value of the scaling coefficient z affects the strength of statistical averaging. If we assume that all species in a community are independent, equally abundant, and have the same z, statistical averaging dampens community variability whenever $z > 1$, although it works most effectively with larger z (see Fig. 2 for graphical example and Tilman 1999 for derivation). In grasslands, z appears to be between 1.2 and 1.4 (Tilman *et al.* 1998; Tilman 1999). More generally, z is thought to be constrained between 1 and 2 (Murdoch & Stewart-Oaten 1989), although z may be as low as 0.6 and as high as 2.8 (Hanski 1982; Taylor & Woiwod 1982). This suggests that statistical averaging may operate in most, but not all, ecological communities (Doak *et al.* 1998; Tilman 1999).

Biological factors such as evenness (Doak *et al.* 1998) and overyielding (Tilman 1999; Hughes & Roughgarden 2000) also influence richness–variability relationships, in part by modifying the strength of the statistical averaging effect. For example, statistical averaging is greatest when all species contribute equally to the aggregate community property (Doak *et al.* 1998). As evenness decreases (i.e. dominance increases), the negative relationship between richness and community variability is dampened (Fig. 3). Eventually, species make such unequal contributions to the aggregate community property that increased richness has no effect on community variability. Overyielding, increases in the mean of an aggregate community property with increased richness, also affects community variability

(a)

(b)
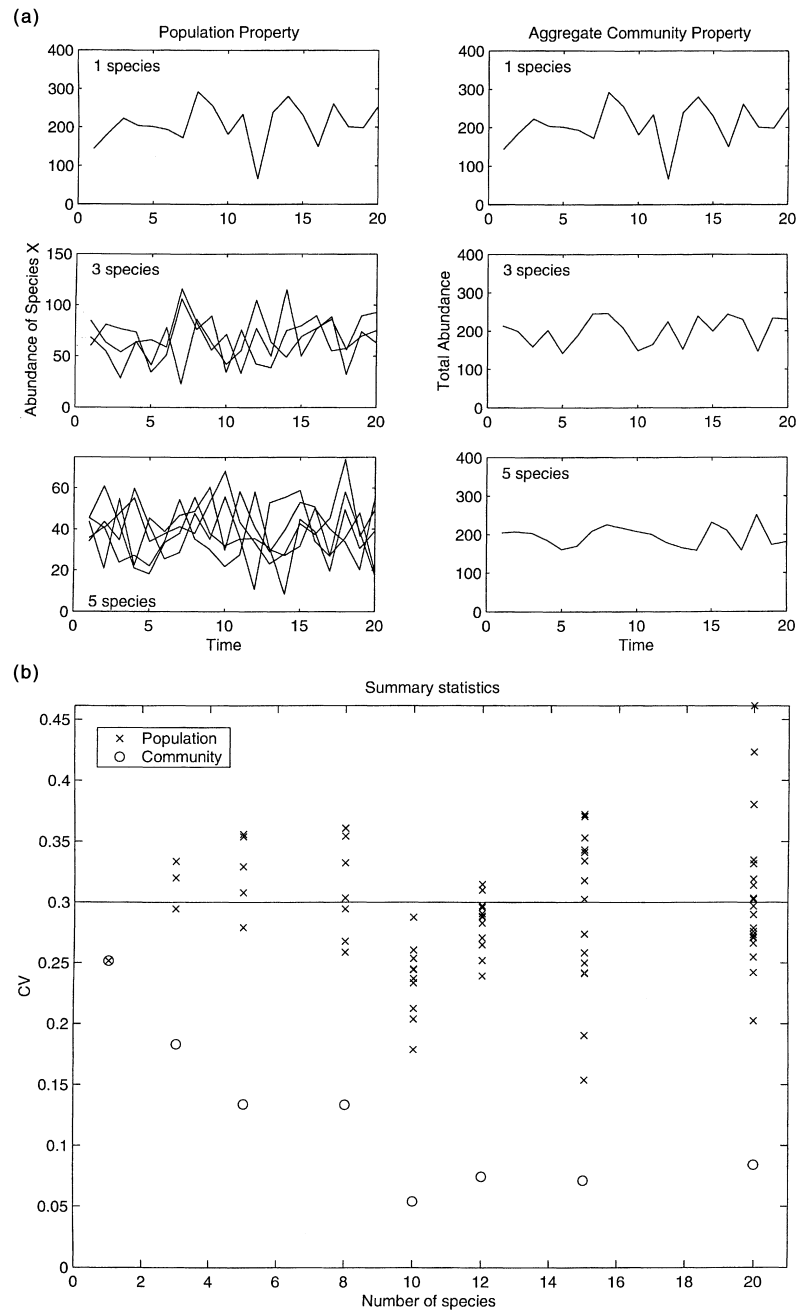
Figure 1 Graphical depiction of statistical averaging (the portfolio effect). A. Simulated fluctuations in the abundances of individual species (abundance of species X, left column) and an aggregate community property created by summing species abundances (total abundance, right column), through time for communities with one, three, and five species. Notice the apparent dampening in community variability as the number of species increases. B. Coefficients of variation (CV) for species abundances (×) and total abundance (○) across a richness gradient, showing a decline in the CV for total abundance with increasing richness. The points for one, three, and five species in (b) are derived from the time series depicted in (a). All data were simulated following equations in Tilman (1999): populations are assumed to be independent, normally distributed, equally abundant, and with the same CV (0.3). Mean total abundance was held constant at 200 individuals.

(Tilman 1999; Hughes & Roughgarden 2000). Greater overyielding (i.e. a larger increase in the community property with additional species) leads to larger decreases in community variability and a broader range of scaling coefficients z for which community variability decreases with increasing species richness. Because overyielding is linked to species coexistence (Tilman *et al.* 1997), mechanisms of coexistence may be an important component of richness–variability relationships (Tilman 1999).

Although there is a long history of invoking competition as a mechanistic explanation for complexity–stability

relationships (McNaughton 1977, 1985; Tilman 1996, 1999), the role of species interactions in richness–variability relationships is currently unclear. Community theory predicts that pairs of competitors should show compensatory responses, such that when one species increases, the other declines; the resulting negative covariance is expected to reduce variability in aggregate community properties (Frost *et al.* 1995; Tilman 1999). However, in complex communities these relationships are often masked by indirect effects (e.g. Connell 1983). In a simulation model including both direct and indirect
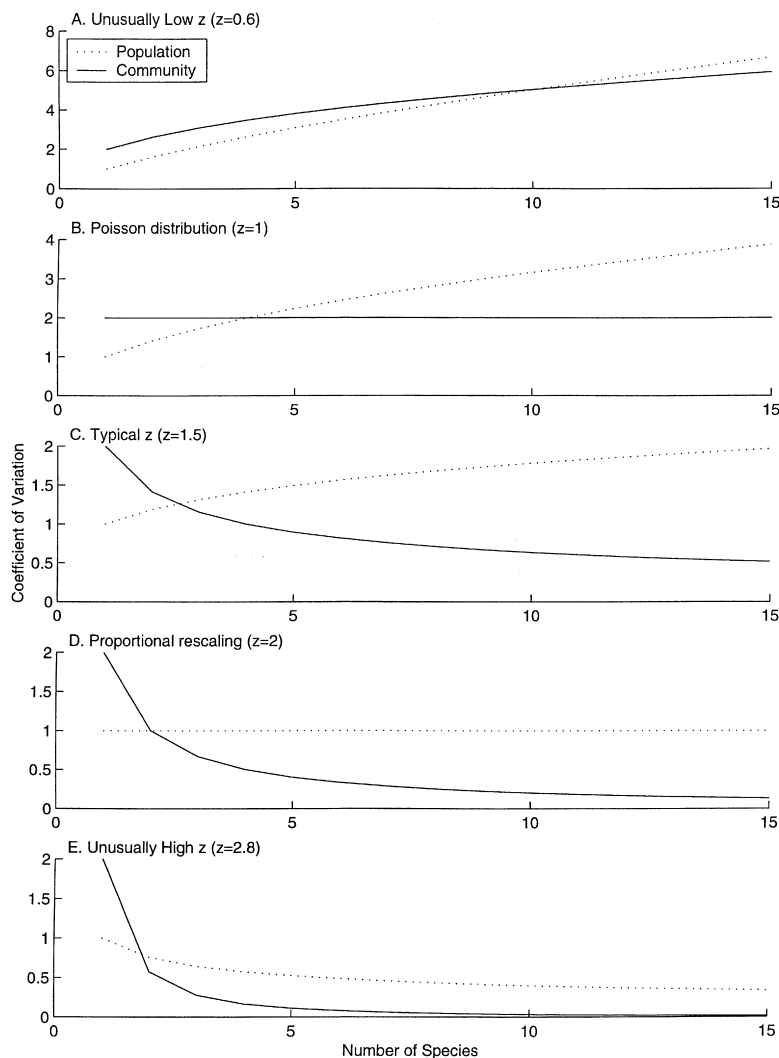
Figure 2 Effect of variance-mean rescaling (as summarised by the scaling coefficient, z) on the relationship between the temporal variability of population and aggregate community properties and species richness when all species are equally abundant and have the same CV. (A) $z = 0.6$, an unusually low value. (B) $z = 1$, typical of the Poisson distribution. (C) $z = 1.5$, a typical value of z based on the work of Murdoch & Stewart-Oaten (1989). (D) $z = 2$, the case where the variance scales as the square of the mean. (E) $z = 2.8$, an unusually high value. Equations for population and community variability were derived from Tilman's (1999) equations for stability (1/CV) as a function of the number of species (N) and the scaling coefficient z. Here, $\text{CV}_{\text{comm}} = \mu N / \sigma N = c^{1/2} m^{(z/2-1)} N^{(1-z)/2}$ and $\text{CV}_{\text{pop}} = (m/n)^{z/2-1}$, where c is a constant and m is the total community biomass (both set to 1.0).

species interactions, Tilman (1999) found that although community variability decreased with increased richness, this trend was due to summed covariances only in communities with < 4 species. Similarly, Ives and colleagues (Ives *et al.* 1999, 2000) used stochastic models and analytical approximations to show that both competition and predator–prey interactions have little effect on the relationship between community variability and species richness. Together, these studies suggest that species interactions may have a much weaker effect on richness–variability relationships than statistical averaging (Ives *et al.* 1999, 2000; Tilman 1999). However, an equilibrium-based model that includes stochastic perturbations to species abundances suggests just the opposite, that competitive interactions between species alter richness–variability relationships and can override the effects of statistical averaging (Hughes & Roughgarden 2000). To date, these contrasting results have not been

reconciled, but differences are likely to be due in part to differences in model structure, parameterization, and assumptions. Careful comparisons across models, and possibly construction of hybrid models, will be necessary to resolve the role of species interactions in richness–variability relationships.

Covariance in species responses to environmental fluctuations appears to strongly influence richness–variability relationships (Doak *et al.* 1998; Ives *et al.* 1999, 2000; Yachi & Loreau 1999). When species respond similarly to environmental fluctuations, the resulting positive covariances weaken, but do not eliminate, the degree to which community variability declines with increased species richness (Doak *et al.* 1998). However, when species respond differently to fluctuations in environmental conditions, the resulting negative covariances buffer aggregate community properties against change (Ives *et al.* 1999, 2000; Yachi & Loreau 1999). This

Effect of Evenness on the Richness–Variability Relationship
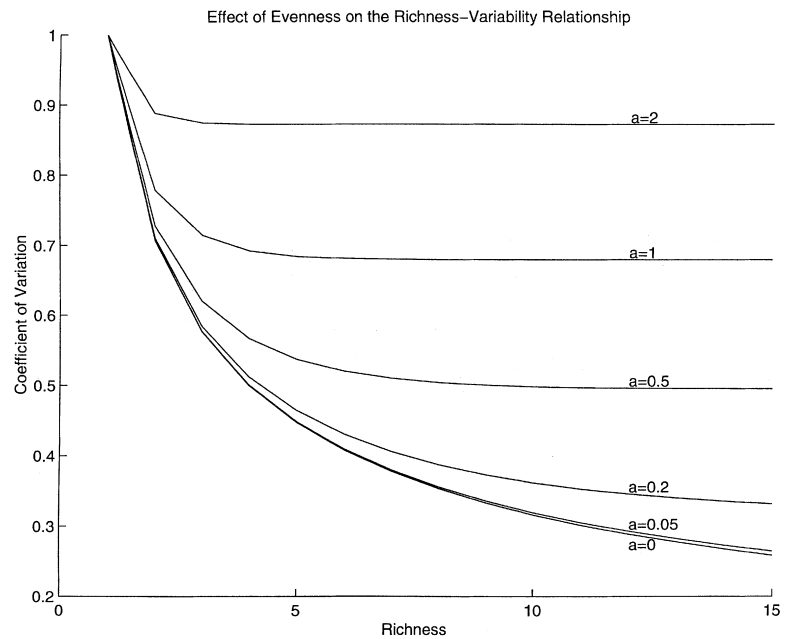
Figure 3 Effect of evenness on the relationship between the CV of an aggregate community property and species richness, derived from equation 3 in Doak *et al.* (1998). When $a = 0$, all species contribute equally to the aggregate community property. As *a* increases, the equity of contributions declines, such that when $a > 0.5$, five or fewer species account for $> 90\%$ of the aggregate community property.

"insurance hypothesis" assumes that the presence of more species increases the probability that at least some species will continue to function as the environment fluctuates (McNaughton 1977; Petchey *et al.* 1999; Yachi & Loreau 1999), and in fact does not work unless increased richness increases the diversity of species responses to environmental fluctuations (Ives *et al.* 1999, 2000). Stochastic dynamic models show that the strength of the insurance effect depends on the ways in which each species responds to environmental fluctuations (Ives *et al.* 1999, 2000; Yachi & Loreau 1999) and how these fluctuations sum to influence the aggregate community property (Yachi & Loreau 1999; Hughes & Roughgarden 2000). These models suggest that maintenance of species with different properties is very important to long-term community stability.

In summary, current theory suggests that variability in aggregate community properties will generally decline with increasing species richness (Doak *et al.* 1998; Tilman *et al.* 1998; Ives *et al.* 1999, 2000; Tilman 1999; Yachi & Loreau 1999; Hughes & Roughgarden 2000). This relationship should be strongest when (1) variance increases at least proportionally to the mean ($z > 1$, Tilman 1999), (2) biomass is evenly distributed among species (Doak *et al.* 1998), (3) overyielding is present (Tilman 1999; Hughes & Roughgarden 2000) and (4) increased richness increases the diversity of species' responses to environmental fluctuations (Ives *et al.* 1999, 2000; Yachi & Loreau 1999).

Empirical studies
Empirical studies generally support the expectation that temporal variability in aggregate community properties

should decline with increasing species richness, although this support is not universal (Table 2). For example, only one of the two studies that manipulated species richness via nutrient additions supported theoretical expectations. When species richness of grassland communities at the Cedar Creek Natural History Area (Minnesota, U.S.A.) was reduced by nutrient enrichment, there were significant negative correlations between the interannual variability of community biomass and the average species richness across experimental plots (Tilman 1996, 1999). In contrast, the relationship between richness and interannual variability was only weakly negative, and rarely significant, in the annually harvested hay meadows of the Park Grass Experiment (Hertfordshire, U.K.) (Dodd *et al.* 1994).

Experimental studies which directly manipulated species richness provided stronger, but not ubiquitous, support for theoretical expectations. For example, temporal variability in CO_2 flux was lowest in species-rich communities in laboratory microcosms constructed from differing numbers of algal, bacterivore, herbivore and predator species (McGrady-Steed *et al.* 1997). Follow-up experiments confirmed that temporal variability in community biomass was significantly negatively correlated with increasing species richness in three of the four functional groups (McGrady-Steed & Morin 2000). Furthermore, reanalysis of data from earlier experiments on the relationship between species richness and various ecosystem functions suggested that the temporal variability of nutrient uptake, community respiration, and primary productivity decreased significantly with species richness (McGrady-Steed *et al.* 1997). However, although systematic removals of major functional groups of

Table 2 Summary of the empirical studies exploring the effects of increased species richness on the variability of (a) aggregate community and (b) population properties. "Richness manipulation" includes both how species richness treatments were created and the trophic level(s) manipulated. "Replicates" indicates the number of replicates per treatment; n/a is used for indirect richness manipulations. "Response to richness" indicates how variability changed with increased species richness: "no change" indicates that there was no change in variability with richness, "decrease" indicates that there was a significant decline in variability with richness, and "increase" indicates a significant increase in variability with richness

Study	Richness manipulation	No. Richness Treatments	No. Replicates	Response variable	Response to richness
A. Variability of aggregate community properties					
Dodd *et al.* (1994)	Fertilization–producers	n/a	n/a	Plant biomass	No change
McGrady-Steed *et al.* (1997)	Direct–multiple levels	8	5–20	CO_2 flux	Decrease
McGrady-Steed & Morin (2000)	Direct–multiple levels	5	5	Bacterial abundance	Decrease
				Producer abundance	No change
				Herbivore abundance	Decrease
				Predator abundance	Decrease
Naeem *et al.* (1995)*	Direct–multiple levels	3	4–6	Net production	
				CO_2 flux	Decrease
Tilman (1996)	Fertilization–producers	9	5–6 per block	Plant biomass	Decrease/No change
				4 blocks	
Tilman *et al.* (1996)*	Direct–producers			Nutrient uptake	Decrease
Wardle *et al.* (1999)	Deletion–producers	5	10 blocks	Plant biomass	No change
				Root biomass	No change
				Active microbial biomass	No change
				Total microbial biomass	No change
				Primary productivity	No change
				Microbial respiration	No change
B. Population variability					
McGrady-Steed & Morin (2000)	Direct–multiple levels	5	5	Pooled species	No change
				Individual species	Mixed
Tilman (1996), Tilman (1999)	Fertilization–producers	9	5–6 per block 4 blocks	Pooled species	Increase
Wardle *et al.* (1999)	Deletion–producers	5	10 blocks	Nematode species	No change

*As reanalysed in McGrady-Steed *et al.* (1997)

primary producers in New Zealand grasslands led to significant reductions in the species richness of functional groups, there was no change in the temporal variability of plant, root, and microbial biomass; net primary productivity; or substrate-induced and basal respiration (Wardle *et al.* 1999). It seems unlikely that differences in power explain why some studies detected richness effects while others did not, since there is no clear relationship between the degree of replication (a crude surrogate for power) and the conclusions about richness–variability relationships drawn from each experiment (Table 2).

Variability In population properties

The relationship between species richness and population variability is considerably murkier than the relationship between richness and community variability. The theoretical results of Tilman (1999) suggest that the relationship between population variability and species richness

depends primarily on the scaling coefficient z (Fig. 2). Specifically, population variability is predicted to increase with species richness if $z < 2$, be independent of richness if $z = 2$ and decline with species richness if $z > 2$. Because z is thought to be constrained between 1 and 2 (Murdoch & Stewart-Oaten 1989), population variability should increase with richness in most natural communities. Tilman (1999) found support for this expectation in a simulation model that included competition and overyielding.

In contrast, empirical studies generally suggest that there is little to no relationship between species richness and population variability. When Tilman (1996) pooled results across grassland plant species and plots within a field, year-to-year variability in the biomass of each plant species was weakly positively correlated with the average species richness in both drought and nondrought years. However, when McGrady-Steed & Morin (2000) pooled results from laboratory microcosms across species and replicates, there was no correlation between temporal

variation in abundance and species richness. Furthermore, when they looked at each of the 24 species in their experiment independently, the temporal variability for 67% of the species populations had no correlation with species richness (McGrady-Steed & Morin 2000). Similarly, the deletion of plant functional groups from New Zealand grasslands did not influence the temporal variability of nematode populations (Wardle *et al.* 1999).

Synthesis: does biodiversity regulate temporal variability?

At present, there is appreciable empirical support for the theoretical expectation that species richness decreases the temporal variability of aggregate community properties, but less support for the expectation that species richness increases population variability. However, three factors preclude us from making definitive statements regarding the relationship between species richness and community variability at the present time. First, some of the discrepancies between theoretical predictions and empirical tests of those predictions could be due to the overly simplistic assumptions made in generating theoretical predictions; we return to this idea in A SUGGESTED RESEARCH AGENDA. Second, the empirical studies reviewed above have been conducted in a narrow range of ecosystems, mainly freshwater microcosms and terrestrial grasslands. Ecosystem- and even site-specificity could be an issue in extrapolating these results to other systems if richness-variability relationships are mediated by factors which vary across systems, such as the strength of interspecific interactions, food web structure, spatial heterogeneity and disturbance. Many of these factors are only beginning to be explored theoretically, and their effects on richness–variability relationships are not yet known. Finally, the findings of many empirical studies can be challenged on methodological grounds, including inadequate experimental designs and problems in how variability was calculated. We explore these methodological limitations in the next section.

METHODOLOGICAL LIMITATIONS TO EXTRAPOLATION FROM PAST STUDIES

We focus our attention here on two types of methodological problems–experimental design and the calculation of temporal variability–that may limit the extent to which we can draw robust conclusions from past studies of richness–variability relationships.

Challenges to effective experimentation

Experimental design, analysis, and interpretation of results are critical issues that must be addressed properly in order to test a scientific hypothesis. Although richness–variability studies have not been directly criticised for experimental design, studies investigating the effects of species richness on ecosystem function have provoked considerable statistical criticism, and many of the concerns are relevant to studies of richness-variability relationships. These criticisms are important, since the method for manipulating biodiversity has inevitable consequences for experimental design and interpretation (Diemer *et al.* 1997; Garnier *et al.* 1997; Huston 1997; Allison 1999).

The adequate isolation of species richness as an experimental variable has been a major challenge to the design of effective experiments to test the consequences of biodiversity. Early studies which took advantage of richness gradients in natural communities created by long-term experimental enrichment (e.g. Dodd *et al.* 1994; Tilman 1996) were severely criticised for "hidden" treatment effects that confounded richness with other factors, including community composition (Givnish 1994; Huston 1997). Consequently, more recent studies have attempted to directly manipulate species richness. This has been achieved by two principal approaches: constructing synthetic communities with the desired richness level *or* removing species from either constructed or natural assemblages.

Constructed communities offer the advantage of directly establishing target richness levels, but they have also been criticised because it can be difficult to isolate the effects of species richness from those of the identity of the particular species used in the experiment (Aarssen 1997; Huston 1997; Hodgson *et al.* 1998; Loreau 1998; Thompson & Hodgson 1998; Wardle 1998; Wardle 1999; but see Naeem *et al.* 1994b; Tilman 1997; Lawton *et al.* 1998; Naeem & Li 1998; van der Heijden *et al.* 1999). Communities can be constructed either randomly or nonrandomly from a species pool; choice of species for this pool is an often unrecognised source of bias. Constructing nonrandom communities requires researchers to choose seemingly appropriate combinations of interacting species (e.g. Naeem *et al.* 1994a), while random community construction involves random selection of species from the predetermined species pool (e.g. Tilman *et al.* 1996). Regardless of strategy, it can be difficult to distinguish the relative effects of species richness from species composition in constructed communities (Tilman 1997; Lawton *et al.* 1998; Naeem & Li 1998; van der Heijden *et al.* 1999). For example, the selection probability effect (SPE), first defined by Huston (1997), allows species-rich communities to outperform species-poor communities when assemblages are constructed randomly since replicates of species-rich treatments have a higher probability of being dominated by species whose unique traits allow them to perform well under the experimental

conditions. Although many regard the SPE as an experimental artefact that confounds the effects of species richness (Huston 1997; Lawton *et al.* 1998; van der Heijden *et al.* 1999; Wardle 1999), others counter that the SPE is a mechanism by which species richness affects ecological communities: without differences in species traits, there would be no effects of richness in a community (Tilman 1997; Lawton *et al.* 1998; Chapin *et al.* 2000; Purvis & Hector 2000). This largely semantic issue has yet to be resolved.

Constructed communities have also been criticised for a lack of realism. For example, Schwartz *et al.* (2000) pointed out that communities with equal abundances of each species are hardly typical in nature. Also, constructed communities rarely stay at their initial species richness, but settle down at some lower, realised richness (e.g. Tilman *et al.* 1996; McGrady-Steed & Morin 2000). Furthermore, because weak vs. strong interspecific interactions have differing effects on community stability, it is important that manipulations of species richness create communities with realistic ratios of weak and strong interactions (McCann 2000). This is difficult to achieve, particularly for randomly constructed communities.

Ecologists have also used selective removals of species or functional groups to investigate the effects of richness on community and ecosystem properties (e.g. Hooper & Vitousek 1998; Wardle *et al.* 1999). This approach is usually justified by the argument that if the global loss of biodiversity is the overarching question of interest, the best systems for examining the effects of species loss are depauperate versions of either natural (Wardle *et al.* 1999) or constructed communities (Naeem *et al.* 1994a; Naeem & Li 1998). Although the strategy of establishing richness treatments by removals holds promise for circumventing some of the challenges to experiments with constructed communities, removal experiments also have their own problems. For example, underlying environmental heterogeneity can create high variance among replicates, and the disturbance involved in removing individuals of some species may alter conditions for remaining individuals.

In both constructed and removal experiments, the need for adequate replication further exacerbates the problems of isolating species richness and creating realistic community structures (Huston 1997; Tilman 1997; Lawton *et al.* 1998). To separate the effects of species richness and species identity, both the richness levels and the combinations of species within each level must be replicated. However, this is a logistical nightmare if there are more than a handful of species or richness treatments. For example, Naeem *et al.* (1996) calculated that adequate replication of their experiment (16 species, 5 levels of species richness), would require 13 827 assemblages containing 221 232 plants! Despite these difficulties,

recent experiments have begun to replicate both richness and compositional effects, as exemplified by the large-scale European BIODEPTH experiment (Diemer *et al.* 1997; Hector *et al.* 1999).

Bias in estimates of temporal variability

Although population ecologists have long wrestled with the question of how to calculate variability from time series data (see e.g. reviews by McArdle *et al.* 1990; Gaston & McArdle 1994), these methodological concerns are not mentioned in the richness–variability literature. Measuring variability is a "deceptively simple task" (McArdle *et al.* 1990, p. 453) that requires attention to, and correction for, factors that create bias in variability estimates. Below, we briefly review these factors, including variance–mean rescaling, autocorrelation and sampling error.

The general tendency for variance to increase with the mean is a major source of bias. Variance–mean rescaling [described earlier using Taylor's power law, Eq. (2)] complicates comparisons of variability across populations or communities because variability estimates need to be benchmarked to similar mean values before they can be compared without bias (McArdle *et al.* 1990). Only two commonly used variability metrics take variance–mean rescaling into account: the coefficient of variation (CV: McArdle *et al.* 1990; Gaston & McArdle 1994) and the standard deviation of log-transformed values (SD[log(X_i)]: Williamson 1984; Gaston & McArdle 1994). Although the two metrics are nearly equivalent when the CV < 0.3, the SD[log(X_i)] is less sensitive to highly skewed distributions than the CV and is not subject to calculation bias if zero values are excluded (McArdle *et al.* 1990). As a result, SD[log(X_i)] has been a popular metric of variability for population ecologists (McArdle *et al.* 1990; Cyr 1997). We believe it could also be quite useful in studies of aggregate community properties, although to date, most variability studies have used the CV.

Unfortunately, neither the CV nor SD[log(X_i)] completely controls for variance–mean rescaling if the scaling coefficient z is not equal to 2 (McArdle *et al.* 1990). If z > 2, both the CV and SD[log(X_i)] will increase with the mean, and if z < 2, both will decrease slightly with the mean (McArdle *et al.* 1990). Either way, the bias will be greater the farther z is from 2. Given that z generally falls between 1 and 2 (Murdoch & Stewart-Oaten 1989), there is likely to be some uncontrollable bias in either metric for many ecological variables. This bias needs to be explicitly recognised in studies of richness–variability relationships where the mean changes across the richness gradient, as would be expected in systems with overyielding.

Other factors that bias estimates of variability include autocorrelation, trend, measurement (sampling) error and the spatiotemporal scale of sampling (Box *et al.* 1978; McArdle *et al.* 1990; Gaston & McArdle 1994; McArdle & Gaston 1995; Cyr 1997). First, positive first-order auto-correlation will cause variability to be overestimated, while negative first-order autocorrelation will cause variability to be underestimated (Box *et al.* 1978, p. 588). Autocorrelation will bias comparisons if the degree of autocorrelation differs between populations or communities, or is highly sensitive to sampling scale. Second, trends can be a problem if the objective is to estimate the variability of underlying dynamics in the absence of long-term directional change (Gaston & McArdle 1994). Third, measurement errors may bias variability estimates because they confound true fluctuations in population densities with apparent fluctuations due to inaccurate sampling (McArdle & Gaston 1995). Finally, estimates of temporal variability are sensitive to both the spatial and temporal scale of sampling (Connell & Sousa 1983; McArdle *et al.* 1990; Cyr 1997), which can complicate the comparison of variability across populations and communities sampled at different scales.

Although there was no mention of biasing factors on estimates of variability in any of the empirical papers we reviewed, bias could be an issue in some empirical studies. For example, because the standard deviation (SD) and standard error of the mean (SEM) are not scaled relative to the mean, the results of McGrady-Steed *et al.* (1997) may be biased because there was overyielding – i.e. mean community respiration and decomposition rates changed with species richness – in their study. Furthermore, autocorrelation, trend, and measurement error could bias any of the studies we reviewed.

The good news is that there are antidotes for most of the biasing factors. For example, calculating variability from the difference between successive samples can reduce bias due to trends and/or strong first-order autocorrelations (reviewed in Gaston & McArdle 1994). Similarly, there are techniques that correct for sampling error, if it is known (e.g. McArdle & Gaston 1995). However, these antidotes need to be used in order to avoid bias in comparisons of temporal variability across richness gradients.

A SUGGESTED RESEARCH AGENDA

In light of the methodological issues reviewed above, we recommend that future research on richness–variability relationships be directed towards three areas: (1) use of existing data to evaluate factors thought to affect richness-variability relationships; (2) theoretical studies with fewer restrictive assumptions and (3) properly designed field experiments in a greater diversity of ecosystems.

Opportunities with existing data

Existing data could be used to advance our understanding of several facets of richness-variability relationships. First, because the experimental designs used to investigate the effects of richness on temporal variability and ecosystem function are often quite similar, the raw data collected by long-running studies of *richness–function* relationships could be reanalysed to determine whether richness influenced temporal variability, bearing in mind the design caveats outlined above. Studies eligible for this data-mining exercise would have sampled each experimental unit at designated intervals over multiple generations of the focal organisms. McGrady-Steed *et al.* (1997) adopted this approach for a subset of richness–function studies with promising (but biased) results; we would like to see their work expanded using a more appropriate metric such as the CV, SD[log(X_i)], or perhaps Levene's test (e.g. Schultz 1985).

Second, time series from both richness–variability and richness–function experiments could be reanalysed to determine how species covariances changed across richness gradients. Two types of analyses seem relevant. Following Tilman (1999), summed variances and summed covariances could be calculated over time for each experimental unit, then plotted against average richness to explore how these metrics change across a richness gradient. In addition, the multivariate autoregressive techniques of Ives and colleagues (Ives *et al.* 1999, 2000) could be used to extract information regarding both species interactions and species responses to environmental fluctuations, thereby providing insight into the extent to which species interactions vs. the insurance effect might have operated in each experiment.

Third, published data on temporal fluctuations for many different populations could be used to determine variance–mean rescaling in different communities. Given Tilman's (1999) predictions regarding the role of the scaling coefficient z in richness–variability relationships, it seems important to gather comparative data on z in order to estimate the potential strength of statistical averaging in a variety of ecosystems. How does z vary for organisms that span a range of sizes and life histories? Is it true that z rarely exceeds 2 in ecological data? How do interspecific and intraspecific interactions affect z? The answers to these questions may help resolve the ambiguity surrounding results of empirical studies, since nonsignificant richness-variability relationships could be due to the values of z for that particular community.

Increased realism of theoretical studies

To date, theoretical models of the relationship between richness and variability have been built from relatively

simplistic and unrealistic assumptions that may limit the degree to which results are likely to apply to natural communities. For example, Tilman and colleagues (Tilman *et al.* 1998; Tilman 1999) assumed that all species within a community are equally abundant, i.e. that evenness is high. However, because natural communities are often dominated by relatively few species, statistical averaging may be irrelevant for real-world systems (Schwartz *et al.* 2000) (although evenness itself may be quite important: Nijs & Roy 2000; Wilsey & Potvin 2000). Similarly, in order to simplify the mathematics, Doak *et al.* (1998) and Tilman *et al.* (1998) assumed that the CV was the same for each species. Ives *et al.* (2000) assumed that $z = 2$ when developing their autoregressive model, while Hughes & Roughgarden (2000) assumed that $z = 0$. These assumptions regarding evenness, CV, and z are unlikely to hold in many, if not most, natural communities. To what extent are results robust to these and other restrictive assumptions? Answers to this question will have important consequences for the degree to which theoretical predictions will be expected to apply to natural communities.

Another interesting opportunity to extend current theory would be to consider the effects of density-dependent functional rates on richness-variability relationships. To date, models have assumed that *per capita* productivity or nutrient cycling is similar at low and high population density. However, it seems likely that this assumption will not hold for many populations. How might results regarding aggregate community variability change if the functional characteristics of each species were explicitly related to population size?

Furthermore, theoretical studies could broaden to include the effects of species richness across a wider range of community types, particularly those that include multiple trophic levels. To date, most studies have focused on species richness within a single trophic level, despite the fact that few natural communities fit this description. Richness–variability relationships might be quite different if the 'community' is defined as including more than one trophic level, since competitors are more likely to be positively correlated than predators and prey. Several empirical studies have addressed the effects of richness in multitrophic level systems (e.g. van der Heijden *et al.* 1998; Knops *et al.* 1999; Wardle *et al.* 1999; McGrady-Steed & Morin 2000; Symstad *et al.* 2000), but there is little theoretical underpinning for this work. Initial theoretical studies involving multiple trophic levels (Ives *et al.* 2000) are promising and worthy of continued development.

Empirical studies

Given the controversy generated by design issues, we recommend that researchers planning richness–variability studies pay particular attention to recent studies exploring the consequences of different experimental designs through simulation (e.g. Garnier *et al.* 1997; Allison 1999). These studies have generated a number of interesting and important results. For example, Garnier *et al.* (1997) demonstrated that comparison of species-rich communities with monocultures grown under identical conditions is essential, and that how mixtures vs. monocultures are established will affect the observed results. Allison (1999) compared six richness designs and found that, although most designs were able to detect an effect of species richness, the designs varied considerably in their ability to discriminate between the effects of richness and species composition. In addition, many designs were sensitive to sample size (Allison 1999), suggesting that adequate replication is essential.

We further recommend that researchers consider the merits of evaluating richness–variability relationships though experiments that simultaneously manipulate species richness through both construction and removal strategies. Since the consensus is that both approaches have their strengths and weaknesses, we may be able to achieve significant new understanding by combining these two approaches.

Based on the interrelationships of species diversity, productivity and scale (Waide *et al.* 1999), we also suggest that spatial extent of experiments be considered either as an experimental variable or as a potentially confounding factor in richness experiments. The European BIO-DEPTH project (cf. Diemer *et al.* 1997) provides a unique approach to the study of both local and regional patterns in richness-variability relationships. Using data from BIODEPTH, Hector *et al.* (1999) found that large-scale patterns did not always reflect patterns observed in 12 small-scale experiments. Because understanding temporal variability across a broad range of spatial scales is essential for the establishment of general conclusions regarding the effects of species richness, we look forward to seeing more researchers join together to replicate the same experiment at multiple sites, as was done quite successfully by the International Tundra Experiment (ITEX; Arft *et al.* 1999).

Finally, we suggest that empirical research on richness–variability relationships be expanded to include a greater array of ecosystems and habitats, especially those currently experiencing high rates of species losses (e.g. tropical rainforests, deserts, and wetlands; Sala *et al.* 2000). To date, most empirical studies of richness-variability relationships have been conducted in either grasslands or aquatic microcosms. Richness–variability studies may be under-represented in other systems because of difficulties associated with constructing diversity treatments (e.g. spatial distributions, complex behaviours, and generation times). However, the rich-

ness–variability relationship must be reliably detected in multiple ecosystems before it can be recognised as a general ecological pattern.

CONCLUSIONS

We began this review with the expectation that we would document a clear relationship between species richness and the temporal variability of population and aggregate community properties. However, we were surprised to find that the evidence for richness–variability relationships is a little more equivocal than we had expected. In hindsight, two factors are likely to have contributed to our expectations. First, although the conclusions of several studies which ostensibly support the hypothesis that biodiversity regulates variability are weakened by methodological difficulties, the critical reviews that point out these difficulties have rarely received the same degree of attention from a general ecological audience as the original papers. Thus, our initial scanning of titles and abstracts did not reveal the degree to which the methods used to evaluate the effects of species richness relationships have been contested. Second, as with other topics of considerable ecological interest, journals may favour studies that claim to demonstrate positive results over studies that report no definitive relationship (Wardle 1998). Such differential publication might have helped fuel our expectation that relationships between biodiversity and temporal variability have already been conclusively established.

Despite the currently equivocal support for a relationship between species richness and the temporal variability of population and community properties, we feel that efforts to clarify this relationship or to demonstrate the lack of a relationship should continue. We currently believe that, as with so many other ecological debates, the answer to the question, "Does species richness regulate temporal variability?" will probably not be a simple "yes" or "no". Instead, the answer will likely be "sometimes": richness is likely to influence temporal variability in some, but not all, systems, and under some, but not all, conditions in a particular system. If this expectation is correct, then future efforts should focus not only on demonstrating *that* species richness regulates temporal variability, but also on identifying *when* this regulation is likely to occur. Such information is essential to increasing our ability to maintain the consistency of ecological function despite the loss of component species–a goal that is important not only to ecologists, but also to policy makers and the general public.

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BIOSKETCH

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