

## PRODUCTIVITY ALTERS THE SCALE DEPENDENCE OF THE DIVERSITY–INVASIBILITY RELATIONSHIP

KENDI F. DAVIES,<sup>1,3</sup> SUSAN HARRISON,<sup>1</sup> HUGH D. SAFFORD,<sup>2</sup> AND JOSHUA H. VIERS<sup>1</sup>

<sup>1</sup>Department of Environmental Science and Policy, University of California, Davis, California USA 95616

<sup>2</sup>USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, California 94592 USA

**Abstract.** At small scales, areas with high native diversity are often resistant to invasion, while at large scales, areas with more native species harbor more exotic species, suggesting that different processes control the relationship between native and exotic species diversity at different spatial scales. Although the small-scale negative relationship between native and exotic diversity has a satisfactory explanation, we lack a mechanistic explanation for the change in relationship to positive at large scales. We investigated the native–exotic diversity relationship at three scales (range: 1–4000 km<sup>2</sup>) in California serpentine, a system with a wide range in the productivity of sites from harsh to lush. Native and exotic diversity were positively correlated at all three scales; it is rarer to detect a positive relationship at the small scales within which interactions between individuals occur. However, although positively correlated on average, the small-scale relationship between native and exotic diversity was positive at low-productivity sites and negative at high-productivity sites. Thus, the change in the relationship between native and exotic diversity does not depend on spatial scale per se, but occurs whenever environmental conditions change to promote species coexistence rather than competitive exclusion. This occurred within a single spatial scale when the environment shifted from being locally unproductive to productive.

**Key words:** California grassland; coexistence mechanisms; competitive exclusion; diversity–invasibility paradox; heterogeneity; invasion; niche partitioning; productivity; serpentine.

### INTRODUCTION

Invasive species are one of the most significant threats to native species diversity, and identifying the factors that make places more or less invulnerable has been one of the most important issues in the study of invasions (Wilcove et al. 1998, Pimentel et al. 2000). Elton (1958) first proposed that a high richness of native species armors sites against invasion by making resources less available to newly arriving species. This idea was supported by many empirical studies that detected negative relationships between native and exotic diversity at small spatial scales, which is the scale of interaction between individuals (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, Levine et al. 2004). Recently, however, Lonsdale (1999) and Stohlgren et al. (1999) surprised invasion ecologists by showing that native and exotic diversity could be positively correlated when scales larger than the scale of interaction are considered. Their results raised the possibility that the processes determining invasibility

and its relationship to diversity depend on spatial scale (see Fridley et al. [2007] for an excellent overview of the diversity–invasibility paradox).

Since the studies of Stohlgren et al. (1999) and others, the potential for scale dependence of the native–exotic relationship has stimulated much research, and studies have reported both negative relationships at small scales and positive relationships at large scales within the same system (Levine 2000, Brown and Peet 2003, Davies et al. 2005, Knight and Reich 2005). Two hypotheses could explain the positive correlation of native and exotic diversity at large scales and why the relationship changes slope. First, the environmental favorability hypothesis suggests that sites or landscapes with favorable environmental conditions for native species also have favorable conditions for exotic species (Levine and D’Antonio 1999, Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003). In other words, factors such as soil fertility or propagule supply rates vary between sites and cause between-site variation in both native and exotic diversity. Shea and Chesson (2002) generalized this idea and showed how a positive relationship at large spatial scales can arise by combining data from a series of negative relationships at smaller scales, where differences in diversity at larger scales were caused by environmental differences in the mean conditions between sites. However, their model only accounts for patterns in the mean diversity (alpha diversity) rather than the cumulative diversity (gamma diversity) of

Manuscript received 15 November 2006; revised 26 February 2007; accepted 8 March 2007; final version received 12 April 2007. Corresponding Editor: T. J. Stohlgren.

<sup>3</sup> Present address: Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA. E-mail: kendi.davies@colorado.edu

communities (Davies et al. 2005). Second, the environmental heterogeneity hypothesis suggests that not only variation in mean conditions between sites (as in the environmental favorability hypothesis) but also heterogeneity of conditions within sites can contribute to the positive relationship of native and exotic diversity at large scales. Davies et al. (2005) suggest that the relationship between native and exotic diversity changes slope as larger spatial scales are considered because, at some spatial scale, enough spatial heterogeneity will be present that strong coexistence mechanisms that depend on spatial heterogeneity, and allow many species to coexist, come into play. These coexistence mechanisms override the mechanisms of competitive exclusion operating at small scales. Davies et al. (2005) provided new insights into the mechanisms behind the scale dependence in the native–exotic diversity relationship; however, the generality of their ideas is unknown. Further work is needed, with both observational and experimental studies.

Thus, while the cause of the small-scale negative relationship between native and exotic diversity has a satisfactory explanation (i.e., that competitive exclusion mechanisms are operating; Grime 1973, Tilman 1999), there is still uncertainty about the general mechanisms behind the large-scale positive relationship between native and exotic diversity and the scale dependence of the relationship. A more general solution is needed and two important questions remain. (1) What is the mechanism behind the positive relationship between native and exotic diversity at large scales? And (2) what is the mechanism behind the scale dependence of the diversity–invasibility relationship?

In this study, we examine these two overarching questions about the roles of competitive exclusion and coexistence in the negative and positive relationships between native and exotic diversity. We examine a California statewide-scale data set for serpentine herbs, composed of 109 sites. Serpentine is a toxic, low-productivity soil that supports a species-rich plant flora, dominated by native species (Kruckeberg 1984). In our system, sites ranged in their herb productivity from barren to relatively lush. We define harsh conditions to mean those that result from physiological or resource stress, resulting in low population densities (Chesson and Huntly 1997). We hypothesized that the harshness of our study system would alter the relationships between native and exotic diversity from what is generally predicted, and thus provide further insight into the mechanisms behind the diversity–invasibility paradox. Although harshness alone cannot lead to lack of saturation (Chesson and Huntly 1997), harshness could reduce saturation by interacting with other processes (e.g., competition, through the storage effect; Chesson 2000). Then, the invasibility of sites may vary with productivity, even at the small spatial scales at which we would otherwise expect competitive exclusion to be the dominant mechanism. We hypothesized that

unproductive sites may be less saturated and competitive exclusion less dominant.

Three broad hypotheses explain how site productivity could determine the relative importance of competitive exclusion at small scales, and therefore, how native and exotic diversity are correlated. (1) Harsh sites are more internally heterogeneous at the 1-m<sup>2</sup> scale than are productive sites. At internally heterogeneous sites, species coexist through mechanisms that depend on heterogeneity, while natives competitively exclude exotics at productive sites that are internally homogeneous (environmental heterogeneity hypothesis). (2) Similarly, coexistence mechanisms that depend on variation in mean resources between quadrats, like soil depth or nutrient availability, result in positive relationships at harsh sites, while competitive exclusion results in negative relationships between native and exotic diversity at productive sites (environmental favorability hypothesis). (3) Facilitation, which may be more likely at harsh sites (Bertness and Callaway 1994), results in positive relationships between native and exotic species at harsh sites, while competitive exclusion results in negative relationships at productive sites.

We asked two questions. (1) What is the slope of the relationship between native and exotic diversity at three spatial scales; quadrats within sites (1 m<sup>2</sup>), sites within blocks (1000–4000 m<sup>2</sup>), and blocks within geographic provinces (~1000–4000 km<sup>2</sup>)? (2) How does the harshness/productivity of sites affect how native and exotic diversity are correlated at the scale of local interaction (small scales)?

In this study, we define small spatial scales as those at which we expect individual plants to experience competition (both intra- and interspecific). For our herb communities, this scale corresponds approximately to our smallest spatial unit, a 1-m<sup>2</sup> quadrat. We define any scale larger than this to be “large,” that is, outside the realm in which we would expect competition to act.

## METHODS

### *Study system*

We surveyed 109 serpentine sites throughout California, USA. Serpentine is a harsh, low-productivity soil that supports a rich flora dominated by native species. “Serpentine” refers to ultramafic rocks, mainly serpentine and peridotite, and the soils derived from them. These rocks and soil tend to be high in Mg and Fe, and low in Ca, N, P, and K. Sometimes serpentine environments also have high heavy metal concentrations and low water holding capacity. Serpentine often excludes some species from surrounding communities and supports endemic species that are unique to the soil type (Kruckeberg 1984).

Our sites occur in four broad, geographically defined provinces: the Klamath-Siskiyou Mountains, the North Coast Range, the South Coast Range, and the Sierra Nevada. Vegetation ranges from forest, woodland, and barrens at higher elevations and latitudes, through

shrublands interspersed by barrens and grasslands, to primarily grasslands toward the southern extent of serpentine in the state (for full details see Harrison et al. [2006b]).

#### Data collection

Between April 2001 and July 2004, we surveyed sites for plant richness and local environmental variables. Sites were selected by using a spatially referenced floristic database to stratify the state into 86 regions that contained serpentine, selecting approximate sampling areas by geology and access, and then using topographic maps to select sites where both a cool (north-northeast) and a warm (south-southwest) slope occurred in close proximity (within 200 m).

At each site, two  $50 \times 10$  m plots were established (one on the north slope, one on the south slope). We recorded the identities of all species in each plot, and in seven  $1\text{-m}^2$  quadrats (five along the central transect and two at opposite corners of the plot). We also recorded percent cover by each species for the  $1\text{-m}^2$  quadrats. In addition, we recorded the percent cover of rocks, bare soil, litter, and animal disturbance (trails, scat, burrowing, etc.) in the  $1\text{-m}^2$  quadrats, and the slope and aspect. We averaged these environmental variables to obtain a mean of each variable for each plot. Finally, we recorded woody species cover, height, and identity along a central 50-m transect. Each site was visited at least three times in two years but data from all visits were combined to create one species list for each site. Soil samples were collected from five of the  $1\text{-m}^2$  quadrats (depth 1–10 cm) and analyzed for N, P, K, Ca, Mg, texture, and trace metals by A & L Laboratories (Modesto, California). Additional site-level environmental variables were obtained from GIS analyses of published maps. These included local spatial variables: area, isolation, perimeter to area ratio; also rainfall, temperature, time since last fire, distance to nearest road, grazed or not, and productivity as measured by the NDVI (normalized differential vegetation index) of an area of radius 250 m surrounding each site (Harrison et al. 2006b). NDVI is a remotely sensed index, which measures the separation between energy reflectivity in the near infrared and red wavelengths. It indicates the density and vigor of plants present.

For the purposes of this paper, our sampling scheme comprised three spatial scales. We defined small spatial scales as those at which we expect individual plants to experience competition or facilitation, both within and between species, which corresponds approximately to our smallest spatial unit, a  $1\text{-m}^2$  quadrat. Any scale larger than this we define as “large”; that is, outside the realm in which we would expect species to interact locally. Thus, these definitions depend on the scale of interaction of the study organisms. We created an intermediate spatial scale by dividing each of the four geographic regions into five to six blocks by grouping sites that were close together in space. This resulted in 23

blocks. We created this intermediate spatial scale because geographic regions tended to form long narrow groupings of sites. Blocking helped to account for the spatial autocorrelation among sites within geographic regions. Thus, our three spatial scales comprised: (1) 14  $1\text{-m}^2$  quadrats within each site (seven from each plot), (2) four to five sites within each block, and (3) five to six blocks within each geographic region (sites and geographic regions are illustrated in Harrison et al. [2006b]). Strictly, there is another spatial scale, geographic regions within California, but there was too little replication to consider this scale in analyses ( $N = 4$ ).

#### Data analysis

We focused our analyses on herb species. We defined diversity as species richness. We used Genstat (Version 9.1, VSN International, Hemel Hempstead, UK) for all analyses. We used regression with a blocking factor (site, block, geographic region) to estimate the slope of the relationship between native and exotic diversity for each scale (Davies et al. 2005): quadrats within sites, sites within blocks, and blocks within geographical regions. 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), and  $\varepsilon_{ij}$  has a normal distribution with mean zero and variance  $\sigma^2$ . 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 started by regressing native and exotic cumulative diversity for all data (109 sites) for all three spatial scales. We investigated the quadrat-within-site scale relationship further by asking whether the slopes of the relationship between native and exotic diversity for individual sites (there were 14 quadrats within each site, and 109 sites in total) were correlated with local productivity. We considered two measures of productivity. First, NDVI was calculated for a 250-m radius around each site. Most likely because of the size of the area measured, this measure of productivity proved to be insensitive in this and other studies (Harrison et al. 2006b), so we considered percent cover as a more local measure of productivity. For this study, cover was measured as the sum of the percent cover of all species in a quadrat, both natives and exotics, averaged for the 14  $1\text{-m}^2$  quadrats at each site. For completeness, we also investigated the relationship between slope and all 30 other environmental variables.

After discovering that the slopes of the relationship between native and exotic diversity for individual sites were correlated with cover, our measure of local productivity (Fig. 1), we divided sites into two groups, those with high productivity ( $N=12$ ) and those with low productivity ( $N=97$ ). We used as our cutoff the point at which the overall regression line crossed zero and became negative, which occurred at 60% cover (Fig. 1). There was also a natural break in the data at this point. For these two groups of sites, low and high productivity, we again regressed native and exotic cumulative diversity for small spatial scales.

### RESULTS

There was a significant negative relationship between productivity and the slopes of the relationships between native and exotic diversity at the smallest spatial scale, quadrats within sites, so that native and exotic diversity tended to be positively correlated at low-productivity sites and negatively correlated at high-productivity sites (Fig. 1). There were 42 sites at which no exotic species, or only one exotic species, was present (the productivity of these sites ranged from 0.35% to 61%). This left us with the problem of whether to include a value for the slope of the relationship between native and exotic diversity for these sites so that these sites could be included in the analysis of the relationship between site slope and productivity. One option was to assign a zero value for these sites, although a zero slope suggests that native and exotic diversity are randomly distributed relative to one another, which we do not necessarily know to be the case for these sites. Thus, we explored the relationship between site slope and productivity two ways: with assignments of a zero slope for these sites, and without including these sites in the analysis. Although the strength of the relationship increases when these sites are removed (with zeroes  $N=109$ ,  $P=0.04$ , adjusted  $R^2=3\%$ , slope  $=-0.002$ , 95% CI  $=-0.0028$  to  $-0.0012$ ; without zeroes  $N=67$ ,  $P=0.005$ , adjusted  $R^2=11\%$ , slope  $=-0.003$ , 95% CI  $=-0.004$  to  $-0.002$ ), the cutoff where the slope of the overall regression line crosses zero and becomes negative does not change, giving us faith in the robustness of the relationship and in the low- and high-productivity groupings. Further, both relationships, and the cutoff point, are robust to the removal of the points with the largest and smallest productivity and to points with high leverage. For completeness, we also investigated the relationship between slope and all 30 other environmental variables and detected no significant relationships.

Considering the relationships between native and exotic diversity and how they varied with scale, we predicted a negative relationship between native and exotic diversity at the smallest spatial scale, and positive relationship at large scales. In contrast to our prediction, we detected positive relationships between native and exotic diversity at all three spatial scales, small through large (Fig. 2).

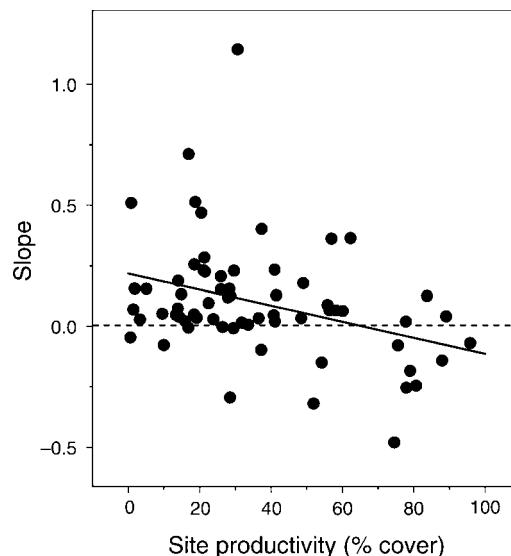


FIG. 1. Relationship between site productivity and the slopes of the relationships between native and exotic diversity at the smallest spatial scale, quadrats within sites:  $P=0.005$ , adjusted  $R^2=11\%$ , slope  $=-0.003$  (95% CI:  $-0.004$  to  $-0.002$ ).

When the relationship between native and exotic diversity and productivity was investigated further at small spatial scales, we found that when low-productivity sites were considered alone, native and exotic diversity were positively correlated (Fig. 3b), but that when high-productivity sites were considered alone, native and exotic diversity were negatively correlated (Fig. 3a; note that the high-productivity sites are well distributed across the study area; they occur in eight different blocks). These results illustrate that the change in the relationship between native and exotic diversity, from negative to positive, does not depend on spatial scale per se.

The makeup of species present at productive and unproductive sites was as follows. There were 825 species in total detected at unproductive sites and, of these, 79 species were exotic (86% annual herbs, 14% perennial herbs) and 746 species native (40% annual herbs, 60% perennial herbs). There were 268 species detected at productive sites (there were many fewer sites). Of these, 47 species were exotic (87% annual herbs, 13% perennial herbs) and 229 species native (60% annual herbs, 40% perennial herbs).

### DISCUSSION

In this harsh and unproductive system, native and exotic diversity were positively correlated at all spatial scales, even the small spatial scales at which individuals interact ( $1\text{ m}^2$ ; Fig. 2). Positive relationships at large scales are expected and common in empirical studies. However, detecting a positive relationship at the small scales at which we expect individuals to interact is rarer in empirical studies (but see Fridley et al. [2007]). Native and exotic plant diversity is expected to be negatively correlated at small scales because competitive neighbor-

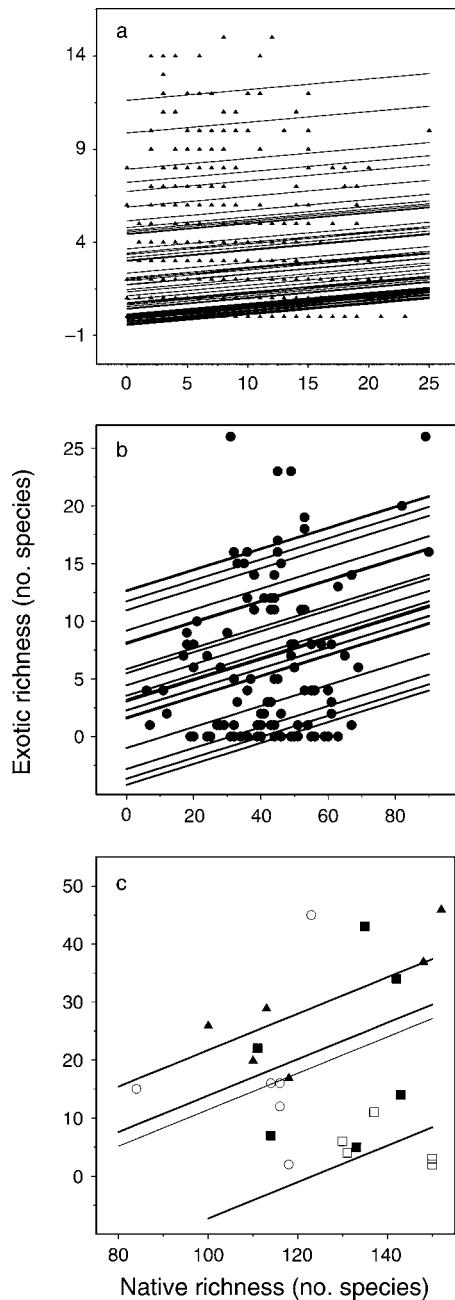


FIG. 2. Relationships between exotic and native diversity, for all sites, at three spatial scales: (a) quadrats within sites ( $P < 0.001$ , adjusted  $R^2 = 79.3\%$ , slope = 0.09), (b) sites within blocks ( $P = 0.005$ , adjusted  $R^2 = 53.3\%$ , slope = 0.57), and (c) blocks within geographic provinces ( $P = 0.07$ , adjusted  $R^2 = 34.5\%$ , slope = 0.31). Different symbols represent different geographic provinces. Exotic and native diversity were positively correlated at all spatial scales.

hoods with many native species have few niche opportunities for potential invaders, while neighborhoods with few natives have many (Elton 1958, Levine et al. 2004). Our result suggests that our sites were not saturated, even at small scales.

We predicted that, along with spatial scale, site productivity could also affect the relationship between native and exotic diversity, especially at small scales where the occurrence of competitive exclusion may vary with productivity. We found that at high-productivity sites, native and exotic diversity tended to be negatively correlated with each other, while at unproductive sites, native and exotic diversity tended to be positively correlated, resulting in a significant relationship between “slope” and productivity (Fig. 1). Because the majority of sites were less productive, the average relationship at small spatial scales for all sites considered together was positive (Fig. 2a). However, when productive and unproductive sites were considered separately, unproductive sites had a common positive relationship between native and exotic diversity, while productive sites had a common negative relationship (Fig. 3).

Three hypotheses explain how productivity interacts with invasibility to explain the differences in the slope of the native–exotic diversity relationship at low- and high-productivity sites at small spatial scales: (1) the

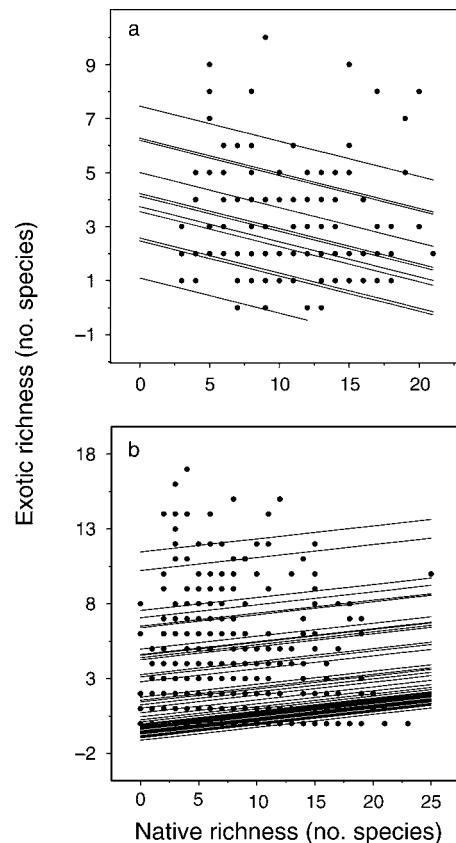


FIG. 3. Relationships between exotic and native diversity at the smallest spatial scale, the scale of local interactions (quadrats within sites) for: (a) high-productivity sites ( $P = 0.002$ , adjusted  $R^2 = 42\%$ , slope =  $-0.13$ ) and (b) low-productivity sites ( $P < 0.001$ , adjusted  $R^2 = 80\%$ , slope = 0.09). Exotic and native diversity were negatively correlated at high-productivity sites and positively correlated at low-productivity sites.

environmental heterogeneity hypothesis, (2) the environmental favorability hypothesis, and (3) facilitation.

The first hypothesis, the environmental heterogeneity hypothesis, postulates that harsh sites are more internally heterogeneous at the 1-m<sup>2</sup> scale than are productive sites, so that in harsh sites, 1-m<sup>2</sup> plots with greater heterogeneity have more niches for both natives and exotics, leading to coexistence and a positive relationship between native and exotic diversity (Davies et al. 2005, Melbourne et al. 2006). In comparison, at productive sites, homogeneity of resources would lead to competitive exclusion of exotics by natives and a negative relationship. First, harsh sites might simply have greater environmental heterogeneity than productive sites at small scales. Sources of heterogeneity within quadrats could include rockiness, soil depth, soil composition, or the availability of critical nutrients. A second possibility, as suggested by Tilman (1987, 1988), is that competition occurs predominantly aboveground at productive sites, where species compete for light, a single limiting resource, and shifts belowground at unproductive sites, where species compete for belowground resources that tend to be more heterogeneous (e.g., Wilson and Tilman 1991, 1993, 1995, Cahill 2003). We were not able to measure heterogeneity directly at the spatial scale of interest because we would have needed multiple samples of each environmental variable within quadrats so that a measure of the variance at the quadrat scale could have been made. However, if heterogeneity was behind these relationships, the presence of greater heterogeneity at unproductive sites should have resulted in greater diversity of both native and exotic species at harsh sites, whereas the opposite was the case; the least productive sites also had the fewest species, making heterogeneity-dependent coexistence an unlikely driver of the change in slope between productive and less productive sites at small spatial scales. Related to these ideas is the multiple resource hypothesis of Byers and Noonburg (2003) that says that more different types of resources allow more species to invade or coexist resulting in a positive relationship (see Melbourne et al. [2006] for discussion); however, this would also require that the least productive sites have the most species.

The second and most likely hypothesis is the environmental favorability hypothesis, which covers coexistence mechanisms that depend on mean conditions rather than heterogeneity in conditions. The environmental favorability hypothesis suggests that native and exotic diversity are positively correlated at large spatial scales because sites with favorable conditions for natives also have favorable conditions for exotics. Although this hypothesis was developed to explain large-scale positive relationships, it can also be applied at small spatial scales. In our system, it is likely that the majority of our sites, except for the small subset with the highest cover, are unsaturated so that there are weaker effects of resident species on the ability of new

species to invade. The positive effects of shared responses to the environment (i.e., shared tolerances) more easily overwhelm the negative effects of competition, resulting in a small-scale positive relationship at harsh sites. For example, the availability of critical nutrients may vary between 1-m<sup>2</sup> quadrats so that quadrats with better conditions harbor both more natives and exotics. In contrast, at productive sites, competitive exclusion results in negative relationships between native and exotic diversity.

Finally, the third hypothesis to consider is facilitation, which can also be more likely to occur at harsh, unproductive sites (Bertness and Callaway 1994, Callaway 1998, Choler et al. 2001, Smith et al. 2004, Von Holle 2005). Theory connecting facilitation to community invasibility is undeveloped, so it is unclear how facilitation would be expected to alter the diversity–invasibility relationship in a metacommunity context (but for invader facilitating invader see Simberloff [1999, 2006]). However, the presence of facilitative rather than competitive local interactions at harsh, compared to benign, sites could result in the relationships that we observed. At a practical level, at harsh sites, quadrats with more native species generate more organic matter and thus soil nutrients, for example, potentially allowing more exotic species to invade.

As far as explaining the positive relationship at large scales, we previously showed that at large spatial scales exotic cover was positively correlated with total native herbaceous richness (Harrison et al. 2006a). However, when the effects of soil chemistry, disturbance, overstory cover, regional rainfall, and elevation were taken into account, there was no indication that exotic cover reduced total richness. Rather, the similarities in the conditions favoring exotic and native species explained the correlation. In other words, exotic cover had no impact on native diversity, and sites with many niches had more niches for both natives and exotics, while sites with fewer niches had fewer for both natives and exotics. We expect different mechanisms to be responsible for relationships detected at small and large scales.

For completeness, we considered that productivity might be correlated with disturbance so that more productive sites were also more disturbed, and that this could affect local invasibility. Of two measures of disturbance, scat count and percent cover of burrowing in 1-m<sup>2</sup> quadrats, only burrowing was weakly correlated with productivity (0.24), so that more productive sites tended to have more burrowing. However, the effects of disturbance are likely small because we would expect disturbance to increase coexistence, whereas native and exotic diversity are negatively correlated at small scales at productive sites.

Finally, we return to the questions posed at the beginning of this paper. First, what is the mechanism behind the positive relationship between native and exotic diversity? Second, what is the mechanism behind the scale dependence of the diversity–invasibility rela-

tionship? Our findings illustrate that the change in the relationship between native and exotic diversity, from negative to positive, does not necessarily depend on spatial scale per se. This means that these questions can be reduced to a single question: Why does the diversity–invasibility relationship change slope? We suggest, as is well accepted, that competitive exclusion results in the negative relationship between native and exotic diversity at small spatial scales, and that the relationship becomes positive wherever native and exotic species coexist, so that locations with more niches or better conditions for natives also have more niches or better conditions for exotics, even at small spatial scales. It is important to note that the coexistence mechanisms that allow natives and exotics to coexist are likely not different from those that allow native species to coexist with one another, and exotic species to coexist with one another. There are many different mechanisms that allow species to coexist (natives with natives, exotics with exotics, natives with exotics), so there are likely equally many reasons why native and exotic diversity are positively correlated. The most promising avenue for future research will be to quantify the contribution of different coexistence mechanisms.

What our result contributes to our understanding of the diversity–invasibility paradox, which has been framed in terms of spatial scale, is that the coexistence mechanism that dominates can be affected by factors other than spatial scale so that we can see both positive and negative relationships within a spatial scale in situations where the coexistence mechanism fundamentally changes from one environment (site) to another. Because the difference in the slope of the relationship between native and exotic diversity (positive vs. negative) is about the coexistence mechanism that dominates at the scale and location of focus rather than spatial scale per se, this could occur, for example, where there is a wide range in the internal heterogeneity of sites, as we move from site to site. Then we might see positive relationships at small-scale heterogeneous sites and negative relationships at small-scale homogeneous sites (heterogeneity hypothesis). Similarly, if conditions varied from site to site so that facilitative relationships were favored at some sites and competitive relationships at others, we might detect small-scale positive relationships between native and exotic diversity at some sites and negative relationships at others. Finally, although this study was undertaken in a harsh study system so that our sites had a particularly wide range of productivity, allowing us to uncover the patterns reported, we should expect to see both positive and negative relationships at small scales in less extreme systems, but for other reasons (e.g., variation between sites in within-site heterogeneity).

#### ACKNOWLEDGMENTS

We thank Brett Melbourne, Marcel Holyoak, and two anonymous reviewers for their comments, which greatly improved the manuscript. We thank all of the people who

provided botanical and geological information and helped with site access. Support was provided by the National Science Foundation (NSF DEB-0075369) to SH.

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