

Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora

SUSAN HARRISON, KENDI F. DAVIES, HUGH D. SAFFORD* and JOSHUA H. VIERS

Department of Environmental Science and Policy, University of California – Davis, Davis, California, USA, and

**USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA, USA*

Summary

1 The relationship of productivity to species diversity is usually positive at regional scales, but is often neutral, unimodal or negative at local spatial scales. Recent studies have pointed out that beta diversity, or among-locality and within-region variation in species composition, must therefore tend to increase with productivity.

2 We tested for a positive relationship of productivity to beta diversity in herbaceous plants at 105 widely distributed sites on serpentine soil in California. We also asked whether any such pattern could be explained, as previously proposed, by increased environmental heterogeneity at higher levels of productivity.

3 We found that one measure of beta diversity (the species dissimilarity between paired 500 m² plots on adjacent north and south slopes) was positively related to productivity (as measured by the normalized difference vegetation index, a remotely sensed index). However, this effect was not strong enough to transform the neutral relationship of productivity with alpha (1 m²) diversity to a positive relationship of productivity with gamma (1000 m²) diversity.

4 The positive effect of productivity on beta diversity was not related to increasing heterogeneity in coarse measures of vegetation structure (percentage cover of shade, litter, rocks, moss, bare soil, animal disturbance). We speculate that the effect may instead have a ‘top-down’ explanation: higher beta diversity may be caused by the positive influence of productivity on the size of the regional species pool.

5 Our study illustrates the principle of a ‘scale transition’, in which an ecological pattern is qualitatively different at different spatial scales. Careful attention to scale-dependence may help narrow the search for mechanisms for such long-studied ecological puzzles as the latitudinal diversity gradient.

Key-words: beta diversity, diversity, heterogeneity, productivity, regional species pool, scale transition, serpentine, spatial scale, species richness

Journal of Ecology (2006) **94**, 110–117

doi: 10.1111/j.1365-2745.2005.01078.x

Introduction

Mechanisms to explain the relationship between productivity and species richness remain highly elusive, and recent studies of this problem have emphasized the need for careful consideration of appropriate spatial scales (Huston 1999; Waide *et al.* 1999; Mittelbach

et al. 2001; Safford *et al.* 2001). Productivity is nearly always found to be positively correlated with diversity at large scales, such as among biomes or geographical regions (Francis & Currie 2003; Hawkins *et al.* 2003), but the relationship is often neutral, weakly unimodal, or negative at smaller scales, such as among field sampling plots (Grime 1973, 2001; Tilman 1982; Grace 1999; Waide *et al.* 1999; Gross *et al.* 2000; Safford *et al.* 2001). The productivity-diversity relationship thus provides a potential example of a ‘scale transition’

(Chesson *et al.* 2005), in which an ecological pattern at a larger scale is qualitatively different to that at a smaller one, and an additional mechanism is required to explain such non-linear scale-dependence.

Chase & Leibold (2002) demonstrated that the scale transition from a non-positive to a positive productivity-diversity relationship must involve an increase in beta diversity, or among-site dissimilarity in species composition. They found that zooplankton diversity within ponds (i.e. local, or alpha, diversity) followed a unimodal relationship to productivity. However, ponds within high-productivity watersheds were more dissimilar from one another in composition (i.e. had higher beta diversity) than ponds within low-productivity watersheds, thus producing a positive relationship between productivity and watershed-scale diversity (i.e. regional, or gamma, diversity). These authors considered, but found no evidence for, one possible mechanism, namely that environmental heterogeneity increases at higher levels of productivity. They speculated that the mechanism instead involved the existence of alternative stable states at high productivity, an idea that later received a modest amount of support from microcosm experiments (Fukami & Morin 2003). Subsequently, lack of connectivity among ponds was implicated as a necessary condition for the increase in beta diversity with higher productivity (Chase & Ryberg 2004).

Higher beta diversity at higher productivity is likely to be a phenomenon of global generality and importance. In a recent review and meta-analysis, Hillebrand (2004) found that the tropical-temperate diversity gradient is virtually always stronger at the regional scale, e.g. among countries or latitudinal bands, than at the local (field plot) scale, even when total latitudinal extent is held constant. In addition, multiple studies have found that the regional latitudinal diversity gradient is very strongly correlated with measures of energy and water availability that control primary productivity (Francis & Currie 2003; Hawkins *et al.* 2003; Hillebrand 2004). Taken together, these results mean that global-scale patterns in productivity are positively associated with beta diversity, i.e. with the ratio of regional richness to local richness. Thus, although we are still far from having a satisfactory mechanistic explanation for either the latitudinal richness gradient or the productivity-diversity relationship, further study of beta diversity is clearly needed.

In this study we ask whether beta diversity increases with productivity in a terrestrial herbaceous plant system. We further ask whether such a relationship can be found at the relatively small scale of tens to hundreds of metres, where beta diversity may be caused by heterogeneity in readily observable microhabitat conditions such as slope and aspect, shading, litter, rock cover and animal disturbance. We hypothesize that increasing mean productivity in our system is associated with greater variation in such local microhabitat conditions, in turn leading to higher small-scale spatial differentiation in species composition. If this is true, ours would

be the first study to find evidence for one of the major proposed explanations for the positive productivity-beta diversity relationship.

We analysed plant species richness in 105 field sites on serpentine soil in California. Serpentine is a harsh, low-productivity soil that supports a rich flora dominated by native species. In earlier work we found that at a regional scale (e.g. 10^2 – 10^4 km 2), species richness in our system was strongly positively correlated with productivity, which in turn was strongly correlated with average annual rainfall (Harrison *et al.* 2000; Harrison *et al.* 2004; Harrison *et al.* 2006). These results were in good agreement with other studies linking regional-scale plant diversity in California to a rainfall-driven gradient in productivity (Richerson & Lum 1980; Hawkins & Porter 2003; Williams *et al.* 2005).

We considered four components of species richness: ‘alpha’ (1×1 m quadrats), ‘within-plot beta’ (dissimilarity among seven quadrats within 50×10 m plots), ‘between-slope beta’ (dissimilarity between pairs of 50×10 m plots on adjacent north and south-facing slopes), and ‘gamma’ (cumulative richness of each pair of 50×10 m plots). Within-plot beta is intended to measure the diversity that is related to general small-scale environmental heterogeneity; between-slope beta is intended to measure the diversity associated with differences in local topography. We only considered herbs, because valid tests of local processes on diversity must sample potentially competing species (Huston 1999), and because we were interested in beta diversity at scales too small for woody species.

We asked three questions. (i) How strongly is variation in the gamma (total) herb richness of our study sites associated with variation in each smaller component of richness (alpha, within-plot beta, between-slope beta)? (ii) How does each component of richness respond to productivity? Specifically, does productivity have a non-positive relationship to alpha, but a positive relationship to beta and gamma diversity? (iii) How does environmental heterogeneity respond to productivity? In particular, is productivity positively associated with either the within-plot variability, or the between-slope variability, in environmental parameters that may affect herb species composition (percentage cover of shade, rocks, bare soil, litter, moss, animal disturbance)?

Using the terminology of Waide *et al.* (1999), our ‘focus’ was small (1×1 m quadrats), but our ‘extent’ was large (our sites spanned roughly 1200 km latitude and 2750 m elevation). This choice of scales should be well suited for the questions we investigated. Most unimodal or negative productivity-diversity relationships are observed in small plots (e.g. Grace 1999; Waide *et al.* 1999; Gross *et al.* 2000) and, in general, many authors advocate defining alpha at a small scale where interspecific interactions should be strong and internal spatial heterogeneity relatively low (e.g. Huston 1999; Loreau 2003). However, our large geographical and ecological extent is appropriate because it ensures an ample natural gradient in primary productivity.

Methods

STUDY SYSTEM

The term ‘serpentine’ as used by ecologists refers to ultramafic (Mg- and Fe-rich) rocks, principally serpentine and peridotite, and the soils derived from them. These rocks originate at the base of the oceanic lithosphere and are exposed on the earth’s surface in zones of tectonic plate convergence and subsequent mountain uplift. Serpentine is an infertile environment for plants because of its low levels of Ca relative to Mg, exacerbated by low nutrient (NPK) levels and, in some cases, metal (Ni and Cr) toxicity and poor water-holding capacity. Distinctive floras occur on serpentine, both because it excludes some plant species from the surrounding communities, and because it may support substrate specialists (endemics) (Kruckeberg 1984; Brooks 1987).

Serpentine in California is found in four broad, geologically defined provinces: the Klamath-Siskiyou Mountains, the North Coast Range, the South Coast Range, and the Sierra Nevada. It supports several thousand plant species including 200+ endemics (Kruckeberg 1984; Safford *et al.* 2005). Very little serpentine is found in adjacent areas outside of the state. The vegetation ranges from forest, woodland and barrens at higher latitudes and in more mesic areas, through shrublands interspersed by barrens and grasslands, to grasslands in more southerly and xeric sites.

SAMPLING

We conducted field sampling of local plant richness and local environmental variables on serpentine from April 2001 to July 2004. To attain geographically representative coverage, we used a spatially referenced floristic data base (Viers *et al.* 2006) to stratify the state into 86 regions that contained serpentine. Within each of these regions, we examined maps of the geology, road layout and land ownership to identify accessible areas and the approximate location of sampling sites without reference to the vegetation. Topographic maps were then used to identify locations where a cool (N–NE) and a warm (S–SW) slope were in close proximity, generally 10–200 m apart. We avoided sites < 50 m from paved roads and sites with obvious signs of human disturbance (mining, logging, off-road vehicles) or recent fire. We sampled 109 sites in 78 regions, with sites spanning 1200 km in north–south extent (from the Oregon border to Catalina Island) and from sea level to 2750 m elevation.

At each site we established two 50 × 10 m plots, one on the north and one on the south slope, to measure the contribution of local topography to species richness. Plot origins were determined by blind tosses of a flag. We recorded the identities of all species in the plots, and in seven 1 × 1 m internal quadrats (five at 10-m intervals along the central transect and two at opposite

corners of the plot). Plots were GPS-located and the plots and subplots were marked. Species were identified using Hickman (1993), supplemented by county floras and local species lists. Within the 1 × 1 m quadrats, we recorded percentage cover by each species and by rocks, bare soil, litter and animal disturbance (trails, burrowing, etc.), and the slope and aspect. We averaged these variables to obtain a mean and CV of each variable for each plot. We recorded woody species cover (i.e. shade), height and identity along the central 50-m transect.

Our sampling schedule was timed to accommodate differences among sites in their peak flowering season based on their latitude and elevation. Because different species were visible and identifiable at different times of year, we sampled each site at least three times in 2 years, with at least one visit early and one visit late in the site-specific flowering season, and accumulated data across sampling dates to obtain one list for each site. Our sampling was sufficiently complete that we very rarely added > 10% of the total species list on the final visit.

To measure productivity, we used the remotely sensed normalized difference vegetation index (NDVI), which measures the separation between energy reflectivity in the near infrared and red wavelengths, and indicates the density and vigour of the plant canopy (Cihlar *et al.* 1991; Hansen *et al.* 2004). The NDVI is a well-studied correlate for leaf area index, net primary productivity and fractional photosynthetically active radiation. The NDVI was an excellent predictor of regional plant diversity on serpentine and other soils in several earlier studies (Williams *et al.* 2005; Harrison *et al.* 2006). Our NDVI data were obtained from the moderate resolution imaging spectroradiometer sensor (MODIS; Carroll *et al.* 2004). We averaged the NDVI spatially for a circle of 250 m radius around each site (in nearly all cases this circle was 100% serpentine). We averaged the NDVI temporally for 2000–04, using the same composite date for each image (calendar day 129: c. 8–23 May) and masking for yearly climatic conditions (i.e. clouds and snow) and known water features. We had to exclude four of our 109 sites because NDVI data were missing, most likely because of cloud cover.

By using the NDVI, we are employing a measure that is closer to potential than to actual productivity, because it does not indicate the degree to which disturbance or herbivory has reduced the biomass of the specific sites that we sampled. Theory suggests that the relationship of diversity to productivity may depend on the level of disturbance (Huston 1999). However, many previous studies of diversity have used potential measures (e.g. rainfall), as well as actual determinations of productivity (e.g. biomass), and a recent meta-analysis found that their results did not differ significantly depending on the measure that was used (Mittelbach *et al.* 2001). Also, previous studies have shown that disturbance has less effect on diversity in serpentine vegetation than in many other plant systems

(Whittaker 1960; Safford & Harrison 2004; Harrison *et al.* 2006).

ANALYSES

As a simple measure of dissimilarity, or beta diversity, we used the proportion of unshared species (one minus the Jaccard index), following numerous other authors (e.g. Colwell & Coddington 1994; Magurran 1998; Chase & Leibold 2002). While more complex beta measures may be preferable when beta diversity is being calculated among sites that vary systematically in their alpha diversity (e.g. among sites spanning latitudinal gradients; Harrison *et al.* 1992; Koleff *et al.* 2003), this is not an issue in our study, where beta diversity was calculated *within*, not among, latitudinally varying sites.

In analysing patterns of alpha diversity and within-plot beta diversity, our sample size was the number of plots ($n = 210$), and our measures of heterogeneity were the within-plot, among-quadrat coefficients of variation (CVs) of the environmental parameters. We refer to these as plot-level analyses. In contrast, in analysing gamma diversity and between-slope beta diversity, our sample size was the number of sites ($n = 105$), and our measures of heterogeneity were the between-slope differences (absolute value of north minus south) in the within-plot average values of the environmental parameters. We refer to these as site-level analyses.

To answer our first question, we used a site-level multiple regression to ask how variation in gamma (total) diversity was associated with variation in average alpha diversity, within-plot beta diversity, and between-slope beta diversity.

To answer our second question, we used multiple regressions to ask how alpha diversity (plot-level) and gamma diversity (site-level) depended on NDVI and $NDVI^2$. We also used simple regressions to test how within-plot beta diversity (plot-level) and between-slope beta diversity (site-level) depended on NDVI.

To answer our third question, we used multivariate analyses of variance to ask how NDVI was associated with, first, the within-plot mean values, secondly, the within-plot coefficients of variation (CVs), and thirdly, the between-slope differences of environmental variables. The variables we examined were the percentage cover of shade (i.e. woody cover), rocks, bare soil, litter, disturbance and moss. We also used multiple regressions to ask whether within-plot beta diversity was related to the CVs of these variables, and whether between-slope beta diversity was related to the between-slope differences in any of these variables.

To avoid possible confounding effects of woody cover, we repeated key analyses using only the subset of 34 sites that had no woody cover. Also, we asked whether our productivity-diversity patterns still held when the percentage of herbaceous cover was used as an additional independent variable in multiple regressions.

Results

CONTRIBUTIONS OF DIVERSITY COMPONENTS TO GAMMA DIVERSITY

Within-plot beta diversity averaged 0.59 ± 0.15 (SD); between-slope beta diversity averaged 0.70 ± 0.13 ; alpha diversity averaged 7.57 ± 5.02 ; gamma diversity averaged 49.74 ± 18.79 .

In a site-level multiple regression, variation in gamma diversity was significantly positively associated with variation in alpha diversity ($r =$ standardized slope = 1.043, $P < 0.001$) and with variation in between-slope beta diversity ($r = 0.408$, $P < 0.001$); it was significantly negatively associated with variation in within-plot beta diversity ($r = -0.110$, $P = 0.04$). The relationship with alpha was much stronger than that with either beta measure, as indicated by the relative slopes.

When only herbaceous sites were considered, the results were little changed: $r = 1.089$ ($P < 0.001$) for alpha, $r = 0.566$ ($P < 0.001$) for between-slope beta, and $r = -0.139$ ($P > 0.10$) for within-plot beta.

RELATIONSHIP OF THE NDVI TO DIVERSITY COMPONENTS

In plot-level analyses, neither alpha diversity nor within-plot beta diversity was significantly related to either NDVI ($P > 0.10$; Fig. 1) or $NDVI^2$. In site-level analyses, between-slope beta diversity was positively related to NDVI ($r = 0.299$, $P = 0.002$) but gamma diversity was not related to NDVI ($P > 0.10$; Fig. 1) or $NDVI^2$.

When only herbaceous sites were considered, the relationship of NDVI to between-slope beta remained significant ($r = 0.511$, $P = 0.003$; Fig. 2). The relationships of NDVI and $NDVI^2$ to alpha, within-plot beta, and gamma diversity remained non-significant ($P > 0.10$).

When herb cover was added as an independent variable to the preceding model (using herbaceous sites only), it showed significant positive relationships to alpha diversity ($r = 0.576$, $P < 0.001$) and to gamma diversity ($r = 0.401$, $P = 0.029$), as well as negative relationships to within-plot beta diversity ($r = -0.421$, $P < 0.001$) and between-slope beta diversity ($r = -0.487$, $P = 0.001$). However, it did not qualitatively alter the relationships of NDVI to the components of diversity: these were still neutral for alpha, within-plot beta and gamma diversity ($P > 0.10$), and positive for between-slope beta diversity ($r = 0.403$, $P = 0.006$).

RELATIONSHIPS OF THE NDVI AND BETA DIVERSITY TO ENVIRONMENTAL HETEROGENEITY

In a plot-level multivariate analysis of variance, NDVI was not associated significantly with the mean values of percentage rock, bare soil, disturbance, litter or moss, but it was positively associated with the mean

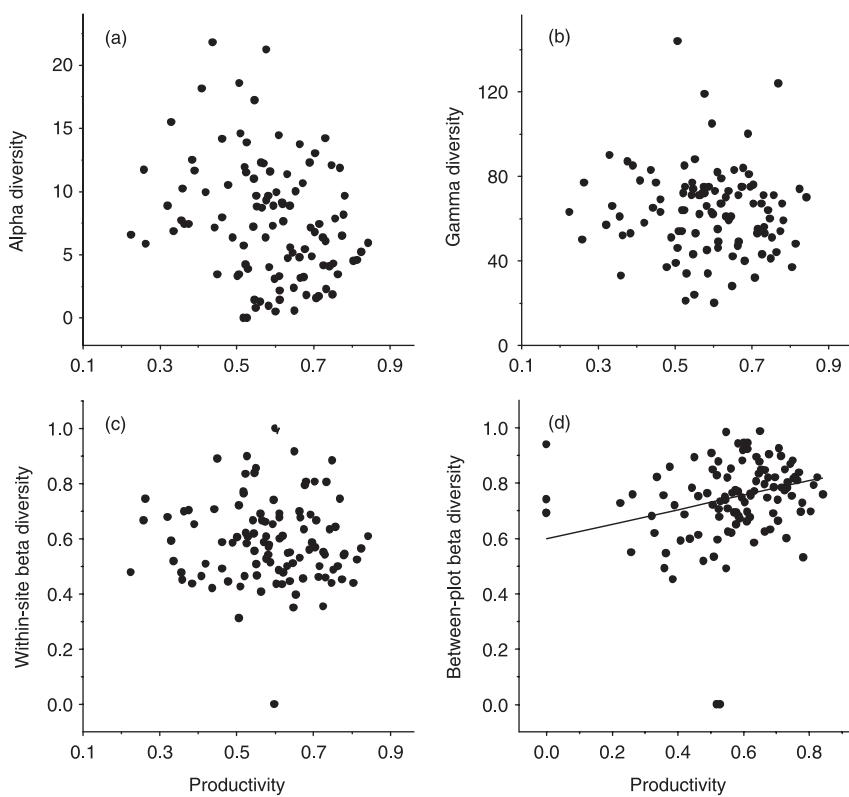


Fig. 1 Relationship of productivity (NDVI) to (a) alpha, (b) gamma, (c) within-plot beta, and (d) between-slope beta diversity, for all sites. The relationship is only significant for between-slope beta ($P = 0.002$; intercept = 0.60 ± 0.05 (SE), unstandardized slope = 0.26 ± 0.01 (SE)).

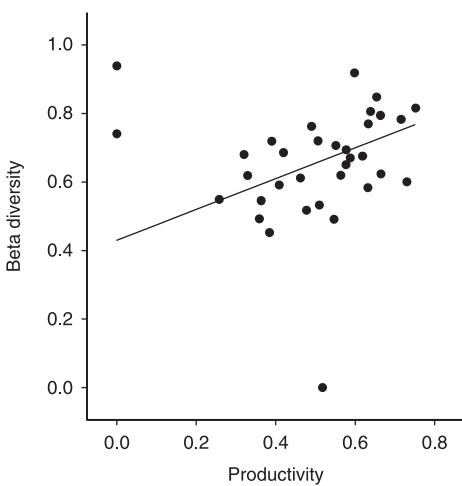


Fig. 2 Relationship of between-slope beta diversity and productivity (NDVI) for the sites with no woody cover. ($P = 0.003$; intercept = 0.43 ± 0.08 (SE), unstandardized slope = 0.45 ± 0.14 (SE)).

value of percentage shade. (For the whole model, Pillai Trace = 0.17, d.f. = 7 and 202, $F = 5.92$, $P < 0.001$; in associated F -tests, $P < 0.001$ for the effect of NDVI on percentage shade, $P > 0.10$ for the effects of NDVI on all other variables.)

In a plot-level MANOVA of the coefficients of variation of the above variables, NDVI was positively associated with the CVs of the percentage cover by rock, bare soil

and animal disturbance. (For the whole model, Pillai Trace = 0.14, d.f. = 7 and 202, $F = 4.67$, $P < 0.001$. In associated F -tests, $P = 0.001$ for the effects of NDVI on CV of rock, $P < 0.001$ for the effects of NDVI on CV of bare soil, $P = 0.027$ for the effect of NDVI on the CV of animal disturbance; $P > 0.10$ for the effects of NDVI on all other variables.)

In a site-level MANOVA, NDVI had no significant relationship to the between-slope differences in the values of any environmental variable (Pillai Trace = 0.06, d.f. = 7 and 97, $F = 0.83$, $P > 0.10$).

In a plot-level multiple regression, within-plot beta was not significantly related to the CVs of any of the environmental variables ($P > 0.10$).

In a site-level multiple regression, between-slope beta was positively related to the between-slope difference in litter, but not to the between-slope differences in any other environmental variables ($r = 0.030$, $P = 0.002$).

Discussion

We found a positive association between productivity and beta diversity, similarly to other authors (Chase & Leibold 2002; Chase & Ryberg 2004). Higher values of the productivity measure NDVI, which, in our study system, largely reflects rainfall, are associated with greater dissimilarity in herb species composition between two plots on adjacent north and south slopes. This result was not an artifact of the effect of productivity on the

relative amounts of woody and herbaceous cover, as it was also true among the subset of sites with no woody cover, and as it was qualitatively unchanged when herb cover was included in the model. We did not find such an effect for beta diversity at a smaller scale, among 1-m² quadrats within 50 × 10 m plots.

We found no evidence for the hypothesis that increasing environmental heterogeneity causes the increase in beta diversity at higher levels of productivity. We did find that several measures of within-plot heterogeneity were positively associated with NDVI, namely the coefficients of variation of rock, bare soil and animal disturbance. However, no measure of between-slope environmental heterogeneity showed an increase with NDVI. As only the between-slope beta diversity was positively associated with NDVI, we conclude that the forms of environmental heterogeneity we measured were not capable of explaining the positive relationship of productivity to beta diversity.

Unlike previous authors, we did not find that increasing beta diversity caused a transition from a non-positive productivity-diversity relationship at a smaller scale to a positive one at a larger scale. Instead, we found non-significant relationships of productivity to diversity at both our smaller (alpha, or 1 m²) scale and our larger (gamma, or 1000 m²) scales. Although such results are not uncommon (Waide *et al.* 1999; Gross *et al.* 2000), it is possible that using a more localized measure of productivity, such as biomass, would have revealed significant relationships at one or both of these scales. Even if we had, we would still be unlikely to have found a scale transition, because the influence of beta diversity on gamma diversity was weak in our system. Variation in gamma diversity was much more strongly associated with variation in alpha diversity ($r^2 = 0.60$) than with variation in either within-plot ($r^2 = 0.01$) or between-slope ($r^2 = 0.10$) beta diversity. This contrasts with other studies that find a strong positive linkage between environmental heterogeneity, beta diversity and gamma diversity (e.g. Williams *et al.* 2002). A scale transition would only be possible if beta diversity responded differently to productivity than did alpha diversity and if beta diversity exerted a strong influence on gamma diversity.

As we know that NDVI is a strong positive predictor of regional diversity in our system (Williams *et al.* 2005; Harrison *et al.* 2006), the scale transition must happen at a larger scale (i.e. a larger site size) than the one we examined. Larger sites would incorporate a higher level of internal heterogeneity, thus increasing the influence of beta relative to alpha diversity. In addition, previous work (Chase & Ryberg 2004) suggests that if our sites were large enough to include spatially discontinuous localities, such as plots on separate serpentine outcrops, our potential to find a scale transition should be enhanced.

We are left in search of a mechanism to explain the positive association of productivity to beta diversity in our system. The only mechanism besides heterogeneity

that has been proposed in the literature is the existence of alternative stable states at high levels of productivity (Chase & Leibold 2002; Fukami & Morin 2003). We do not think this is likely in our system, because serpentine vegetation is characterized by slow growth, infrequent disturbance and generally late-successional conditions (e.g. Whittaker 1960; Safford & Harrison 2004; Harrison *et al.* 2006). Also, our quadrats and plots were spatially continuous with one another, so it seems unlikely that they could exist in alternative stable states. Instead, we propose an explanation based on regional control of local community patterns (Cornell 1993; Karlson *et al.* 2004; Ricklefs 2004).

Species-energy theory (Hawkins *et al.* 2003) predicts that, as productivity increases, regional diversity increases not as a scaled-up consequence of local processes, but because of mechanisms that intrinsically act at a regional scale, for example lower rates of species extinction due to higher regional population sizes. At the same time, resource competition (Tilman 1982; Grime 2001) and assemblage-level thinning (Oksanen 1996; Stevens & Carson 1999) can prevent the additional diversity associated with higher productivity from being absorbed into small localities. Putting these two pieces together, one would predict what we found: an increase in beta diversity with increasing productivity that is not associated with an increase in environmental heterogeneity. Instead, increasing beta diversity could be the by-product of a greater regional number of species ‘spilling over’ among localities as the same number (or fewer) of them are able to coexist within localities. This agrees with the model of Weitz & Rothman (2003), in which the scale transition to a positive productivity-diversity relationship arises from an increase in the size of the regional species pool without any change in local dynamics.

Our proposed explanation is intrinsically difficult to prove because it switches the emphasis from easily observable, local phenomena to regional-scale and long-term processes that are much harder to study (see Ricklefs 2004 for a review of historical explanations for richness gradients). Nonetheless, our results suggest it is valuable to focus on spatial scale as a way of refining the search for explanations of species diversity patterns. We conclude by speculating that beta diversity is higher in the tropics, not necessarily because tropical species have narrower climatic tolerances, as proposed by Janzen (1967), but for reasons similar to those we suggest here. That is, small localities cannot fully absorb the abundance of species that are produced at the regional scale by the high rates of speciation and/or low rates of extinction that are characteristic of highly productive regions.

Acknowledgements

The people who helped us with botanical and geological information, site access and/or field hospitality are too numerous to list, but we are extremely grateful to

them all. F. Caplow and P. Maloney provided expert field assistance. Support was provided by the National Science Foundation (NSF DEB-0075369). We thank H. V. Cornell, L. Haddon, B. A. Melbourne, R. Turkington and two anonymous reviewers for helpful comments on the manuscript.

References

- Brooks, R.R. (1987) *Serpentine and its Vegetation: a Multidisciplinary Approach*. Dioscorides Press, Portland.
- Carroll, M.L., Dimiceli, C.M., Sohlberg, R.A. & Townshend, J.R.G. (2004) 250m MODIS Normalized Difference Vegetation Index (2000–04). The Global Land Cover Facility, College Park, Maryland.
- Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature*, **416**, 427–430.
- Chase, J.M. & Ryberg, W.A. (2004) Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecology Letters*, **7**, 676–683.
- Chesson, P., Donahue, M.J., Melbourne, B.A. & Sears, A.L. (2005) Scale transition theory for understanding mechanisms in metacommunities. *Metacommunities: Spatial Dynamics and Ecological Communities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 279–306. University of Chicago Press, Chicago.
- Cihlar, J., St-Laurent, L. & Dyer, J.A. (1991) Relation between the normalized vegetation index and ecological variables. *Remote Sensing of Environment*, **35**, 279–298.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society London (Series B)*, **345**, 101–118.
- Cornell, H.V. (1993) Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schlüter), pp. 243–252. University of Chicago Press, Chicago.
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *American Naturalist*, **161**, 523–536.
- Fukami, T. & Morin, P.J. (2003) Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, **424**, 423–426.
- Grace, J.B. (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution, and Systematics*, **2**, 1–28.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. Wiley, Chichester.
- Gross, K.L., Willig, M.R., Gough, L., Inouye, R. & Cox, S.B. (2000) Species density and productivity at different spatial scales in herbaceous plant communities. *Oikos*, **89**, 417–427.
- Hansen, M., Defries, R., Townshend, R., Sohlberg, R., Dimiceli, C. & Carroll, M. (2004) MODIS Normalized Difference Vegetation Index. The Global Land Cover Facility, College Park, Maryland.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, **61**, 141–148.
- Harrison, S., Safford, H.D., Grace, J.B., Viers, J.H. & Davies, K.F. (2006) Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs* (in press).
- Harrison, S., Safford, H.D. & Wakabayashi, J. (2004) Does the age of exposure of serpentine explain variation in endemic plant diversity in California? *International Geology Review*, **46**, 235–242.
- Harrison, S., Viers, J.H. & Quinn, J.F. (2000) Climatic and spatial patterns of diversity in the serpentine plants of California. *Diversity and Distributions*, **6**, 153–161.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.-F., Kaufman, D.M. et al. (2003) Energy, water, and broad-scale patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist*, **161**, 40–49.
- Hickman, J.C. (1993) *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley, California.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192–211.
- Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86**, 393–401.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *American Naturalist*, **101**, 233–250.
- Karlson, R.H., Cornell, H.V. & Hughes, T.P. (2004) Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature*, **429**, 867–870.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.
- Kruckeberg, A.R. (1984) *California Serpentines: Flora, Vegetation, Geology, Soils and Management Problems*. University of California Press, Berkeley.
- Loreau, M. (2003) Are communities saturated? On the relationship between alpha, beta, and gamma diversity. *Ecology Letters*, **3**, 73–76.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B. et al. (2001) What is the observed relationship between diversity and productivity? *Ecology*, **82**, 2381–2396.
- Oksanen, J. (1996) Is the humped relationship between species richness and biomass an artifact of plot size? *Journal of Ecology*, **84**, 93–295.
- Richerson, P.J. & Lum, K.-L. (1980) Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist*, **116**, 504–536.
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.
- Safford, H.D. & Harrison, S. (2004) Fire effects on plant diversity in serpentine versus nonserpentine chaparral. *Ecology*, **85**, 539–548.
- Safford, H.D., Rejmanek, M. & Hadač, E. (2001) Species pools and the ‘hump-back’ model of plant species diversity: an empirical analysis at a relevant spatial scale. *Oikos*, **95**, 282–290.
- Safford, H.D., Viers, J.H. & Harrison, S. (2005) Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño*, **52**, in press.
- Stevens, M.H. & Carson, W.P. (1999) The significance of assemblage-level thinning for species richness. *Journal of Ecology*, **87**, 490–502.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Viers, J.H., Thorne, J.H., Quinn, J.F. (2006) Caljep: a spatial distribution database of Calflora and Jepson. *San Francisco Estuary and Watershed Science*, in press.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G.G., Gough, L., Dodson, S.I. et al. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.

- Weitz, J.S. & Rothman, D.H. (2003) Scale-dependence of resource-biodiversity relationships. *Journal of Theoretical Biology*, **225**, 205–214.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Williams, S.E., Marsh, H. & Winter, J. (2002) Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology*, **83**, 1317–1329.
- Williams, J.W., Seabloom, E.W., Slayback, D., Stoms, D.M. & Viers, J.H. (2005) Anthropogenic impacts upon plant species richness and net primary productivity in California. *Ecology Letters*, **8**, 127–137.

Received 11 July 2005

revision accepted 13 September 2005

Handling Editor: Roy Turkington