

DISPERSAL LIMITATION AND ENVIRONMENTAL HETEROGENEITY SHAPE SCALE-DEPENDENT DIVERSITY PATTERNS IN PLANT COMMUNITIES

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Abstract. Understanding the large-scale distribution of species diversity requires distinguishing two of the primary factors that cause compositional differences: dispersal limitation and environmental variation. In a community with a naturally discontinuous spatial structure, we asked (1) at what scale(s) nonrandom variation in species composition occurs and (2) at what scale(s) such variation is associated with spatial separation, indicative of dispersal limitation, and at what scale(s) variation is associated with environmental heterogeneity? We sampled 50 seeps (small wetlands) on five serpentine outcrops. Using a randomization model, we showed that additive beta diversity (a measure of community dissimilarity) was lower than random within seeps and higher than random among both seeps and outcrops. Using Mantel tests, we showed that plant community dissimilarity, in both the full seep assemblage as well as in a subset of seep endemics, at the two larger scales was associated with different forms of environmental heterogeneity and, at the largest scale, was also associated with geographic distance. We conclude that diversity in this system is shaped by multiple scales of heterogeneity and by dispersal limitation at the largest scale.

Key words: additive partitioning; beta diversity; community dissimilarity; dispersal limitation; environmental heterogeneity; metacommunity; patchiness; scale; serpentine seep.

INTRODUCTION

Understanding spatial patterns in species diversity is fundamental to both community ecology and conservation biology. Regional diversity patterns are a result of local processes, underlying environmental heterogeneity, and species dispersal among local communities (Ricklefs and Schluter 1993). Beta diversity, the difference among local communities in species composition or richness, can be used to measure how variation among local communities contributes to regional diversity. Beta diversity can be due to large habitat differences (i.e., different community types), habitat gradients (i.e., gradual changes within a community type), and dispersal limitation (a combination of species traits, spatial arrangement of local communities, and historical factors). Within community types, the relative roles of habitat gradients and dispersal limitation in determining beta diversity have important implications for competitive coexistence, responses to enrichment, responses to fragmentation, and species invasions (Chesson 2000, Fahrig 2003, Mouquet and Loreau 2003, Davies et al. 2005).

Much recent theory addresses the processes governing diversity in “metacommunities,” or networks of local communities connected by dispersal. Leibold et al. (2004) outline four alternative metacommunity modeling paradigms that differ in the relative roles of habitat heterogeneity and dispersal. However, the contributions of habitat heterogeneity and dispersal are likely to be dependent on spatial scale (Seabloom et al. 2005), suggesting that different modeling paradigms may be appropriate at different scales even within the same system. Thus, understanding the scale dependence of factors that contribute to diversity represents one of the major challenges in metacommunity ecology (Leibold et al. 2004, Loreau 2000).

Several studies have compared the relative influences of habitat heterogeneity and dispersal in either a single system at a single spatial scale (Cottenie et al. 2003) or among different systems that were defined at different scales (Cottenie 2005). In the present study, our goal was to pursue a unified understanding by exploring how these influences change across multiple scales within a single system. Our hypotheses test a priori predictions about how diversity is structured across a multi-scale spatially discontinuous landscape and which causal influences dominate at each scale. Although models and micro- and mesocosms have provided valuable insights, studies that evaluate the importance of metacommunity processes to diversity patterns across scales in natural, large-scale systems are much needed.

Manuscript received 23 May 2006; revised 9 March 2006; accepted 3 April 2006; final version received 8 May 2006.
Corresponding Editor: J. A. Jones.

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PLATE 1. Photograph of a serpentine seep in the University of California McLaughlin Natural Reserve (North Coast Range, California, USA). Photo credit: B. D. Inouye.

We analyzed the spatial structure of species diversity in a naturally patchy system consisting of plants in seeps (small wetlands) found within discrete outcrops of serpentine soil. This study system is ideal for a metacommunity analysis because it is clearly discontinuous at multiple scales (Kolasa 1989). In addition, serpentine-seep species operate as a metacommunity, in that colonization and extinction contribute to the distributions of species among seeps (Harrison et al. 2000). A priori, we expected a significant part of beta diversity in this system to be caused by dispersal limitation, because the habitat is discontinuous. However, it was not obvious which spatial scales of habitat discontinuity would be most important (e.g., separate geologic outcrops, or among seeps within an outcrop). In other systems, because of sampling biases and a lack of clearly defined spatial boundaries, it may be much harder to detect the role of dispersal limitation at reasonable and realistic geographic scales.

We determined the relationships between plant beta diversity, spatial scale, environmental gradients, and distances between seeps, by sampling 25 seeps across five serpentine outcrops (regional scale), and sampling an additional 25 seeps within a single serpentine outcrop (outcrop scale). We used two measures of beta diversity in order to address both species richness and species composition. To test for nonrandom distributions of species richness among spatial scales, we compared an additive measure of beta diversity in species richness at multiple nested spatial scales (Lande 1996) to randomized null models (Gotelli and Graves 1996, Gering et al. 2003). We hypothesized that we would detect non-

random beta diversity, especially at the largest spatial scales.

To test the associations of community composition with habitat gradients and distance, we used the complement of the Jaccard index of community similarity (J) as a measure of community dissimilarity ($1 - J$). We hypothesized that beta diversity would be associated with environmental gradients at all spatial scales, since both fine- and coarse-scale environmental variation can shape community composition in the face of species' relative competitive abilities and physiological tolerances. We also hypothesized that beta diversity would be correlated with distance at larger spatial scales. While at least one seep species is known to disperse via water within seeps (Waser et al. 1982), between-seep dispersal is expected to be reduced due to lack of habitat connectivity, an effect that is likely to increase at greater geographic distances. In addition, our seep plant community includes several species that are completely restricted to serpentine seeps, although most species are also found in non-serpentine wetlands. We repeated our analyses of community dissimilarity using a subset of five strict serpentine-seep species, as a test of the hypothesis that the beta diversity of these habitat specialists would be more strongly affected by distance than the beta diversity of the community as a whole.

Other studies have tested for nonrandom additive beta diversity (e.g., Crist et al. 2003, Gering et al. 2003) or have analyzed environmental correlates of beta diversity in other communities (e.g., Harrison 1999, Harrison and Inouye 2002, Williams et al. 2002). However, to our knowledge, ours is the first study to use both species richness and species composition to

investigate both environmental heterogeneity and spatial discontinuity at multiple large, naturally defined scales of a single system.

METHODS

Study system and sampling design

Serpentine soils are high in magnesium and heavy metals and low in nutrients (Kruckeberg 1984), and a diverse endemic flora has evolved to tolerate these harsh conditions. Serpentine seeps (see Plate 1) harbor a subset of species that tolerate the serpentine soils as well as the seasonally flooded wetland soils. Forty serpentine seep species occur in the Napa, Lake, and Yolo county portions of the North Coast Range, California (Appendix A; A. L. Freestone, *personal observation*) including five species that are considered strictly endemic to serpentine seeps in this region (referred to as “endemics”; California Native Plant Society 2001: list 4b). Although the remainder of the flora may persist in non-serpentine habitats elsewhere, they are locally restricted to serpentine seeps. Serpentine seeps have very heterogeneous soils (Kruckeberg 1984) and hydroperiods (A. L. Freestone, *personal observation*). Although little is known about many of the seep species, including their various dispersal methods, Harrison et al. (2000) demonstrated distance-dependent colonizations and extinctions in several seep endemics, suggesting that between-seep dispersal was important to their regional persistence. These findings, in addition to the seeps’ spatial structure and location within the same biogeographical region, support their consideration as a metacommunity.

As originally defined by Whittaker (1960), local (α) and differential (β) components of regional (γ) diversity are related in a multiplicative fashion, that is, $\alpha \times \beta = \gamma$, but the recently popularized additive approach (i.e., $\alpha + \beta = \gamma$ [Allan 1975, Lande 1996, Gering et al. 2003]) provides a tractable alternative when diversity is partitioned over multiple scales. Additive partition components have the same units and can easily be compared and interpreted within and between spatial scales (Lande 1996, Crist et al. 2003). For nested spatial scales, diversity of the smallest spatial unit is α_1 . Diversities of the hierarchical scales are then α_2 , α_3 , and so forth. Because these are nested scales, α_3 would also include α_2 and α_1 ; β_x would then be the incremental change in diversity at each hierarchical step up in scale. Under the additive model, $\alpha_2 - \alpha_1 = \beta_1$. For a region with four nested spatial scales, an additive model is $\alpha_1 + (\alpha_2 - \alpha_1) + (\alpha_3 - \alpha_2) + (\alpha_4 - \alpha_3) = \gamma$, or simply $\alpha + \beta_1 + \beta_2 + \beta_3 = \gamma$.

Given the patchiness of seeps within and among outcrops, the spatial structuring of seep habitat is fully nested. As we define it, alpha diversity (α) represents the average richness at the local scale; β_1 represents the average differential diversity between local-scale plots within contiguous seeps; β_2 represents the average differential diversity between seeps within outcrops,

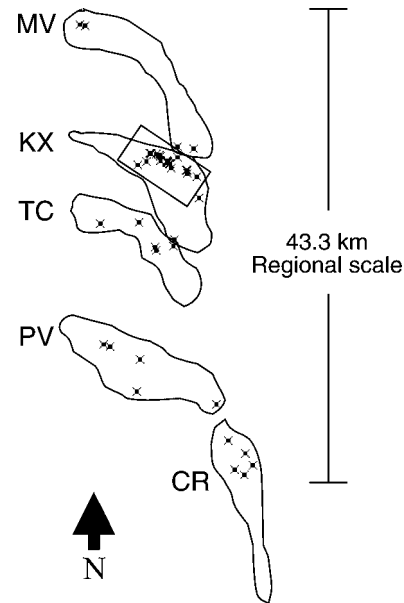


FIG. 1. Map of study area showing spatial relationships among sampled seeps. Seeps are indicated by their GPS locations (x). The outcrop scale is indicated by the box ($38^{\circ}51'55.8''$ N– $38^{\circ}50'46.1''$ N). The regional scale includes the five outcrops ($38^{\circ}58'14.3''$ N– $38^{\circ}36'10.7''$ N). The two seeps most distant from one another are 43.3 km apart.

which is the smallest spatial scale with discrete patchiness of this plant community; and β_3 represents the average differential diversity between outcrops in a region. Therefore, the partitioning equation is $\alpha + \beta_1 + \beta_2 + \beta_3 = \gamma$ for a regional scale that includes multiple outcrops and $\alpha + \beta_1 + \beta_2 = \gamma$ for a scale including seeps on only one outcrop.

We studied 50 serpentine seeps in the inner North Coast Range, California. Twenty-five are spread over five serpentine outcrops (five seeps per outcrop) over 46 800 ha (i.e., “regional scale”; Fig. 1). We used Trimble GeoExplorer III GPS units (Trimble Navigation 1996–2000, Sunnyvale, California, USA) to record coordinates of each seep transect midpoint. Mean distance between two seeps at this scale is 15.6 km (0.29–43.3 km). The remaining 25 seeps cluster within a portion of one serpentine outcrop (430 ha) and form a subset of the region (i.e., “outcrop scale”; Fig. 1). Mean distance between seeps for the outcrop scale is 1.65 km (0.02–4.76 km).

We haphazardly chose study seeps within the context of either the regional or the outcrop scale being represented; mean slope and aspect conditions of seeps did not vary between scales (results not shown). We then established a 50-m transect along the central drainage of each seep. At 5-m intervals, a contiguous array of 1-m² quadrats (local-scale [α] sampling) ran from a random side of the transect line to the edge of the seep; 1543 quadrats were sampled across all seeps. We surveyed

seeps for plant diversity twice each year (early and late season) during May through July 2001 and 2002. Presences of the 40 seep species were recorded in each quadrat and pooled across seasons and years. Plants in all life stages were counted, including seedlings, providing a fair approximation of the resident community as well as its recent colonizers. During 2002, we also recorded presences of seep species in all seep tributaries contiguous with the transect, up to 300 m away. Most seep tributaries are shorter than 300 m, and we rarely found new species beyond this area.

We used a soil-moisture meter (Lincoln Irrigation, Lincoln, Nebraska, USA) that ranks soil moisture from zero to ten to record four soil-moisture readings per quadrat during early- and late-season sampling, 2002. At five 10-m intervals along the transect, we randomly chose a quadrat for soil sampling. We determined this scale of sampling to be a feasible method that accounts for within-seep soil heterogeneity. We analyzed soil for organic matter, estimated N release, P, extractable cations (K, Mg, Ca, Na), H, pH, cation exchange capacity, percentage cation saturation, nitrate-N, sulfate-S, Zn, Mn, Fe, Cu, B, soluble salts (A&L Western Agricultural Laboratories, Modesto, California, USA), and texture (DANR Analytical Lab, University of California, Davis, California, USA). Results for the five soil samples were averaged to yield values for each seep; variances and ranges of values among seeps at the two scales were also calculated.

Additive diversity null models

To test for nonrandom beta diversity we generated null distributions using a randomization routine that reshuffled the observations, according to standard methods (Gotelli and Graves 1996, Manly 1997, Gering et al. 2003). These randomizations maintained the same frequency distributions for every species and distributions of sampling effort as in the original data (i.e., sums of rows [species] and columns [sites] were held constant). Note that the values of both α and γ diversity were therefore constrained to the observed values. Randomizations assigned each species observation to a quadrat (α scale), without replacement. We estimated seep-scale diversity by grouping the randomly filled quadrats, using the same distribution of quadrats per seep as the original data, in order to account for unequal distribution of sampling effort. Diversity patterns at larger scales were estimated by grouping the randomized seep-scale partitions into outcrops. Randomizations were repeated 1000 times, yielding null distributions for the additive partitioning of species richness at each scale. In addition, we also used a bootstrapping randomization that differs from the first method in that species observations are assigned to quadrats with replacement; that is, row (species) but not column (sites) sums were maintained. Therefore site diversity is not constrained.

Spatial and environmental correlations

To analyze relationships between beta diversity and environmental heterogeneity, we calculated the similarity of species composition between seeps with the Jaccard index of community similarity (Krebs 1999), which is based on species presence/absence data and ranges from 0 to 1. We used the Jaccard index in this portion of the study because it allowed us to calculate pairwise compositional differences without designating a regional diversity as required by the additive model. For the beta diversity matrices, entry $[i, j]$ was calculated as $(1 - J_{ij})$, where J_{ij} is the Jaccard index for seeps i and j , respectively. We used $(1 - J_{ij})$ instead of J_{ij} so that the matrices would reflect community dissimilarity, that is, so that a value of 0 would indicate identical species lists and 1 would indicate a complete lack of overlap. Values of $1 - J$ were calculated for both the full suite of seep species and the five endemics. Analyses were also completed using Sorensen's Index, but results were quantitatively similar to those from Jaccard and will not be presented. Mantel tests were used to calculate correlations between matrices that described pair-wise differences between the 25 seeps at each scale (Manly 1997, Fortin and Gurevitch 2001).

To describe differences among seeps' soil chemistry using a single metric, we ran a principal-components analysis (PCA) based on the correlation matrix among variables, using all 24 soil variables (including sand and silt percentages from the texture analysis; clay is redundant in the PCA). We then calculated Euclidian distances between seeps in the multidimensional PCA space, after weighting the distances along each PCA axis by the variance explained by that axis. Seeps that differed strongly in PC axis 1 therefore had a larger entry in the matrix than seeps that differed strongly only on PC axes 2 and higher. A similar method was used to construct metrics for texture (using sand and silt percentages), for differences in the serpentine gradient using the 'serpentine variables' (Ca, Mg, and pH), and for Mg alone. Ca, Mg, and pH levels are known to characterize serpentine soils (Kruckeberg 1984) and explain variation in plant assemblages on serpentine grasslands (Harrison 1999). Geographic distances between seeps for the "distance" matrix were calculated from GPS coordinates.

We used the soil-moisture data to calculate hydrological differences between seeps. Because we were interested in the heterogeneity of soil moisture to which the plants would be exposed, we used the distribution quantile of soil-moisture readings that maximized the variance in moistures among seeps, as opposed to average moisture values. Because most early-season moisture readings were high, variance among seeps was maximized by use of a lower quantile, whereas later in the season, when most soil samples were dry, variance was maximized by higher quantiles. At the outcrop scale, we used the 25th and 90th quantiles for early- and

TABLE 1. Results of the randomization models.

Parameter	Regional		Outcrop	
	Expected	Observed	Expected	Observed
α_1	5.9†	5.9	5.89†	5.89
β_1	24.8 ± 0.27	11.2**	17.5 ± 0.69	8.51**
β_2	7.0 ± 0.35	14.3**	15.6 ± 0.79	24.6**
β_3	2.3 ± 0.51	8.6**	NA	NA
γ	40†	40	39†	39

Notes: The regional scale is represented by 25 seeps distributed across five serpentine outcrops (46 800 ha). The outcrop scale is represented by 25 seeps distributed across one outcrop (430 ha). Local diversity (α_1) and total diversity (γ) are constrained in the model, because row and column sums were held constant; β_1 is the species turnover among quadrats within a seep, β_2 is the species turnover among seeps within outcrops, and β_3 is the species turnover among outcrops. For the 25 seeps across a region, observed β diversity values were lower than expected by chance at the contiguous within-seep spatial scale (β_1) and greater than expected at the non-contiguous among-seep (β_2) and among-outcrop (β_3) spatial scales. For the 25 seeps within one outcrop, observed values were also lower than expected at the within-seep spatial scale (β_1) and greater than expected at the between-seep scale (β_2). Expected values are given as ranges. “NA” indicates not applicable.

† Constrained.
** $P < 0.001$.

late-season soil moisture, respectively; at the regional scale, the 20th and 57th quantile were used.

All Mantel tests were calculated by S-Plus 6.1 (Insightful Corporation, Seattle, Washington, USA), according to the algorithm from Manly (1997), with 5000 randomizations to estimate P values. Partial Mantel tests (Smouse et al. 1986, Fortin and Gurevitch 2001) calculate the partial correlation between matrices **A** and **B**, with respect to matrix **C**, by using matrices **A'** and **B'**, which consist of the residuals from linear regressions of **A** on **C** and **B** on **C**. Two-tailed P values were estimated by the number of matrix randomizations out of 5000 that produced an absolute value of the test statistic greater than or equal to the observed correlations.

RESULTS

Additive diversity partitions

For the 25 seeps across the five-outcrop region, observed beta diversity values were lower than expected by chance at the within-seep scale (β_1), where habitats are contiguous. In contrast, observed beta diversity values were greater than expected by chance at the non-contiguous among-seep (β_2) and among-outcrop (β_3) scales (Table 1). For the 25 seeps within one outcrop, observed beta diversity values were again lower than expected at the within-seep scale (β_1) and were greater than expected by chance at the between-seep scale (β_2 , Table 1). The null model with bootstrapping gave quantitatively similar results, showing that these diversity partitions are robust to relaxing the assumption constraining site diversities (results not shown).

Spatial and environmental correlations

At the regional scale, community dissimilarity ($1 - J$ Jaccard index) for the full suite of seep species was positively correlated with distance, and dissimilarity in serpentine soil variables (composite of Ca, Mg, and pH) and soil texture (composite of sand and silt), and was marginally correlated with dissimilarity of the metric for all soil components (Mantel tests, Table 2). The endemics had qualitatively similar responses with several additional sensitivities; $1 - J$ was correlated with distance, and dissimilarity in soil variables, serpentine soil variables, soil moisture (both early- and late-season), and Mg, and was marginally correlated with dissimilarity in texture and early-season soil moisture (endemics Mantel tests, Appendix B). The positive correlation between community dissimilarity of both suites of species and distance was significant even when the effects of dissimilarities in soil chemistry, texture, and serpentine variables were removed, however the correlations for the endemic species were not any higher than for the community as a whole (partial correlations, Appendix C, D).

TABLE 2. Mantel tests for correlations among community dissimilarity (full suite of species), distance, and environmental factors.

Variable	Description	Regional		Outcrop	
		r with $1 - J$	P	r with $1 - J$	P
$1 - J$	$1 - J$ Jaccard index	1		1	
Distance	spatial distance between seeps	0.27*	0.004*	-0.03	0.44
Soil	PCA of all soil components	0.22	0.09	0.21	0.08
Serpentine	PCA of Ca, Mg, and pH	0.20*	0.03*	-0.06	0.33
Texture	PCA of sand and silt	0.27*	0.01*	0.51*	0.005*
Moisture	PCA of early- and late-season soil moisture	-0.08	0.24	0.21	0.06
Early moisture	quantile of early-season soil moisture	-0.06	0.27	0.26*	0.03*
Late moisture	quantile of late-season soil moisture	-0.06	0.31	-0.008	0.59
Mg		0.08	0.26	-0.03	0.47

Notes: P values are from two-tailed tests. At the regional scale, $1 - J$ (Jaccard index) was positively correlated with distance and dissimilarity in key environmental components. At the outcrop scale, it was also correlated with environmental components but not distance.

* Correlations significant at $P < 0.05$.

At the outcrop scale, community dissimilarity of the full suite of species was correlated with dissimilarity in soil texture and early-season moisture and was marginally correlated with the metric for all soil components and soil moisture (both early- and late-season; Mantel tests, Table 2). Again, the endemics had qualitatively similar responses in that $1 - J$ was marginally correlated to dissimilarity in soil variables and early-season soil moisture, as well as to dissimilarity in serpentine variables (Mantel tests, Appendix B). Distance was not significantly correlated with community dissimilarity of the full suite of species at this scale whether or not dissimilarity in the metrics for soil, texture, and serpentine components was taken into account (Table 2, Appendix C). However, dissimilarity of the endemics became marginally correlated with distance given dissimilarity of serpentine variables (partial correlations, Appendix D). Variances and ranges for environmental components of interest did not show consistent differences between regional and outcrop scales (Appendix E).

DISCUSSION

Spatial discontinuity of the serpentine-seep habitat was consistently associated with nonrandom differences in species richness, in that beta diversity was lower than expected by chance within contiguous habitats (seeps) and greater than expected by chance among both separate seeps and outcrops. This result implies that landscape patchiness may limit species' distributions, such that the plant communities we observed within habitat patches may be the result of a scale-dependent combination of local environmental conditions and propagule availability. Higher than expected beta diversity at larger scales was also found by Gering and colleagues (Crist et al. 2003, Gering et al. 2003) for beetle communities in contiguous deciduous forest.

Although higher beta diversity in species richness consistently occurred among spatially discontinuous seep habitat across both a single outcrop and a region of outcrops, these scales differed in the relative influences of dispersal limitation and environmental variability. Across the region, beta diversity ($1 - J$) for both suites of species was highly correlated with distances between seeps. Even after the removal of environmental differences, assemblages farther apart in space were more different than those closer together. For seeps within an outcrop, however, distance did not affect compositional differences in the full suite of species. Because seeps at the regional scale are further apart and also often separated by non-serpentine soils, dispersal limitation probably affects beta diversity at this scale. However, at the outcrop scale, distance was marginally correlated to compositional differences in the endemic species when serpentine soil variation was removed. This result suggests that these less common and highly restricted species are slightly more sensitive to dispersal limitation at the outcrop scale than the full community. Harrison et al.'s (2000) finding that the

configuration of seeps across the outcrop scale influenced population fluctuations of the endemic species supports this conclusion.

Spatial patterning in species absences across the region also provides evidence for dispersal limitation. Detailed examination shows that most species' absences were not randomly distributed across seeps; rather, absences occurred across entire outcrops or adjacent outcrops. Because of accessibility, sampling did not include all seeps on each outcrop, but even the intense outcrop scale sampling (25 seeps/outcrop) revealed only one more species than the regional sampling protocol (5 seeps/outcrop) for the same outcrop, showing that sampling five seeps per outcrop can be sufficient to record nearly all seep species present on an outcrop. In addition, PCAs of soil, serpentine, and moisture variables (i.e., the same data that show correlations with diversity patterns within the region) show no separation among outcrops, so these absences are unlikely to be correlated with environmental differences. Therefore, this large-scale pattern of species absences supports the idea that dispersal limitation may occur at the regional scale and thus contribute to among-seep and among-outcrop beta diversity.

Research on serpentine dryland plant communities also showed an increase in beta diversity with habitat patchiness, especially for serpentine endemics (Harrison 1997, 1999, Harrison and Inouye 2002). In a neotropical forest system, Condit et al. (2002) found that dispersal limitation may structure beta diversity at different scales and specifically that dispersal limitation may occur at a scale of 0.2–50 km. This scale of dispersal limitation is remarkably consistent with our finding that serpentine-seep species could be dispersal limited at a scale of 0.29–43.3 km.

Environmental heterogeneity appeared to influence community dissimilarity at both the regional and outcrop scales, but the importance of certain variables was scale dependent. For example, among seeps at the regional scale, differences in both endemic species and the whole communities were correlated with differences in serpentine variables, but at the outcrop scale differences in composition were notably not correlated with serpentine variables (Table 2, Appendix D). The regional scale includes five serpentine outcrops, which may encompass a broader gradient of serpentine than a single outcrop. Mg varied over 2.5 times more across the region, and its range was also greater (Appendix E). High levels of Mg are characteristic of serpentine and are known to influence plant responses to these soils (Kruckeberg 1984). The community may therefore only be sensitive to the broader regional serpentine gradient, further intensified by a high sensitivity of the endemics to Mg at this scale (Appendix B). Habitat differences can affect community composition by interacting with species' relative competitive abilities, physiological tolerances, or resilience after disturbance, and are also known to drive beta diversity in other taxa (Williams et

al. 2002, Davies et al. 2003). However, if the influences of different components vary with scale, then ecologists must be cautious when predicting the effects of environmental heterogeneity on beta diversity across scales.

Our results indicate that the spatial discontinuity of serpentine-seep habitat acts in concert with stark environmental gradients to dictate species coexistence and diversity in this system. Although habitat fragmentation often is associated with a loss in biodiversity, studies indicate that fragmentation per se, as opposed to habitat loss, may actually have positive effects on biodiversity (Fahrig 2003). Similarly, in our study system, natural fragmentation of the landscape promoted beta diversity at the regional scale, which probably enhances regional coexistence and diversity beyond what would be expected in contiguous habitat. These patterns would probably differ though in human-fragmented systems in which species have a different evolutionary relationship with the landscape.

The appropriateness of neutral versus niche-based community and metacommunity models is an active source of current debate (Gilbert and Lechowicz 2004, Leibold et al. 2004, Cottenie 2005). Neutral theory predicts that local dispersal creates a systematic increase in beta diversity with distance between sites (Hubbell 2001). This expectation contrasts with niche-based models, which predict community change due to species-specific evolved habitat specificities and competitive abilities along environmental gradients (Tilman 1982). The proposed four metacommunity paradigms (Leibold et al. 2004) also range from neutral to niche-based (i.e., species sorting) modeling alternatives. Empirical studies lend support for niche-based models (Gilbert and Lechowicz 2004) or a combination of both (Cottenie et al. 2003, Tuomisto et al. 2003, Freestone and Harrison 2006). Our results indicate that spatial scale is likely to influence the suitability of these models in predicting beta diversity patterns. We found evidence of dispersal limitation occurring at a 0.29–43.3 km scale for the full suite of species, and marginal evidence for dispersal limitation of endemics at a smaller scale (0.02–4.76 km), thus supporting neutral theory predictions. However, beta diversities at both scales were sensitive to environmental gradients as per niche-based model expectations. Therefore, the mechanisms driving coexistence and diversity in this system appear scale-dependent. Community and metacommunity models may need to integrate the dominance of different mechanisms at different scales to reconcile the maintenance of multi-scale patterns of diversity.

ACKNOWLEDGMENTS

We thank S. Harrison for support and guidance; J. Callizo for help with plant identifications; H. Cornell, K. Davies, M. Holyoak, T. E. Miller, N. Underwood, and anonymous reviewers for comments on earlier drafts; A. B. Thistle for editing; R. Archiga and many others for field assistance; and the University of California Natural Reserve System for use of

the McLaughlin Reserve. Funding was provided by an NSF Graduate Research Fellowship (A. L. Freestone), UCD Consortium for Research at McLaughlin, UCD Public Service Research Program, UCD Jastro-Shields Award, California Native Plant Society, the UC Natural Reserve System, and NSF grants DEB-0075369 to S. Harrison and DEB-03009177 to B. Inouye.

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APPENDIX A

Serpentine seep species of Yolo, Lake, and Napa counties, California, USA (*Ecological Archives* E087-147-A1).

APPENDIX B

Mantel tests for correlations among community dissimilarity ($1 - J$, for endemic species), distance, and environmental factors (*Ecological Archives* E087-147-A2).

APPENDIX C

Select partial Mantel tests showing correlations among community dissimilarity ($1 - J$, full suite of species), distance, and environmental factors, accounting for the variation in an additional given factor (*Ecological Archives* E087-147-A3).

APPENDIX D

Select partial Mantel tests showing correlations among community dissimilarity ($1 - J$, endemic species), distance, and environmental factors, accounting for the variation in an additional given factor (*Ecological Archives* E087-147-A4).

APPENDIX E

Ranges and variances for selected environmental variables across regional and outcrop scales (*Ecological Archives* E087-147-A5).