

SPATIAL HETEROGENEITY EXPLAINS THE SCALE DEPENDENCE OF THE NATIVE–EXOTIC DIVERSITY RELATIONSHIP

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Abstract. While small-scale studies show that more diverse native communities are less invadable by exotics, studies at large spatial scales often find positive correlations between native and exotic diversity. This large-scale pattern is thought to arise because landscapes with favorable conditions for native species also have favorable conditions for exotic species. From theory, we proposed an alternative hypothesis: the positive relationship at large scales is driven by spatial heterogeneity in species composition, which is driven by spatial heterogeneity in the environment. Landscapes with more spatial heterogeneity in the environment can sustain more native and more exotic species, leading to a positive correlation of native and exotic diversity at large scales. In a nested data set for grassland plants, we detected negative relationships between native and exotic diversity at small spatial scales and positive relationships at large spatial scales. Supporting our hypothesis, the positive relationships between native and exotic diversity at large scales were driven by positive relationships between native and exotic beta diversity. Further, both native and exotic diversity were positively correlated with spatial heterogeneity in abiotic conditions (variance of soil depth, soil nitrogen, and aspect) but were uncorrelated with average abiotic conditions, supporting the spatial-heterogeneity hypothesis but not the favorable-conditions hypothesis.

Key words: *alpha diversity; beta diversity; California (USA) grassland; coexistence; competitive exclusion; diversity–invasibility paradox; gamma diversity; invasion; serpentine soil; spatial heterogeneity.*

INTRODUCTION

For some time ecologists have been interested in whether diverse communities are less invadable (Elton 1958). Currently, a paradox exists in the literature. Models and experiments at small spatial scales have tended to find negative relationships between native and exotic diversity (Elton 1958, Turelli 1981, Case 1990, Tilman 1997, Knops et al. 1999, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000, Lyons and Schwartz 2001, Brown and Peet 2003). This has been interpreted to mean that native diversity armors a community against invasion. In contrast, observational studies at large spatial scales have tended to find positive relationships between native and exotic diversity suggesting that diverse communities are more invadable (Lonsdale 1999, Stohlgren et al. 1999, 2003).

These opposing patterns are thought to be the result of different processes operating at different spatial

scales (Levine and D’Antonio 1999, Stohlgren et al. 1999, Levine 2000, Shea and Chesson 2002). Small-scale studies tend to detect negative relationships because they are more likely to be at spatial scales at which competition operates, and thus, are more likely to detect the effects of competition (Huston 1999). Large-scale studies are likely to detect the effects of site-wide extrinsic factors that covary with diversity, so that sites that have favorable conditions for exotics also have favorable conditions for natives (Levine and D’Antonio 1999). Extrinsic factors can be biotic or abiotic factors like resource availability or propagule supply rate (Levine and D’Antonio 1999, Shea and Chesson 2002). In other words, it is thought that niche partitioning and competitive exclusion drive the relationship between native and exotic diversity at small scales but that at large scales, the effects of extrinsic factors override the effects of competition and in turn determine how communities are structured.

However, there is not yet a general explanation for why native and exotic species diversity should increase with favorable environmental conditions. While variation in propagule supply (Levine 2000) is one plausible mechanism, it may not generalize easily to other

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systems, especially at larger scales. Soil fertility and other aspects of resource supply, on the other hand, are not well supported by theory. That is, very little community theory makes the prediction that more species should be able to coexist at higher resource levels (Wright et al. 1993, Hawkins et al. 2003). We need to identify a general mechanism that is consistent with both theory and evidence, to explain the qualitative shift from negative relationships (indicating competitive exclusion) to positive ones (indicating competitive coexistence) with increasing spatial scale.

In one of the first attempts to address this problem theoretically, Shea and Chesson (2002) showed how a positive relationship at a large scale can arise by combining data from a series of negative relationships at smaller scales (Fig. 1). To detect the small-scale relationship, differences in diversity at larger scales, perhaps due to different extrinsic conditions, must also be accounted for. This idea is the basis for a statistical theory of multiscaled diversity–invasibility relationships. Shea and Chesson consider mean diversity at large spatial scales (alpha diversity). However, researchers working at large spatial scales are generally concerned with cumulative diversity (Stohlgren et al. 1999, 2003, Lonsdale 1999).

Here we extend the ideas of Shea and Chesson (2002) to cumulative diversity (gamma diversity). First, we define alpha and gamma diversity as follows: *alpha diversity* (α) is species richness measured for a small-scale unit; *gamma diversity* (γ) is species richness in a larger spatial unit, in other words the cumulative diversity over all the smaller units within the larger unit. Alpha diversity for the larger unit is the mean diversity over the smaller units. Gamma is related to alpha through *beta diversity* (β), a measure of the spatial heterogeneity in species composition. Beta diversity can be defined multiplicatively so that $\gamma = \beta\alpha$ (Whittaker 1960), or additively so that $\gamma = \beta + \alpha$ (Allan 1975, Lande 1996). We prefer the multiplicative definition because it relates more naturally to the species–area relationship (Harte and Kinzig 1997, Harte et al. 1999). The multiplicative form can be transformed to additivity by using the logarithm scale: if $A = \ln \alpha$, $B = \ln \beta$, and $G = \ln \gamma$, then $\gamma = \beta\alpha$ can be restated as $G = A + B$.

To understand how the relationship of native and exotic diversity can be positive or negative, recall that the sign of the slope in a linear relationship is determined by the covariance. For beta diversity defined multiplicatively, the covariance of the cumulative diversities is

$$\text{Cov}(G_N, G_E) = \text{Cov}(A_N, A_E) + \text{Cov}(B_N, B_E) + \text{Cov}(A_N, B_E) + \text{Cov}(A_E, B_N) \quad (1)$$

where A_N and A_E are the mean diversity and B_N and B_E are the beta diversity. For beta diversity defined ad-

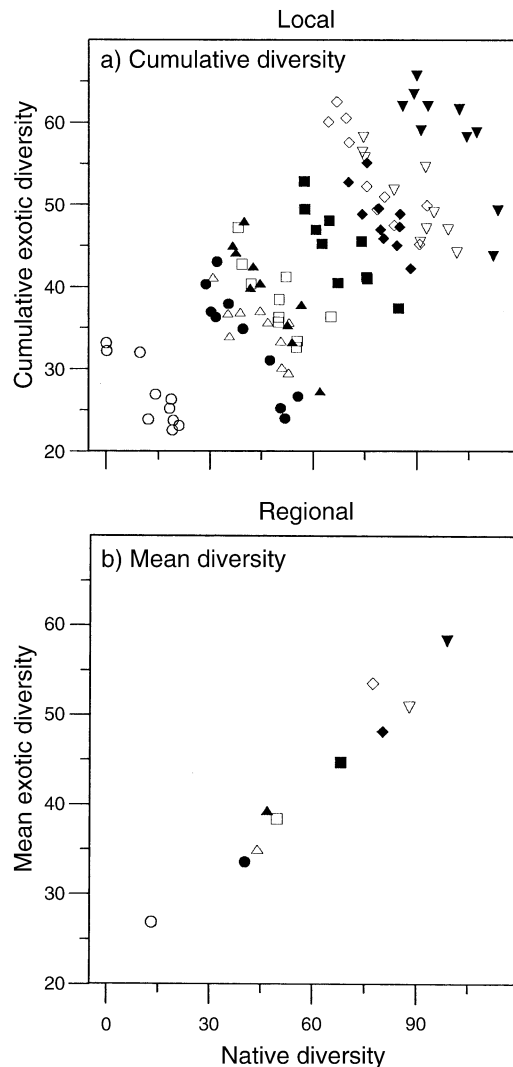


FIG. 1. The conceptual model of Shea and Chesson (2002). There are three spatial scales (for illustrative purposes: quadrats within sites within a region). If we collected data in 10 quadrats at each of 10 sites within a region (for each site, quadrats are represented by a distinct symbol type in [a]), then the relationship at the smallest scale (quadrats within sites) is negative. However, in (a) the cloud of points for all quadrats has a positive trend. In (b) the mean exotic and mean native diversity for each of the 10 sites within the region forms a positive relationship.

ditively, the covariance of the cumulative densities is

$$\text{Cov}(\gamma_N, \gamma_E) = \text{Cov}(\alpha_N, \alpha_E) + \text{Cov}(\beta_N, \beta_E) + \text{Cov}(\alpha_N, \beta_E) + \text{Cov}(\alpha_E, \beta_N) \quad (2)$$

Here, γ_N and γ_E are the cumulative species richness (gamma diversity) of native and exotic species, respectively, at the larger scale (say sites), α_N and α_E are the corresponding mean species richness (alpha diversity) of the smaller-scale units (say quadrats within sites), and β_N and β_E are the between-quadrat beta di-

versities. Thus, the sign of the slope of the relationship between native and exotic cumulative diversity depends on both the sign of the slope for mean diversity and the sign of the slope for the beta diversities.

Our model leads to an alternative hypothesis for why the relationship between native and exotic cumulative diversity changes from negative to positive as spatial scale increases: as we increase the spatial scale, coexistence mechanisms that depend on spatial heterogeneity in the environment come into play, overriding the competitive exclusion that operates at smaller scales. Thus, landscapes with more spatial heterogeneity can sustain both more native and more exotic species, leading to a positive correlation of native and exotic diversity at large scales. This hypothesis has a stronger mechanistic basis than the idea of favorable environmental conditions, since much coexistence theory predicts that greater spatial heterogeneity in a resource will allow more species to coexist (Connell 1979, Chesson and Huntly 1997, Chesson 2000).

Our aim was to test the implications of our model in a nested data set for grassland plants. In particular, could our model help to explain the diversity–invasibility paradox? We asked three questions. (1) Does the slope of the relationship between native and exotic diversity change between spatial scales so that it is negative at small scales and positive at large scales? (2) If the slope of the diversity–invasibility relationship differs between spatial scales, what drives the change in sign? Is it (a) the relationship between native and exotic mean (alpha) diversity, (b) the relationship between native and exotic beta diversity, or (c) both? (3) What is the role of extrinsic conditions (e.g., abiotic factors) in the relationship between native and exotic diversity at large scales? Were diversity patterns caused by mean abiotic conditions or by the spatial heterogeneity in abiotic conditions?

In this study, we define small spatial scales as those at which we expect individual plants to experience competition (both intra and interspecific). At these scales we might expect to detect a negative relationship between native and exotic diversity. For our grassland communities, this scale corresponds approximately to our smallest spatial unit, a 1-m² quadrat. We define any scale larger than this to be “large,” that is, outside the realm in which we would expect competition to act. As we consider larger spatial scales, we expect heterogeneity in the environment within the larger scale to increase, leading to a positive correlation of native and exotic diversity at the larger scale. Thus, these scale definitions depend on the scale of interaction of the study organism.

METHODS

Data collection

Our survey site was located in patchy serpentine and non-serpentine grassland in the McLaughlin University

of California Reserve (38°51' N, 123°30' W), 120 km north of San Francisco, California; USA. We collected data at 96 sites that comprised a 550 × 350 m grid, in the spring of 2001 and 2002. Sites were located 50 m apart in 12 rows and 8 columns. At each site, we collected plant composition data in four 1-m² quadrats, located around a central marker. In total, we detected 163 grass and forb species, of which 118 species were native and 45 species were exotic. We collected soil samples, 10 cm deep, 30 cm from the central marker at each site. Soil chemical composition and texture was analyzed at A and L Western Laboratories (Modesto, California, USA) (for organic matter, pH, Ca/Mg, N, P, Zn, Fe, Cu, K, Na, H, % Sand, % Silt, % Clay, texture). We measured slope and aspect at the central marker, and measured soil depth at five random locations within 2 m of the central marker by hammering a 12-mm-diameter, 120-cm-long, steel rod into the ground until bedrock was encountered (up to a maximum of 60 cm).

The grid comprised four spatial scales: (1) four 1-m² quadrats within each site (quadrat: 1 m²), (2) four sites within each subblock (site: 16 m²), (3) four subblocks within each block (subblock: 2516 m²), and finally (4) six blocks within the grid (block: 23 716 m²). Ideally, the local scale is the scale at which individuals interact with individuals of their own and other species. Operationally, we defined this as the smallest spatial unit, a 1-m² quadrat, although the scale of interactions is likely to have been somewhat smaller than this. Means were calculated with the local scale as the grain for both the diversity and beta diversity analyses.

Data analysis

We defined diversity as “species richness.” We used Genstat (Version 6.1, VSN International, Hemel Hempstead, UK) for all analyses. We used regression with a blocking factor (site, subblocks, blocks) to estimate the slope of the relationship between native and exotic diversity for each scale: quadrats within sites, sites within subblocks, subblocks within blocks, and blocks within the grid. We ran separate analyses for mean diversity and cumulative diversity. The statistical model was:

$$E_{ij} = a_i + bN_{ij} + \varepsilon_{ij}, \quad \varepsilon_{ij} \sim \mathcal{N}(0, \sigma^2)$$

where i indexes units at the larger scale (e.g., sites) and j indexes units at the smaller scale (e.g., quadrats within sites). For example, for quadrats within sites, E_{ij} is exotic richness in site i , quadrat j , N_{ij} is native richness in the same quadrat, a_i is the y -axis intercept for each site and b is the slope of the linear relationship of exotic vs. native richness at the quadrats-within-sites scale. The important feature of this model is that b is the common slope at the smaller scale, whereas the intercept a_i varies between units at the larger scale. This corresponds to the nested model of Shea and Chesson (2002) and contrasts with the widely used but incorrect regression model that has a common intercept.

We regressed native exotic diversity on both the natural and logarithm scales because the logarithm scale is more appropriate biologically but the natural scale was more appropriate statistically. On the natural scale, we used Box-Cox transformations of the response variable where appropriate to reduce departures from linear regression assumptions (Box and Cox 1964).

For each spatial scale we also looked at whether the beta diversity of native and exotic species covaried. We used both the multiplicative ($\gamma = \alpha\beta$, Whitaker 1960) and additive (Allan 1975, Lande 1996) versions of beta diversity for two reasons. First, although we believe that the multiplicative version is more correct (in line with the species–area relationship, species accumulate as area is increased in a proportional rather than additive manner), we wanted to compare our results for multiplicative beta diversity with results for additive beta diversity, because the additive metric is popular (Loreau 2000, Gering and Crist 2002, Veech et al. 2002). Second, regression assumptions were satisfied better on the natural scale (additive beta diversity) than on the logarithm scale (multiplicative beta).

Because beta diversity requires information about how diversity varies at a lower spatial scale, we could not calculate beta diversities for our smallest spatial scale. That is, we could not calculate a within-quadrat beta diversity. Again, we used regression with a blocking factor (subblock, block) to determine the slope of the relationship between native and exotic beta diversity for each of the three higher spatial scales (sites within subblocks, subblocks within blocks, blocks within the grid). The cross covariances of α - and β -diversity in Eqs. 1 and 2 were also examined using regression.

We also regressed the logarithm of native and exotic diversity and beta diversity against the mean and the variance of each abiotic variable (i.e., soil chemical composition and texture variables, slope, aspect, and soil depth). For each spatial unit (e.g., each subblock or each block), a Box-Cox transformation (Box and Cox 1964) was applied to obtain independence between the mean and variance. We then tested for independence of the mean and variance with regression. Because the abiotic data were collected at the site scale, we could only analyze data for the two larger spatial scales: subblocks within blocks and blocks within the grid.

RESULTS

Cumulative and mean diversity

We examined the relationship between native and exotic diversity at four spatial scales, for both mean and cumulative diversity (Figs. 2 and 3). The slopes of the relationships for mean diversity and cumulative diversity were different (Figs. 2 and 3). For means, the relationship between native and exotic diversity was negative at all four spatial scales, small through large. In contrast, for cumulative diversity, the relationship

between native and exotic diversity was negative at the two smallest spatial scales and positive at the two largest scales. Thus, the pattern that we detected for cumulative diversity, of negative relationships at small scales and positive relationships at large scales, is the pattern that is most commonly detected in the literature where small-scale studies tend to detect negative relationships and large-scale studies tend to detect positive relationships.

While most of the slopes were significantly different from zero, for both the logarithm and natural scales, some of the slopes for cumulative, mean, and beta diversity at the larger spatial scales were only marginally significant. Nonetheless, the linear relationships appear to be a good fit to the data and the opposing sign of the slope for mean vs. cumulative diversity is obvious (Figs. 2 and 3). As there were only six replicates at the largest spatial scale, we had low power to detect a significant relationship at this scale because there were fewer replicates than other scales (a large block size was necessary in the nested design to test relationships at smaller scales). To be sure that regression slopes changed sign at larger scales we did additional tests at the largest spatial scale, blocks within the grid. We regrouped the data into slightly smaller blocks (nine sites per block) to give 12 replicate blocks instead of 6 replicates. With 12 replicates, all of the larger-scale relationships were significant, as follows: (1) natural scale: cumulative diversity, $P = 0.04$, $R^2 = 28.0\%$; mean diversity, $P = 0.05$, $R^2 = 26.4\%$; additive beta diversity, $P = 0.008$, $R^2 = 47.2\%$; (2) logarithm scale: cumulative diversity, $P = 0.008$, $R^2 = 47.4\%$; mean diversity, $P = 0.04$, $R^2 = 26.2\%$; multiplicative beta diversity, $P = 0.05$, $R^2 = 24.4\%$. Thus, we were satisfied that the slope changed to positive at larger scales for cumulative but remained negative for means, as reflected in Figs. 2 and 3.

Beta diversity

We also examined the relationship between native and exotic beta diversity for the three larger spatial scales for both multiplicative and additive beta diversity. At the smaller spatial scale (sites within subblocks), native and exotic beta diversity was unrelated (Figs. 2 and 3). However, at the two larger spatial scales, the slope of native and exotic beta diversity was positive (Figs. 2 and 3). Thus, the beta diversity of natives and exotics was positively correlated at the spatial scales at which we detected positive relationships between cumulative native and exotic diversity but was not correlated at the scales for which we detected a negative relationship between cumulative native and exotic diversity.

One outlier was removed from the multiplicative beta diversity relationship for blocks within the grid. This point had a large residual (twice as large as the response) and when it was included, the model could not be fitted. For this relationship, with the point re-

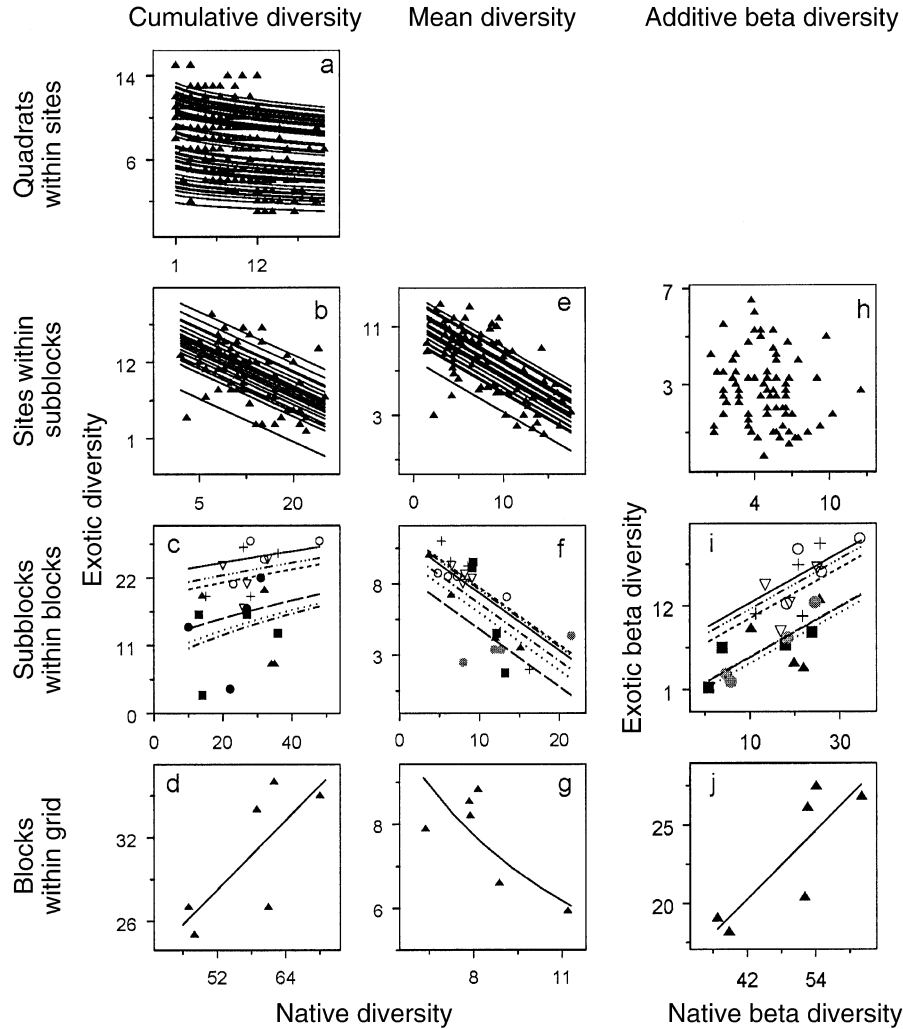


FIG. 2. Natural-scale relationships between native and exotic diversity for cumulative diversity, mean diversity, and additive beta diversity ($\beta = \gamma - \alpha$), at four spatial scales (quadrats within sites, sites within subblocks, subblocks within blocks, and blocks within the grid) showing how beta diversity drives the relationship between native and exotic cumulative diversity. Each block has a distinctive symbol type. P values and adjusted R^2 are as follows: (a) $P = 0.05$, $R^2 = 86.4\%$, (b) $P < 0.001$, $R^2 = 48\%$, (c) $P = 0.26$, $R^2 = 50.2\%$, (d) $P = 0.08$, $R^2 = 47.1\%$, (e) $P < 0.001$, $R^2 = 40\%$, (f) $P = 0.003$, $R^2 = 50.6\%$, (g) $P = 0.05$, $R^2 = 55.5\%$, (h) $P = 0.40$, $R^2 = 22.9\%$, (i) $P = 0.002$, $R^2 = 67.3\%$, (j) $P = 0.036$, $R^2 = 63.4\%$. With more replication at the block-within-grid scale ($n = 12$, i.e., smaller blocks): cumulative diversity, $P = 0.04$, $R^2 = 28.0\%$; mean diversity, $P = 0.05$, $R^2 = 26.4\%$; beta diversity, $P = 0.008$, $R^2 = 47.2\%$.

removed, exotic beta diversity tends to plateau while native beta diversity continues to increase, probably because the exotic species tend to be generalists and so at this larger spatial scale the upper limit of between-quadrat differences in species composition is reached. A cubic smoothing spline with two degrees of freedom was a better fit to the data ($P = 0.03$, not shown).

Other components of the model

There are four components in Eq. 1 and 2 that determine the covariance of cumulative exotic and native diversity. The first two, the covariance of native and exotic mean diversity (α) and the covariance of native and exotic beta diversity (β) are described above. The

remaining two covariance components are the covariances of the reciprocal α - and β -diversities. We will call these the “cross-covariance” terms of the model.

The covariance of cumulative diversity (and hence the slope) was dominated by the covariance of the mean diversities and the covariance of the beta diversities, and not by the cross-covariance terms in Eq. 1 and 2. We found that for the covariance of mean native diversity and exotic beta diversity on the natural scale: blocks within grid, $P = 0.16$, adjusted $R^2 = 26\%$; subblocks within blocks, $P = 0.82$, adjusted $R^2 = 47\%$; sites within subblocks, $P = 0.04$, adjusted $R^2 = 33\%$. For the covariance of native beta diversity and exotic mean diversity on the natural scale: blocks within grid,

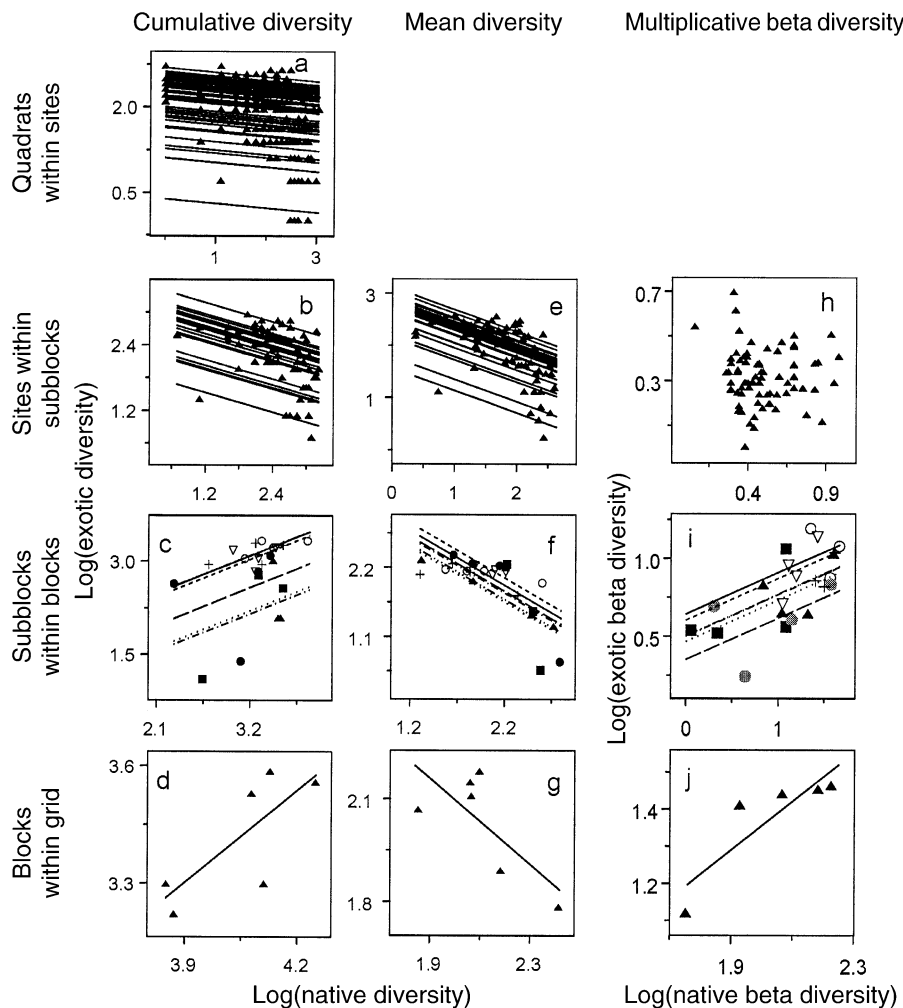


FIG. 3. Logarithm-scale relationships between native and exotic diversity for cumulative diversity, mean diversity, and multiplicative beta diversity ($\beta = \gamma/\alpha$), at four spatial scales showing how beta diversity drives the relationship between native and exotic cumulative diversity. Each block has a distinctive symbol type. P values and adjusted R^2 are as follows: (a) $P = 0.07$, $R^2 = 86.9\%$, (b) $P = 0.02$, $R^2 = 33.5\%$, (c) $P = 0.11$, $R^2 = 36.0\%$, (d) $P = 0.07$, $R^2 = 48.6\%$, (e) $P = 0.002$, $R^2 = 40\%$, (f) $P < 0.001$, $R^2 = 45.4\%$, (g) $P = 0.09$, $R^2 = 42.0\%$, (h) $P = 0.20$, $R^2 = 30.0\%$, (i) $P = 0.047$, $R^2 = 39.7\%$, (j) $P = 0.05$, $R^2 = 69.0\%$. With more replication at the block-within-grid scale ($n = 12$, i.e., smaller blocks): cumulative diversity, $P = 0.008$, $R^2 = 47.4\%$; mean diversity, $P = 0.04$, $R^2 = 26.2\%$; beta diversity, $P = 0.05$, $R^2 = 24.4\%$.

$P = 0.52$, adjusted $R^2 = 12\%$; subblocks within blocks, $P = 0.7$, adjusted $R^2 = 16\%$; sites within subblocks, $P = 0.04$, adjusted $R^2 = 23\%$. For the covariance of mean native diversity and exotic beta diversity on the logarithm scale: blocks within grid, $P = 0.57$, model cannot be fitted even with one outlier removed, subblocks within blocks, $P = 0.06$, adjusted $R^2 = 36\%$; sites within subblocks, $P = 0.85$, adjusted $R^2 = 34\%$. For the covariance of native beta diversity and exotic mean diversity on the logarithm scale: blocks within grid, $P = 0.25$, adjusted $R^2 = 14\%$; subblocks within blocks, $P = 0.02$, adjusted $R^2 = 47\%$; sites within subblocks, $P = 0.11$, adjusted $R^2 = 6\%$. Thus, most of these relationships were not significant, although some were significant. Moreover, the covariances for the two cross-covariance terms were consistently an order of

magnitude smaller than the covariance of the means or the covariance of the beta diversities. Thus, for these data, the cross-covariance terms had little influence on the relationship between cumulative native and exotic diversity.

Correlation of abiotic variables with diversity components

At the two larger spatial scales native and exotic diversity, and beta diversity, were positively correlated with spatial heterogeneity in abiotic conditions but not with mean abiotic conditions. At the largest scale (blocks within the grid) both native and exotic richness were positively correlated with variance in soil depth within blocks (Fig. 4a and b). That is, blocks with more heterogeneity in soil depth had more native and exotic

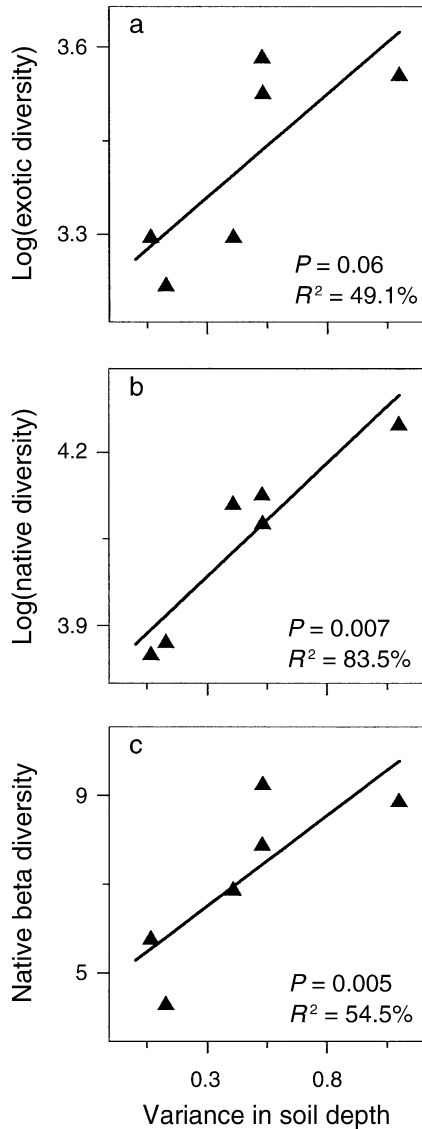


FIG. 4. Relationships between the variance of soil depth and (a) exotic diversity, (b) native diversity, (c) native beta diversity ($\beta = \gamma/\alpha$) for the largest spatial scale (blocks within the grid). Relationships are from least-squares regression; the adjusted R^2 is shown.

species. Further, native beta diversity (multiplicative version) was positively correlated with spatial heterogeneity in soil depth (Fig. 4c). Exotic beta diversity was not correlated with the variance of any abiotic variables but it varied little between blocks. Native diversity, exotic diversity, native beta diversity, and exotic beta diversity were not correlated with the within-block mean of any of the abiotic variables.

At the second largest scale (subblocks within blocks), exotic diversity was positively correlated with the spatial heterogeneity in aspect ($P = 0.06$, adjusted $R^2 = 50\%$), native diversity was positively correlated with the heterogeneity in aspect ($P < 0.001$) and soil

nitrogen content ($P = 0.002$), and negatively correlated with the average soil depth ($P = 0.005$, adjusted $R^2 = 74\%$). Further, native beta diversity (multiplicative version) was positively correlated with the spatial heterogeneity of the soil calcium-to-magnesium ratio ($P = 0.038$, adjusted $R^2 = 31\%$). This ratio is an indication of serpentine soil, as serpentine soils typically have low calcium and high magnesium content. Exotic beta diversity was not correlated with the mean or variance of any abiotic variables.

DISCUSSION

Our results are consistent with the idea that processes operating at different spatial scales cause the diversity-invasibility paradox. We reasoned that if the opposing patterns of negative relationships at small scales and positive relationships at large scales are the result of different processes operating at different spatial scales, as hypothesized in the literature (Levine and D'Antonio 1999, Stohlgren et al. 1999, Levine 2000, Shea and Chesson 2002), then we should be able to detect both relationships within the same data set with a change in scale. Within our grassland data set, we detected negative relationships between native and exotic diversity when our focus was small spatial scales and positive relationships when our focus was large spatial scales, consistent with the hypothesis.

Further, our results support our hypothesis that spatial heterogeneity in species composition and the environment are responsible for the positive relationship between native and exotic diversity at large spatial scales. We found that spatial heterogeneity in species composition (beta diversity) drove the positive relationship between native and exotic diversity. Further, for both native and exotic species, at large spatial scales, cumulative diversity was positively correlated with spatial heterogeneity in abiotic conditions. Importantly, cumulative species diversity was not correlated with mean abiotic conditions, which represents environmental favorability.

This finding contrasts with what is predicted in the literature about the large-scale relationship. Our finding highlights a potential central role for heterogeneity in extrinsic (abiotic) conditions, whereas previous studies have emphasized mean extrinsic conditions. The prominent hypothesis in the literature is that sites with favorable extrinsic conditions for native species also have favorable conditions for exotic species (Levine and D'Antonio 1999, Naeem et al. 2000). Extrinsic factors are measured as mean site-wide biotic or abiotic factors that covary with diversity (Levine and D'Antonio 1999). For example, in a large-scale vegetation survey, the greater average availability of resources (in particular, C and N) was correlated with invasibility (Stohlgren et al. 1999). In another example, average propagule supply rate was considered the extrinsic factor responsible for downstream tussocks being both more invaded and more diverse because both

water and seeds predominantly move downstream in river systems (Levine 2000).

However, theory in community ecology contrasts with these empirically derived hypotheses about extrinsic factors. At its essence, diversity and invasibility is about species coexistence but there is little coexistence theory that predicts that more of a resource, such as nitrogen, will allow more species to coexist (Wright et al. 1993, Hawkins et al. 2003). Rather, much of coexistence theory says that more heterogeneity in a resource will allow more species to coexist (Connell 1979, Chesson and Huntly 1997, Chesson 2000). Thus, our finding that greater heterogeneity in species composition and in extrinsic conditions is correlated with both more native and more exotic species is more consistent with community ecology theory than hypotheses regarding mean extrinsic conditions.

Spatial and temporal habitat heterogeneity have previously been considered as extrinsic factors but only in very few studies and, at least in empirical studies, not as a central mechanism driving the relationship between native and exotic diversity at large scales. First, in a theoretical study, using a simulation approach, Byers and Noonburg (2003) showed that a competition-based model that exhibits a negative relationship at small scales can become positively correlated when the number of available resources across the community is changed. However, their focus was mean diversity, not cumulative diversity. It is unclear what role their mechanism plays in the relationship for cumulative diversity. Second, in a conceptual model, Davis et al. (2000) suggest that communities are more invulnerable when resources surge and temporarily go unused, providing an opportunity for invaders to capitalize on free resources. Their concept concerns only temporal heterogeneity. Third, in an empirical example, when explaining a positive relationship between native and exotic diversity at a large scale, Stohlgren et al. (1999) noted that sites with high beta diversity had a greater percentage of exotic species. Finally, in another empirical example, MacDonald et al. (1989) found a positive relationship between native and exotic diversity in South African nature reserves. They attributed this to greater environmental heterogeneity in diverse reserves. These studies comprise a small portion of the literature on the relationship between native and exotic diversity, which in contrast emphasizes the role of average extrinsic conditions in the positive relationship at large scales. Our findings strongly suggest that heterogeneity in extrinsic conditions may play a more central role than has previously been suggested.

Finally, our largest spatial scale is smaller than the largest scale of some other studies (Lonsdale 1999, Stohlgren et al. 1999), yet we still found a positive relationship at this larger scale. The definitions of small and large depend on the scale of interaction of individuals, and the importance of heterogeneity to the relationship between native and exotic diversity depends

on how much heterogeneity is present relative to those scales, not on the physical size of the study area. In our system, heterogeneity in environmental conditions at small scales was great. Levine (2000) detected a positive relationship between native and exotic species in a study of similar spatial extent, and Stachowicz et al. (2002) suggest that the negative relationship detected at their larger scale was due to the homogeneity of the environment.

In conclusion, in our grassland system, spatial heterogeneity in abiotic conditions drove the positive relationship between native and exotic diversity at large spatial scales, and not mean abiotic (extrinsic) conditions. We suggest that native and exotic diversity is positively correlated at large spatial scales because coexistence mechanisms that depend on spatial heterogeneity in the environment come into play at larger scales, overriding the competitive exclusion that operates at small scales (a similar idea appears in Tilman [2004]). In future work, we will test this hypothesis by directly quantifying the contribution of coexistence mechanisms. Future work could also use our framework (Eqs. 1 and 2) to test other ideas about the diversity-invasibility paradox (e.g., Davis et al. 2000, Rejmanek 2003).

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