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Changes in ecological stability across realistic biodiversity gradients depend on spatial scale

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ABSTRACT

Aim It is unclear how the stability of natural ecosystems and populations varies with biodiversity at spatial scales relevant to resource managers. This study evaluates whether theory and prior experiments adequately predict how stability varies with a measure of biodiversity, plant species richness, at multiple scales in naturally assembled ecosystems and assesses mechanisms through which biodiversity is proposed to affect stability.

Location Chihuahuan desert. Historically, grasslands represented the dominant vegetation type in this landscape and shrubs were uncommon. Desertification has degraded many native grassland regions into one of several alternate states dominated by different shrub species and these regions differ in biodiversity.

Methods Researchers at the Jornada long-term ecological research site have amassed 12 years of data on the primary productivity of individual plant species in 735 permanent 1-m² plots distributed among 15 regions that were all historically grasslands. I used this information to describe the relationship between biodiversity and stability at the local (1 m²) and regional (3721 m²) scale and to evaluate mechanisms through which biodiversity is proposed to affect stability.

Results At the local scale, ecosystem stability increased linearly with biodiversity while population stability tended to decline with biodiversity. At the regional scale, both ecosystem and population stability increased as a saturating function of biodiversity. Scale-dependent change in the biodiversity–stability relationship can be explained by the spatial insurance hypothesis, asynchrony in the local productivity dynamics of the average species, and a change in species evenness with scale that weakens statistical averaging.

Main conclusions Results from small-scale experimental studies may not directly translate to larger spatial scales but they appear to predict patterns in natural communities at small spatial scales. These results suggest that the maintenance of high biodiversity over a large spatial area is essential for maintaining ecosystem services and reducing the potential for further species extinctions.

Keywords

Chihuahuan desert, ecosystem dynamics, grasslands, population dynamics, scale dependence, synchrony.

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INTRODUCTION

Anthropogenic activity is causing our planet's biodiversity to decline at an alarming rate (Pimm *et al.*, 1995; Vitousek *et al.*, 1997; Sala *et al.*, 2000) and it is essential to understand how this loss affects the functioning and stability of natural systems if

society is interested in conserving or restoring ecosystems and species (Kinzig *et al.*, 2001; Loreau *et al.*, 2002; Kareiva & Levin, 2003; Novacek, 2008). Ecologists have made great progress in studying the effects of biodiversity on ecosystem processes and have found that the number of species present (species richness) has consequences for how efficiently ecosystems perform critical

functions (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2006; Isbell *et al.*, 2011). Less certain are the effects of biodiversity on ecological stability, due in part, to the need for long-term data (Cottingham *et al.*, 2001; Valone & Hoffman, 2003a; Tilman *et al.*, 2006). Stability has several meanings (Pimm, 1984) but a commonly used meaning (the inverse of the coefficient of variation) focuses on the extent of temporal variability of a system property (e.g. primary productivity) relative to the temporal average of the system property (Cottingham *et al.*, 2001; Tilman *et al.*, 2006). Enhancing our understanding of how biodiversity affects stability is important because ecosystems with low stability are less reliable in their ability to perform ecosystem functions and populations with low stability are more vulnerable to extinction (Cottingham *et al.*, 2001). I focus on the association between stability and a commonly studied metric of biodiversity, species richness.

Results of long-term experiments using small-scale artificially assembled ecosystems have reported that a reduction in plant biodiversity reduces ecosystem stability (i.e. temporal variability in total annual aboveground net primary production of all plant species) but enhances population stability (i.e. temporal variability in a population's annual aboveground net primary production averaged across all species) (Tilman *et al.*, 2006; Bezemer & van der Putten, 2007; van Ruijven & Berendse, 2007; Hector *et al.*, 2010). Jiang & Pu's (2009) meta-analysis affirms this general finding in experimental studies of single trophic level systems, and this finding is consistent with expectations from ecological theory (May, 1974; Tilman, 1996; Tilman *et al.*, 1998; Lehman & Tilman, 2000). Such consistent results are important as they clearly indicate that plant biodiversity exerts a causal influence on both ecosystem and population stability. Nonetheless, these experimental studies focus on responses measured at a small spatial scale (geographic grain of analyses $\leq 4 \text{ m}^2$) in artificially constructed ecosystems experiencing unrealistic (random) patterns of species loss. This is a frequent criticism of experimental work examining how biodiversity affects ecosystem function and ecological stability (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Duffy, 2009; Griffin *et al.*, 2009). An essential issue is whether similar responses are observed in naturally assembled ecosystems experiencing realistic patterns of species loss and at a larger spatial scale (i.e. a geographic grain $> 4 \text{ m}^2$) that is more relevant to conservation managers and policy makers. Some have proposed that the importance of biodiversity to ecological stability will be more evident at larger spatial scales than smaller spatial scales (Loreau *et al.*, 2003).

A scale-dependent change in the association between biodiversity and ecological stability may occur if the mechanism(s) whereby biodiversity affects stability vary with spatial scale. Mechanisms proposed to explain how species richness affects stability include statistical averaging (or the portfolio effect), overyielding, and reduced temporal covariance in the biomasses of species occurring in the community (i.e. compensatory dynamics) (Tilman *et al.*, 1998; Lehman & Tilman, 2000) (Table 1). Several pieces of information and new theory suggests that the influence of these mechanisms is likely to vary with

spatial scale (Table 1) but empirical evidence documenting scale-dependent change in these mechanisms is absent.

In this study, I present results demonstrating that the relationship between biodiversity (plant species richness) and stability depends on spatial scale, and describe how the mechanisms associated with this relationship change with scale (i.e. grain of the analysis). The approach I employ utilizes data from natural ecosystems that vary in biodiversity as the result of the desertification of native grasslands. The need for studies examining how stability varies across real gradients of biodiversity that are created by 'local (habitat) and landscape factors' causing alternative community states has been presented as essential to increase the applicability of research on the association between biodiversity and stability (Griffin *et al.*, 2009). Although I present results for how stability varies across a natural biodiversity gradient, one should not interpret the results reported here as the primary evidence indicating that changes in biodiversity cause changes in ecological stability. Such evidence is provided by the experimental studies described above. Instead, one should interpret the results reported here as evidence for whether insights gained from theory and small-scale experimental studies of artificially assembled ecosystems adequately explain variation in the stability in natural ecosystems and at spatial scales too large to conduct experiments.

METHODS

I assessed the relationship between biodiversity and stability at two spatial scales (i.e. geographic grain) for plant communities at the Jornada long-term ecological research (LTER) site in New Mexico (NM), USA. Grasslands represent the historically dominant vegetation type in southern NM where upland areas were dominated by black grama grass (*Bouteloua curtipendula*) and lowland areas (playas – ephemeral lakebeds) that become wetter were dominated by other grasses, including tobosa (*Pleuraphis mutica*), vine mesquite (*Panicum obtusum*) and alkali sacaton (*Sporobolus airoides*) (Huenneke *et al.*, 2002; Peters & Gibbens, 2006). Although shrubs have been present in the landscape for at least 4000 years they did not dominate the landscape (Grover & Musick, 1990). Desertification during the past 100 years, however, has resulted in shrubs becoming a much more dominant part of the landscape (Buffington & Herbel, 1965; Gibbens & Beck, 1988). Grasses still dominate some regions of the landscape at the Jornada LTER, but some regions which were historically grasslands have become dominated by one of three species of shrub: tarbush (*Flourensia cernua*), creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) (Huenneke *et al.*, 2002; Peters & Gibbens, 2006). Despite regional differences in the identity of dominant species present (i.e. vegetation types), the species pool for all of these regions is the same as most taxa can be found in any of the regions and all species found in regions dominated by shrubs are also found in regions dominated by grasses (Huenneke, 1996).

Researchers at the Jornada LTER have amassed 12 years (1990–2001) of species-specific data on aboveground net primary productivity on 735 permanent 1-m² plots distributed

Table 1 Summary of mechanisms and scale-dependent influences involving the relationship between ecological stability and species richness.

Mechanism	Scale-dependent influence
<p>1. Statistical averaging: statistical averaging is a mathematical product of the scaling coefficient (z) describing how the temporal variance of a population's productivity (s^2) varies with its mean productivity (m) when described as a power function, $s^2 = cm^z$, where c is a constant. Statistical averaging is expected to cause species richness to enhance ecosystem stability and reduce population stability when $1 < z < 2$ but cause species richness to enhance both ecosystem and population stability when $z > 2$ (Tilman <i>et al.</i>, 1998)</p> <p>2. Overyielding/underyielding: overyielding, an increase in the temporal average productivity with an increase in species richness, causes species richness to enhance stability when stability is defined as the ratio between the temporal average productivity and the temporal variability in productivity (Tilman <i>et al.</i>, 1998; Lehman & Tilman, 2000). Change in average productivity would be expected if increasing species richness alters the strength of competitive or facilitative interactions among species or if species differ in their ability to use different resources (i.e. niche complementarity). I refer to the reduction of average productivity with species richness as underyielding</p> <p>3. Compensatory dynamics/species asynchrony: asynchronous fluctuations in productivity dynamics of different species enhance ecosystem stability because species compensate for each other in a manner that maintains ecosystem productivity across years. Both competitive interactions and differences in the way in which species respond to changing environmental conditions can produce asynchronous fluctuations in productivity dynamics among species (Tilman <i>et al.</i>, 1998; Lehman & Tilman, 2000)</p> <p>4. Patch asynchrony*: greater species richness at larger spatial scales enhances population stability at larger spatial scales because the presence of more species in the region causes the productivity dynamics of a species to fluctuate asynchronously across patches</p>	<p>(a) Statistical averaging has a weaker effect on the association between species richness and stability when species evenness is low (Doak <i>et al.</i>, 1998; Cottingham <i>et al.</i>, 2001) and species evenness decreases with area (Wilson <i>et al.</i>, 1999). Consequently, the association between species richness and stability will be weaker at larger spatial scales if statistical averaging is an important mechanism linking species richness and stability</p> <p>(b) Spatial heterogeneity at larger scales increases the scaling coefficient to increase above that typically observed at a local scale (Murdoch & Stewart-Oaten, 1989) which could cause the biodiversity–stability relationship to change with spatial scale if statistical averaging is an important mechanism linking species richness to stability</p> <p>(a) Spatial averaging hypothesis (Benedetti-Cecchi, 2005): spatial heterogeneity in local diversity causes regional productivity to be lower than expected if productivity varies with local diversity in an increasing but saturating manner. Scale dependence in the stability–biodiversity relationship will arise from spatial averaging if diverse regions are more heterogeneous in local diversity than less diverse regions</p> <p>(b) Spatial insurance mechanism 1 – regional niche complementarity (Loreau <i>et al.</i>, 2003; Gonzalez <i>et al.</i>, 2009): spatial heterogeneity in species composition at the regional scale ensures the presence of species that differ in their ability to utilize resources in different localities. Resource heterogeneity is likely to be greater at larger spatial scales than smaller scales so the effect of niche complementarity will be greater at large spatial scales</p> <p>(a) Spatial insurance mechanism 2 – regional scale species asynchrony (Loreau <i>et al.</i>, 2003; Gonzalez <i>et al.</i>, 2009): greater spatial heterogeneity in species composition at larger spatial scale ensures the presence of taxa at larger spatial scales that are more likely to differ in their response (and hence fluctuate asynchronously) to changing environmental conditions. The odds of encountering species with different responses to environmental conditions increase in larger areas</p> <p>(a) Does not operate at local scale but operates at regional scale</p>

*This mechanism was not identified as a potential mechanism prior to the interpretation of the results reported in this manuscript.

equally among 15 regions that were all historically grasslands (i.e. 49 plots/region): three regions dominated by black grama grass, three grass-dominated playas, three regions dominated by creosote bush, three regions dominated by mesquite and three regions dominated by tarbush (Huenneke *et al.*, 2001, 2002) (see Huenneke *et al.* (2002) for a map of the study regions). Plots within each region were arranged within a 7×7 grid and the distance between adjacent plots was 9 m; consequently a region covered an area of 3721 m². Each of these regions differ in the extent of temporal variability in ecosystem production (Huenneke *et al.*, 2002) but temporal variation in productivity was not associated with temporal variability in precipitation (Huenneke & Schaffer, 2006). I used data collected for the studies of

Huenneke *et al.* (2001, 2002) to evaluate how stability varies across a biodiversity gradient at a site where the historically dominant vegetation type has degraded into multiple, alternative states (vegetation types) that tend to differ in biodiversity.

Researchers measured the amount of aboveground biomass of every species found within each study plot. Biomass was estimated non-destructively by estimating volume during the autumn, winter and spring of each year and then applying species-specific regressions that predict biomass on the basis of volume estimates (Huenneke *et al.*, 2001). The annual productivity of a species within a plot for a particular year was estimated as the sum of the positive increments in aboveground biomass for that species between: (1) autumn and winter, (2)

winter and spring, and (3) spring and autumn (Huenneke *et al.*, 2001). Annual ecosystem productivity within a plot for a particular year was estimated as the sum of the annual productivities of all plant species within the plot. Productivity within a region (either for an ecosystem or for a particular population) for a particular year was estimated as the sum of annual productivities of all plots within the region. Huenneke *et al.* (2001) have demonstrated that these methods provide sufficiently accurate estimates of annual aboveground net primary productivity at the Jornada LTER.

I estimated ecosystem stability, population stability and plant biodiversity (species richness) at two spatial scales for each region: the scale of a plot within each region (local) and the scale of the entire region (regional). Stability of an ecosystem or a population was estimated as μ/σ where μ represents the average (across the 12 years of study) annual productivity within a plot or region and σ represents the standard deviation (across the 12 years of study) of annual productivity values within a plot or region (Tilman *et al.*, 2006). Population stability was measured for each species and then averaged across all species present within each plot or region. The metric of stability employed here assumes there is no temporal trend in average productivity but this assumption is valid in this case as productivity did not vary predictably with time within any region (P -values from linear regressions between productivity and year for each site were all > 0.12 , median P -value = 0.61). Local biodiversity was represented by the average (across years) number of species found within a particular plot and regional biodiversity was the average (across years) number of species found within a region.

To avoid pseudoreplication of local estimates within regions, I averaged stability and biodiversity estimates across all 49 plots within a region prior to statistical analysis (Srivastava, 1999; Harrison & Cornell, 2008; Canning-Clode *et al.*, 2010) to produce one estimate of biodiversity, ecosystem stability, and population stability at the local scale for each region. Thus, the number of data points associated with analyses at each spatial scale was the same (15) and scale-dependent patterns cannot be attributed to differences in sample size. Given that the biodiversity gradient considered here resulted from degradation of a historically dominant vegetation type into multiple, alternative states (vegetation types) that tend to differ in biodiversity, it is important to determine how much variability in stability can be attributable to: (1) variation in biodiversity among vegetation types, (2) variation in biodiversity that is independent of that due to vegetation type, (3) variation in the properties of vegetation types that are not associated with differences in biodiversity, and (4) other unknown sources of variation not associated with any of the first three sources of variation. I quantified how much variation in stability was associated with each of these four sources of variation by comparing coefficients of determination of general linear models which differed in the combinations of predictor variables (biodiversity and vegetation type) (see Appendix S1 in Supporting Information for a description of the models) included in the model. This approach allows one to conclude: (1) whether a change in biodiversity associated with the degradation of historical grassland to other vegetation types

provides an adequate explanation for why regions differ in stability, and (2) whether differences in biodiversity among vegetation types explain more of the variability in stability than do differences in biodiversity that are independent of variation in vegetation type.

To evaluate whether stability varied with biodiversity I employed least-squares regression analysis. Two forms of regression models were performed to evaluate how stability varied with biodiversity: a quadratic regression on untransformed data, and a linear regression on log-transformed data. I employed the quadratic regression model as it can detect linear, asymptotic and modal relationships and each of these kinds of relationship are of interest. I employed the linear regression of log-transformed data because it may capture nonlinear but asymptotic relationships better than the quadratic regression model. The regression model explaining the greatest amount of variation in stability was reported and this was the quadratic regression model in all cases. To reduce collinearity between linear and quadratic components of biodiversity, biodiversity estimates were centred on their grand mean prior to analysis. A significant quadratic effect in a quadratic regression would mean that the association between stability and biodiversity is modal or asymptotic (e.g. having a nonlinear but saturating association) but a test developed by Mitchell-Olds and Shaw (MOS; Mitchell-Olds & Shaw, 1987) can discriminate between modal and asymptotic relationships. The MOS test evaluates whether the value of biodiversity where stability is expected to peak (B^*) on the basis of a quadratic regression is significantly lower than the largest observed biodiversity estimate (B_{\max}) and significantly higher than the lowest observed biodiversity estimate (B_{\min}). If B^* is different from both B_{\min} and B_{\max} the relationship is deemed modal (Chase & Ryberg, 2004). On the other hand, if B^* is different from either B_{\min} or B_{\max} , but not both, the relationship is deemed asymptotic (Chase & Ryberg, 2004). Details associated with statistical methods used to evaluate mechanisms through which biodiversity may affect stability and whether the influence of these mechanisms changed with spatial scale are provided in Appendix S1.

RESULTS

The majority of the variation in stability among regions at local and regional scales was attributable to differences among vegetation types (Table 2, A + B). Much, but not all, of the variation in stability attributable to vegetation type was associated with vegetation types differing in biodiversity (Table 2, A versus B) rather than differences in properties of vegetation type that are not associated with differences in biodiversity. One exception to this pattern was for population stability at the local scale; differences in vegetation type explained the majority of variation in stability but little of this variation was explained by vegetation types differing in biodiversity. Consequently, differences in biodiversity among vegetation types account for much variation in stability but biodiversity is not the only property of vegetation type that contributes to variation in stability among vegetation types. Differences in biodiversity among vegetation types

Table 2 Partitioning of variability in ecological stability at two different spatial and hierarchical scales. Numbers presented are percentages. The sum of A and B corresponds to how much of the variability in ecological stability is due to differences in vegetation type and the sum of B and C corresponds to how much of the variability in ecological stability is attributable to variation in species richness (biodiversity) regardless of the source of variation in species richness. Numbers in bold represent how much variability in stability was explained by differences in species richness that was the result of either vegetation types differing in species richness or differences in species richness that were not attributable to differences in vegetation type.

Spatial scale	Hierarchical scale	Variability due to:			
		Vegetation type:			Unknown (D)
		Differences in properties of vegetation types that are not associated with species richness (A)	Differences in species richness among vegetation types (B)	Differences in species richness that are not attributable to vegetation types (C)	
Region	Ecosystem	38.1	36.2	11.6	14.1
	Population	33.1	35.6	0.6	30.7
Plot	Ecosystem	46.2	45.3	2.7	5.8
	Population	76.9	8.0	4.0	11.1

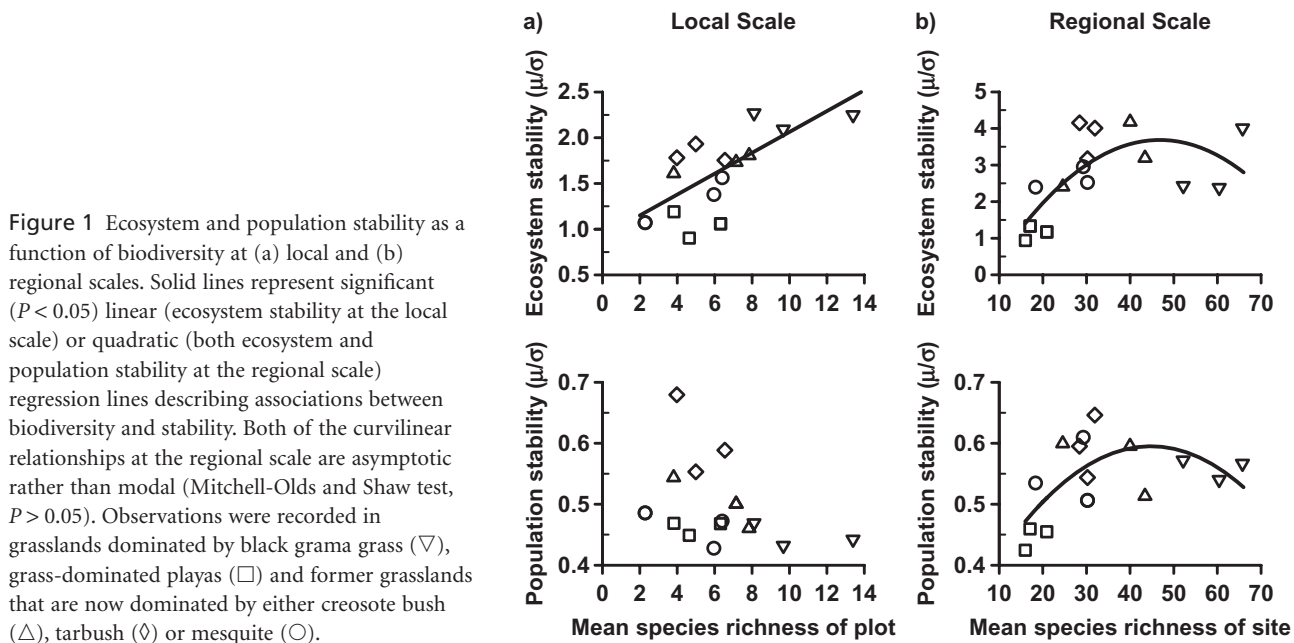


Figure 1 Ecosystem and population stability as a function of biodiversity at (a) local and (b) regional scales. Solid lines represent significant ($P < 0.05$) linear (ecosystem stability at the local scale) or quadratic (both ecosystem and population stability at the regional scale) regression lines describing associations between biodiversity and stability. Both of the curvilinear relationships at the regional scale are asymptotic rather than modal (Mitchell-Olds and Shaw test, $P > 0.05$). Observations were recorded in grasslands dominated by black grama grass (∇), grass-dominated playas (\square) and former grasslands that are now dominated by either creosote bush (Δ), tarbush (\diamond) or mesquite (\circ).

explained more variation in stability than differences in biodiversity that were independent of those associated with vegetation type (Table 2, B versus C).

Ecosystem stability within plots increased linearly with local biodiversity (linear effect: $F_{1,12} = 10.97$, $P = 0.006$; quadratic effect: $F_{1,12} = 0.11$, $P = 0.749$; $R^2 = 0.48$), while population stability at the local scale did not covary significantly with biodiversity at the local scale (linear effect: $F_{1,12} = 1.62$, $P = 0.228$; quadratic effect: $F_{1,12} = 0.02$, $P = 0.901$; $R^2 = 0.12$) (Fig. 1a). There was considerable variation in ecosystem stability at the local scale but the region with the lowest local diversity had an ecosystem stability that was 52% lower than the region with the highest local

diversity. At the regional scale, an increase in biodiversity was associated with a nonlinear increase in both ecosystem (linear effect: $F_{1,12} = 5.31$, $P = 0.039$; quadratic effect: $F_{1,12} = 5.70$, $P = 0.034$, $R^2 = 0.48$; MOS test: $P_{B^*} < B_{\max} > 0.05$, $P_{B^*} > B_{\min} < 0.05$) and population stability (linear effect: $F_{1,12} = 1.92$, $P = 0.191$; quadratic effect: $F_{1,12} = 4.89$, $P = 0.047$; $R^2 = 0.36$) (Fig. 1b). Regression models indicate that ecosystem and population stability at the regional scale peak at 47 and 44 species, respectively. Consequently, the most diverse region would need to lose 33% of its species before either ecosystem or population stability would be expected to decline. A reduction in biodiversity to levels observed in the least diverse region, however, would

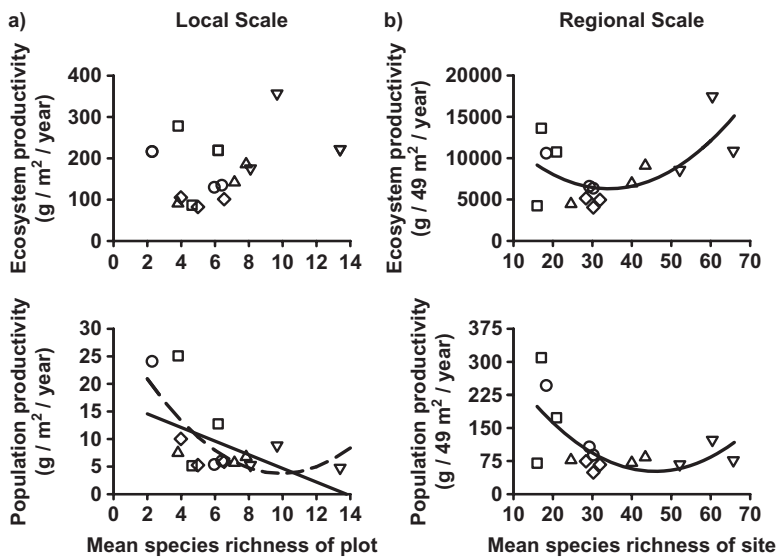


Figure 2 Ecosystem productivity and the productivity of an average species as a function of biodiversity at (a) local and (b) regional scales. Solid lines represent significant ($P < 0.05$) linear (population productivity at the local scale) or quadratic (both ecosystem and population productivity at the regional scale) regression lines that describe the association between biodiversity and productivity. The dashed line represents a strong quadratic trend ($P = 0.064$) in the association between biodiversity and population productivity at the local scale. All of the curvilinear relationships at the regional scale are asymptotic rather than modal (Mitchell-Olds and Shaw test, $P > 0.05$). Observations were recorded in grasslands dominated by black grama grass (∇), grass-dominated playas (\square) and former grasslands that are now dominated by either creosote bush (\diamond), tarbush (\diamond) or mesquite (\circ).

be associated with an ecosystem and population stability that is 62% lower than the asymptotic estimates for ecosystem and population stability.

The scaling coefficient describing the association between a population's temporal mean productivity and the population's temporal variance in productivity at the local ($z = 1.84$, $SE_z = 0.01$) and regional ($z = 1.78$, $SE_z = 0.01$) scale at the Jornada were both greater than 1 but less than 2 ($t_{11} > 17.39$, $P < 0.001$). Species evenness was significantly lower at the regional scale than at the local scale (average difference in evenness between scales for each region = 0.299, $t_{14} = 9.778$, $P < 0.001$).

Ecosystem productivity only increased with biodiversity at the regional scale after a region had more than 46 species present (the value of biodiversity where the quadratic regression estimates productivity is at a minimum) (linear effect: $F_{1,12} = 3.23$, $P = 0.098$; quadratic effect: $F_{1,12} = 4.94$, $P = 0.046$; $R^2 = 0.41$; MOS test: $P_{B^*} < B_{\max} < 0.05$, $P_{B^*} > B_{\min} > 0.05$) but ecosystem productivity did not vary with biodiversity at the local scale (linear effect: $F_{1,12} = 2.04$, $P = 0.179$; quadratic effect: $F_{1,12} = 0.45$, $P = 0.514$; $R^2 = 0.17$) (Fig. 2). The average productivity of a population declined with biodiversity in an asymptotic manner at the local (linear effect: $F_{1,12} = 5.86$, $P = 0.032$; quadratic effect: $F_{1,12} = 4.16$, $P = 0.064$; $R^2 = 0.46$; MOS test: $P_{B^*} < B_{\max} > 0.05$, $P_{B^*} > B_{\min} < 0.05$) and regional (linear effect: $F_{1,12} = 3.45$, $P = 0.088$; quadratic effect: $F_{1,12} = 4.79$, $P = 0.049$; $R^2 = 0.41$; MOS test: $P_{B^*} < B_{\max} > 0.05$, $P_{B^*} > B_{\min} < 0.05$) scale (Fig. 2).

The summed covariances in the productivity dynamics among different species comprising an ecosystem did not vary with biodiversity at either the local (linear effect: $F_{1,12} = 0.74$, $P = 0.408$; quadratic effect: $F_{1,12} = 3.76$, $P = 0.077$; $R^2 = 0.27$) or regional scale (linear effect: $F_{1,12} = 0.18$, $P = 0.682$; quadratic effect: $F_{1,12} = 0.47$, $P = 0.504$; $R^2 = 0.05$). A form of the covariance effect could also cause scale-dependent changes in the association between ecological stability and biodiversity if the biodiversity of a region is associated with the extent of synchrony in productivity dynamics among patches within the

region. For example, an increase in population stability with biodiversity at the regional scale could occur despite the fact that population stability appears to decline with biodiversity at the local scale (Fig. 1a versus Fig. 1b) if the extent of synchrony in local patch dynamics within a region declines with the biodiversity of the region. For the average species, the (log) summed temporal covariance of productivity dynamics across all plots within a region declined as (log) regional biodiversity increased ($F_{1,13} = 9.33$, $P = 0.009$, $R^2 = 0.42$; Fig. 3a). For the ecosystem (i.e. all primary producers), there was a trend for the (log) summed temporal covariance of productivity dynamics among patches to decrease with (log) biodiversity in the region but this trend was not statistically significant ($F_{1,13} = 2.12$, $P = 0.169$, $R^2 = 0.14$; Fig. 3b).

DISCUSSION

The results reported here demonstrate that stability varied across a biodiversity gradient at the Jornada LTER that stemmed from the degradation of native grasslands into vegetation types that were not previously present in the landscape. This study found that the stability of both ecosystems and populations in naturally assembled communities varied differently across a biodiversity gradient at a large spatial scale than at a small spatial scale. In general, biodiversity was a good predictor of stability as it explained, on average, 30% and 42% of the variation in stability at the local and regional scales, respectively. The work reported here provides one explanation for why Jiang & Pu (2009) found that the relationship between population stability and biodiversity within a trophic level varied between experimental studies (small-scale studies) and observational studies (large-scale studies).

Stability–biodiversity relationships at the local scale (Fig. 1a) were consistent with theoretical models (May, 1974; Tilman, 1996; Lehman & Tilman, 2000) and the findings of small-scale experimental studies conducted in artificially assembled ecosystems (Tilman *et al.*, 2006; Bezemer & van der Putten, 2007; van

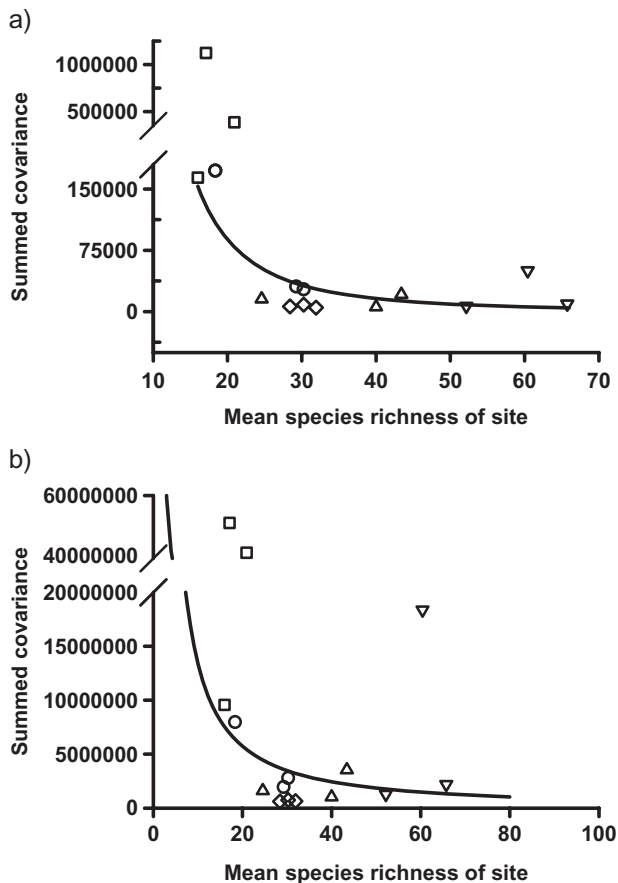


Figure 3 Synchrony in productivity dynamics of (a) the average species and (b) the ecosystem (all primary producers) among localities in regions varying in biodiversity. The solid line represents the relationship between a log-transformed measure of synchrony (the sum of temporal covariances in productivity estimates among plots within a region) and the log of regional biodiversity. The regression accounts for a statistically significant amount of the variation in (a) ($P = 0.009$) but not (b) ($P = 0.169$). Note that the scale above and below the y-axis break is different in order to more clearly show the slope of the regression line while also including all data points. Observations were recorded in grasslands dominated by black grama grass (∇), grass-dominated playas (\square) and former grasslands that are now dominated by either creosote bush (\triangle), tarbush (\diamond) or mesquite (\circ).

Ruijven & Berendse, 2007; Hector *et al.*, 2010). Such congruence in results is encouraging as it suggests that theory and experiments provide sufficient insight to predict how stability varies with biodiversity in the real world. In contrast to observations at the local scale, stability–biodiversity relationships at the regional scale (Fig. 1b) are consistent with theory predicting similar effects of biodiversity on ecosystem and population stability under some conditions (McCann *et al.*, 1998; Tilman *et al.*, 1998). The increasing but saturating effect of biodiversity on stability at regional scales suggests that biodiversity loss will reduce stability but the effect of biodiversity loss on stability will be greater in regions with fewer species than in regions with more species because the slope of the relationship between biodiversity and stability is greater in areas with fewer species.

A nonlinear decline in stability with regional biodiversity has important implications for efforts designed to conserve and restore biodiversity. Given that extinction risk is influenced more by temporal variability in population size than average population size (Belovsky *et al.*, 1999), populations in regions with low biodiversity are expected to be at greater risk of extinction despite the fact that they are more productive (Fig. 2b) because they are less stable (Fig. 1b). Consequently, the persistence of a species in a regional community could greatly depend on conservation efforts designed to preserve the diversity of other species in the community. The nonlinear association between stability and biodiversity at regional scales also suggests that benefits of species restoration efforts on regional stability will decline as regional biodiversity is enhanced. Furthermore, conservation efforts in regions with low biodiversity may not protect as many species but such efforts could prevent more dramatic reductions in stability that induce even more extinctions and greater loss in the reliability of the region in providing important ecosystem services. It is important to note, however, that ecosystem productivity at the regional scale did not reach a plateau as regional biodiversity increased (Fig. 2b). This suggests that conservation efforts targeted at diverse regional communities can be important to maintain high levels of average ecosystem productivity (one important ecosystem function) even though such regions are less susceptible to changes in their stability induced by biodiversity loss.

The work reported here supports the conclusions of experimental studies demonstrating how biodiversity loss from artificially assembled ecosystems will alter ecological stability at small spatial scales but it also demonstrates how these responses may change in naturally assembled ecosystems at the spatial scales that are more relevant to resource managers. Such scale dependence should not be taken to mean that small-scale experimental work with artificial ecosystems is irrelevant. Indeed such experiments demonstrated that variation in biodiversity causes variation in stability. Instead, it points out that integrating results from small-scale experiments and theory with observational studies of natural ecosystems experiencing species loss can enhance our understanding of how biodiversity affects the stability of natural systems at scales too large to feasibly conduct experiments with the same rigour as conducted at small scales. Together, this body of work suggests that the continued loss of our planet's biodiversity could reduce the ability of our natural ecosystems to reliably provide critical ecosystem services and enhance the likelihood of further extinctions in the future.

Mechanisms

The observed values of the scaling coefficient (z) at the Jornada LTER were such that ecosystem stability is expected to increase with biodiversity and population stability is expected to decrease with biodiversity if statistical averaging was an important mechanism driving the association between biodiversity and stability (Table 1). Consequently, statistical averaging may have contributed to: (1) the observed increase in ecosystem stability with biodiversity at both scales, and (2) the observed trend for

population stability to decline with biodiversity at the local scale. Species evenness was lower at the regional than the local scale, however, and statistical averaging has a weaker effect on the association between biodiversity and stability when species evenness is lower (Doak *et al.*, 1998; Cottingham *et al.*, 2001). Thus, statistical averaging probably had a weaker effect on the biodiversity–stability relationship at the regional scale than at the local scale. Furthermore, statistical averaging does not explain why population stability increased with biodiversity at the regional scale, because the scaling coefficient describing the association between mean annual productivity of a species and temporal variance in the productivity of a species was greater than 1 but less than 2, a condition that causes biodiversity to reduce population stability via statistical averaging (Tilman *et al.*, 1998). The decline in evenness with scale and the discrepancy between the observed and predicted pattern (based on the z coefficient) between biodiversity and stability at the regional scale suggest that statistical averaging is not an important mechanism through which biodiversity affects stability at larger spatial scales.

Biodiversity is also expected to affect stability if an increase in biodiversity either enhances (i.e. overyielding) or reduces (i.e. underyielding) the productivity of a population or ecosystem (Table 1). The productivity of the average species declined with biodiversity at both the local and regional scale at the Jornada LTER (Fig. 2), suggesting that biodiversity may suppress the productivity of a species via more intense competitive interactions. Nonetheless, species removal experiments conducted at the Jornada LTER in a region dominated by creosote bush found limited evidence for competitive interactions, but the authors suggest that responses to removals may occur over longer time intervals than that considered in their study (Buonopane *et al.*, 2005). Although the decline in the average productivity of a population with increasing biodiversity may have contributed to the decline in population stability with biodiversity at the local scale it does not explain why population stability increased with biodiversity at regional scales. Instead, another process (see below) must counteract the underyielding effect of biodiversity to allow biodiversity to enhance population stability at larger scales.

Ecosystem productivity did not vary with biodiversity at the local scale but increased with biodiversity at the regional scale (Fig. 2). Thus, biodiversity could not cause the observed increase in ecosystem stability via overyielding at the local scale but it could be a contributing factor at the regional scale. Others, however, have presented evidence that biodiversity enhances ecosystem stability at the local scale via overyielding (Valone & Hoffman, 2003a, b; Tilman *et al.*, 2006; van Ruijven & Berendse, 2007). Given that overyielding of ecosystem productivity occurs as the result of greater niche complementarity and/or facilitation among species (Table 1), the observations reported here suggest that the extent of niche complementarity or the importance of facilitation at the local scale at the Jornada LTER is rather low in comparison to these other study sites. The importance of niche complementarity and/or facilitation at the Jornada LTER appears to increase with spatial scale given the increase in ecosystem productivity with biodiversity at the

regional scale. The greater importance of niche complementarity at regional scales than local scales is consistent with one aspect of the spatial insurance hypothesis: species diversity–productivity associations will be stronger at regional scales than local scales due to the fact that spatial heterogeneity in species composition and differential responses of taxa to local conditions enhances resource use at large spatial scales (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). The absence of a downward concave relationship between biodiversity and ecosystem productivity at the local scale indicates that spatial averaging was not an important mechanism associated with a scale-dependent change in the association between productivity and biodiversity (Benedetti-Cecchi, 2005; Gonzalez *et al.*, 2009).

Biodiversity can also enhance ecosystem stability if it reduces synchrony (i.e. the amount of positive covariance) in the productivity dynamics of different species within the ecosystem (Table 1). There is no evidence that biodiversity reduces synchrony in the productivity dynamics of different species at the Jornada LTER at either local or regional scales. Several studies have reached the same conclusion regarding the covariance effect (Valone & Hoffman, 2003a; Tilman *et al.*, 2006; van Ruijven & Berendse, 2007; Valone & Barber, 2008), but a more recent study which focused on assemblages with either one or two species present found that the covariance effect promoted stability at local scales (Hector *et al.*, 2010). Clearly more work is needed to evaluate the extent to which biodiversity stabilizes ecosystems via the covariance effect. Nonetheless, this study does not find support for an aspect of the spatial insurance hypothesis which posits that larger areas that are more diverse will be more stable because they are more likely to contain taxa that differ in their response to changing environmental conditions (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009).

Different mechanisms contributed to the manner in which ecosystem stability varied with biodiversity at the local (statistical averaging) and regional (weak statistical averaging effect and overyielding that is the result of niche complementarity aspects of the spatial insurance hypothesis) scales and to the manner in which population stability varied with biodiversity at the local scale (statistical averaging and underyielding). None of the previously proposed mechanisms explain why population stability increased with biodiversity at the regional scale at the Jornada LTER. Instead, the mechanism contributing to the increase in population stability with biodiversity at the regional scale is the result of biodiversity reducing synchrony in the productivity dynamics of a species among different patches (i.e. plots) (Fig. 3a) (see Table 1). This mechanism stabilizes fluctuations in population productivity of a species at a large spatial scale even though population stability does not vary with biodiversity at a small scale. Such asynchrony appears to be sufficient to counteract the underyielding effect of biodiversity on the productivities of individual species at the regional scale.

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SUPPORTING INFORMATION

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Appendix S1 Methods used to partition sources of variability in ecological stability and to evaluate particular mechanisms associated with biodiversity–stability relationships.

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BIOSKETCHES

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