

## ‘Structured’ beta diversity increases with climatic productivity in a classic dataset

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**Abstract.** Despite a surge of interest in the measurement of beta diversity, there remain only a modest number of well-supported explanations for variation in naturally occurring levels of beta diversity. Among the few emerging generalizations is that beta diversity tends to increase with productivity; it remains to be determined whether the mechanism(s) involves habitat specialization or random factors in community assembly. We examined this question using the classic dataset of Whittaker (1960), who first defined beta diversity in a study of plant communities along multiple abiotic gradients related to productivity. With increasing productivity along climatic gradients (elevation or topography), though not a soil fertility gradient, we found increases in the levels of ‘structured’ beta diversity, i.e., the turnover associated with each of the other gradients, consistent with greater habitat specialization. ‘Unstructured’ beta diversity, i.e., the among-site variation not associated with gradients, varied idiosyncratically among different combinations of environmental factors. These results were robust to the use of either presence-absence or relative abundance data. We conclude that habitat specialization along gradients may tend to increase either with productivity itself, or with regional (gamma) diversity, which tends to be higher in more productive climates and conceivably ‘spills over’ in ecological or evolutionary time to enhance structured beta diversity.

**Key words:** community; dissimilarity; elevation; floristic diversity; gradient; Klamath-Siskiyou; plant; R. H. Whittaker; serpentine; species richness; topography.

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### INTRODUCTION

Beta diversity, or community differentiation among sites, is a key aspect of global patterns in biodiversity, including the richness of tropical forests (e.g., Condit et al. 2002, Tuomisto et al. 2003) and coral reefs (e.g., Dornelas et al. 2006, Cornell et al. 2007, Belmaker et al. 2008). Beta diversity is not only a product of heterogeneity in the environment, but is also promoted by narrow environmental tolerances (Janzen 1967, Ghalam-

bor et al. 2006, Fine et al. 2008), competitive exclusion (MacArthur 1965, Caswell and Cohen 1993, Loreau 2000), spatial isolation and stochastic effects (Chase and Leibold 2002, Chase 2010), and other factors. Regions may therefore vary greatly in the levels of beta diversity associated with a given level of environmental heterogeneity, a facet of global biodiversity that is not fully understood. For example, Qian and colleagues (Qian et al. 2005, 2009, Qian and Ricklefs 2007, Qian 2008) have shown that even at equivalent

spatial and climatic distances, the beta diversity of vascular plants is higher in East Asia than Eastern North America, and that the beta diversity of both plants and animals along climatic gradients declines sharply at high latitudes. Similar variation in environment-beta relationships may also occur at much smaller scales; for example, Hofer et al. (2008) observed that topographic heterogeneity generated beta diversity within 1-km<sup>2</sup> Swiss landscapes, but only in grasslands and not in woody communities.

Among the few emerging generalizations about beta diversity is that it often increases with productivity (Chase and Leibold 2002, Chalcraft et al. 2004, Harrison et al. 2006) as well as with decreasing latitude (Koleff and Gaston 2003, Rodriguez and Arita 2004, Qian and Ricklefs 2007, Sojininen et al. 2007, Qian 2008, Qian et al. 2009). The latitudinal pattern may be the result of macroevolutionary processes such as glaciation history at high latitudes, or faster speciation at lower latitudes, either of which would tend to produce smaller range sizes and hence higher beta diversity at lower latitudes (Qian et al. 2005, 2009). Alternatively, an explanation that could apply to both the latitudinal relationship and to smaller-scale productivity-beta relationships is that higher levels of environmental energy may promote greater randomness in community assembly. Some experimental evidence (Chase 2010) supports such a linkage between productivity and community divergence within similar environments ('unstructured' beta diversity, or 'variation' sensu Anderson et al., *in press*). A third, non-exclusive possibility is that high productivity is associated with increased specialization along environmental gradients, perhaps because productivity intensifies the competitive pressure that leads to habitat specialization in either evolutionary or ecological time (MacArthur 1965). In this case, it is specifically the community divergence associated with unit changes in environmental gradients (e.g., soils, elevation, or ocean depth; 'structured' beta diversity, or 'turnover' sensu Anderson et al. in 2011) that should increase at higher levels of productivity, as some studies suggest (e.g., Harrison et al. 2006, Qian and Ricklefs 2007, Qian 2008, Qian et al. 2009).

The partitioning of diversity into alpha (local),

beta (turnover), and gamma (regional) components was first devised by Robert Whittaker (1960) in a study of the flora of the Siskiyou Mountains (Oregon, USA), a plant diversity hotspot (Ricketts et al. 1999). Whittaker (1960) sampled communities along gradients of elevation, soil, topographic microclimate, and coastal to interior climate. One of his major observations was that the effects of these four abiotic gradients on plant community composition were consistently interactive. For example, the beta diversity associated with topographic heterogeneity differed among soil types as well as declining with elevation; the beta diversity associated with different soil types varied with topographic position and with elevation; and interior climates manifested higher beta diversity along all three of the other abiotic gradients than coastal climates (Whittaker 1960, pp. 320–322). He also observed a tendency for alpha and beta diversity to covary positively in the communities he studied (Whittaker 1960, p. 322). While he did not try to explain these patterns, he used them to illustrate the role of beta diversity in building larger-scale diversity patterns, such as the higher overall diversity of the interior than the coastal Siskiyou (Whittaker 1960, 1961). He used no formal statistical analyses, relying instead on simple comparisons of the mean values of his newly devised metric ( $\beta = \gamma/\alpha$ ) as well as other measures (e.g., percentage similarity).

Since Whittaker's (1960) seminal paper, diversity partitioning has become immensely popular. Recent literature addresses whether beta metrics should be multiplicative or additive (e.g., Gering and Crist 2002, Crist et al. 2003); use presence-absence relative abundance data (e.g., Jost 2007); or be statistically independent of alpha and gamma (e.g., Jost 2007, 2010, Ricotta 2008, Veech and Crist 2010). Debate also concerns methods for analyzing environmental patterns in beta diversity (e.g., Legendre et al. 2005, Anderson et al. 2006, *in press*, Tuomisto 2010). Since community composition is a multivariate problem, there may be no single way to measure beta diversity that performs best in all ways or for all questions (e.g., Ricotta 2008, 2010, Veech and Crist 2010, Anderson et al., *in press*). However, Whittaker's simple original beta metric is often found to perform surprisingly well (Wilson and Shmida 1984, Vellend 2001, Jost 2007).

While this interest in methodology of diversity partitioning has generated a vast literature, leading to >1,000 citations of Whittaker (1960), the actual ecological conclusions drawn in Whittaker's classic study have been largely overlooked, such as his insight that gradients may interact to shape beta and thus regional diversity. We used Whittaker's (1960) original data and modern statistical methods to test three hypotheses: (1) *Gradients interact to influence beta diversity*; thus, the degree of community distinctiveness of any given site depends on its joint position along two (or more) abiotic gradients, Env1 and Env2. More specifically, (2) *Productivity enhances 'structured' beta diversity*; thus, the compositional turnover among communities along one gradient ( $\beta_{\text{Env1}}$ ) tends to increase as productivity increases on the second gradient, Env2. (An example of this is Whittaker's observation that the beta diversity along gradients of topography was higher at more-productive low elevations than less-productive high elevations.) Alternatively, and not mutually exclusively, (3) *Productivity enhances 'unstructured' beta diversity*; thus, the variation in community composition among plots within any given level of Env1 tends to increase as productivity increases on Env2. (A hypothetical example would be if the variation among communities *within* any given level of topography or soil fertility were higher at lower than higher elevations.)

A recent review found that the two most important properties of beta metrics are the inclusion or exclusion of joint absence information, and the use of presence-absence vs. abundance data (Anderson et al., *in press*). To represent the wide array of available methods, we used both abundance-based (Bray-Curtis) and presence-absence metrics (Whittaker's original beta wherever possible; the Jaccard coefficient otherwise) and we also employed several alternative techniques for relating beta diversity to gradients (see Methods for further details). We did not use any metrics that included joint absences, since these are considered inappropriate for analyses involving gradients (Anderson et al., *in press*).

## METHODS

The Siskiyou Mountains (Oregon, USA) are the

northernmost range of the Klamath-Siskiyou region, long known for its complex vegetation and outstanding floristic diversity (Whittaker 1960, Ricketts et al. 1999). In an effort to develop methods for describing plant community variation, Whittaker (1960) sampled ~400 sites representing gradients of soil fertility (infertile serpentine, intermediate gabbro, and fertile diorite-derived substrates), topographic microclimate (lush northerly slopes and streamsides to hot, dry southerly and southwesterly slopes), and elevation (500–2100 m on diorite soils, 400–1200 m on serpentine and gabbro soils). He also sampled the gradient from coastal to interior climates, but his coastal samples were too sparse for analysis.

Whittaker selected sites haphazardly and established 1000-m<sup>2</sup> plots within which he recorded numbers of woody plants by species and lists of herb species present in the plot. He also counted herb individuals and estimated herb cover by species in 25, 1-m<sup>2</sup> subplots along the plot center lines. We used his herb count data from the subplots to calculate local species richness and abundances for each plot. For full descriptions of the study system and Whittaker's data, see Whittaker (1960), Damschen et al. (2010), Harrison et al. (2010), and Grace et al. (*in press*).

We analyzed each pairwise combination of the three environmental gradients: elevation, topographic microclimate (Whittaker's 'topographic moisture gradient' or TMG, on which low scores indicate lush conditions and high scores indicate harsh conditions), and soil (diorite vs. gabbro vs. serpentine). Tree densities confirm that plant productivity increases with decreasing elevation and TMG scores, and also with the progression of soil fertility from serpentine to gabbro to diorite (Whittaker 1960; Grace et al., *in press*).

The data do not contain all possible combinations of environmental factors (e.g., there are no gabbro or serpentine plots >1200 m elevation, so comparable subsets of data were used for each analysis as follows (also see Table 1). Topographic microclimate (TMG) and elevation, when considered as Env2, were divided into discrete categories (soil is already categorical). For topography, we used four categories of Whittaker's topographic moisture gradient:  $\text{TMG}_1 < 0.15$ ,  $0.15 < \text{TMG}_2 \leq 0.45$ ,  $0.45 < \text{TMG}_3 \leq 0.75$ ,  $\text{TMG}_4$

Table 1. Number of plots at different levels of each environmental gradient.

Elevation	Soil type	Topographic moisture gradient			
		(1) <0.15	(2) 0.15–0.449	(3) 0.45–0.75	(4) >0.75
<700 m	Diorite	4	12	9	11
	Gabbro	5	11	20	11
	Serpentine	4	6	6	9
700–1220 m	Diorite	7	21	28	24
	Gabbro	0	0	2	2
	Serpentine	1	12	10	7
>1220 m	Diorite	5	39	40	43
	Gabbro	0	0	0	0
	Serpentine	0	0	0	0

> 0.75 (see Damschen et al. 2010 for a full description of TMG scores). For elevation, we used different cutoffs between low and high for the separate analyses with TMG and soil. For elevation vs. TMG, only sites on diorite soils were analyzed, and we classified plots at <1220 m elevation as low and plots  $\geq$ 1220 m as high. For elevation vs. soil, we used only sites <1220 m to ensure a comparable range of elevations for different soils, and we set the low vs. high cutoff at  $\sim$ 700 m; plots on gabbro soils were excluded from this analysis as only four plots occurred at  $\geq$ 700 m.

### Statistical analyses

We compared results obtained from beta metrics using relative abundance data (Bray-Curtis), and presence-absence data (Whittaker's beta; Jaccard coefficient). We report the Bray-Curtis results first, since abundance-based metrics should be less affected than presence-absence metrics by the random occurrences of rare species (Jost 2007), and thus should be most indicative of deterministic patterns. When considering presence-absence-based results, we present Whittaker's beta wherever possible for the sake of continuity with Whittaker (1960), and where this is not possible (i.e., when using PRIMER software) we present Jaccard's index of dissimilarity, which is a monotonic transformation of Whittaker's beta (Vellend 2001). We use multiple analytic techniques, as described below, to relate these dissimilarity metrics to the abiotic environmental variables.

To test Hypothesis 1 (i.e., whether Env1 and Env2 have interactive effects on beta diversity), we used PERMANOVA models, which are multivariate analogues of ANOVA with signifi-

cance testing via permutation to accommodate the frequent violation of the assumptions of MANOVA in community data (Anderson 2001). PERMANOVA with multiple predictor variables is a semi-parametric technique in which significant effects can be due either to differences in the average species composition between levels of a factor (i.e., structured beta diversity), or differences in the among-plot variability in species composition across different levels of a factor (i.e., unstructured beta) (Anderson et al. 2008). Thus, we pose the general hypothesis that multiple environmental gradients have interactive effects on beta diversity, and subsequently (hypotheses 2 and 3) focus on distinguishing structured and unstructured beta. For each pair of environmental variables, we analyzed Bray-Curtis dissimilarities between each pair of sites as a function of the two environmental variables and their interaction. Both environmental variables were treated as categorical (categories described below); identical results in terms of significance tests were found when either environmental variable was treated as continuous, or when we used the Jaccard presence-absence metric in place of the Bray-Curtis metric (results not shown). These analyses were implemented in PERMANOVA+ for PRIMER (Anderson et al. 2008).

To test Hypothesis 2 (i.e., whether 'structured'  $\beta_{\text{Env1}}$  increases with productivity on Env2), for the subset of plots at each categorical level of Env2, we expressed  $\beta_{\text{Env1}}$  in three ways: (i) The strength of correlation between pairwise Bray-Curtis community dissimilarities and pairwise differences in Env1 ("Mantel's  $r$ "); 95% confidence intervals for Mantel's  $r$  were used to assess differences among levels of Env2. (ii) The percent

variance in species composition explained by Env1 in constrained ordinations (“% variance”); we report results for constrained analyses of principal co-ordinates (CAP) based on a matrix of Bray-Curtis dissimilarities between each pair of sites (capscale function in *vegan* v. 1.17–3 for R v. 2.11.1). (iii) The mean pairwise Bray-Curtis dissimilarity between pairs of plots at different levels of Env1 divided by the mean pairwise dissimilarity of plots at the same level of Env1 (“pairwise  $\beta$  ratio”). These methods cover the range of techniques for measuring structured beta diversity (Anderson et al. *in press*). For both (ii) and (iii), statistical significance was assessed using randomization tests in which the values of Env1 were permuted across sites, with the constraint that the number of plots at each level of Env1 and Env2 remain unchanged. We repeated all three analyses using Whittaker’s beta.

To test Hypothesis 3 (i.e., whether ‘unstructured’  $\beta$  at a given level of Env1 increases with productivity on Env2), we calculated multivariate dispersion (Anderson et al. 2006) among plots at different levels of each environmental factor, using the PERMDISP function in PRIMER (Anderson et al. 2008). Starting with a matrix of community dissimilarities between all pairs of plots (we used both Bray-Curtis and Jaccard), multivariate dispersion is the average dissimilarity of each plot to the centroid of a defined group of plots (e.g., plots at low elevation, on diorite, and low TMG). By starting with the matrix of pairwise dissimilarities, as in each of our other analyses, multivariate dispersion as a metric of unstructured beta diversity maximizes comparability across analyses. In addition, multivariate dispersion is closely related to the method of calculating the mean pairwise dissimilarity among plots, but avoids the issue of inflating the sample size given that the number of pairwise comparisons is much greater than the number of plots (Anderson et al. 2006). Consistent with our data subsets described earlier, two analyses were conducted. First, using the 1220 m elevational cutoff, multivariate dispersion was calculated for 16 combinations of the three environmental factors: 3 soil types  $\times$  4 TMG classes (all at low elevation) + 4 TMG classes at high elevation. Second, using only sites <1220 m and a 700 m elevational cutoff, multivariate

dispersion was calculated for diorite and serpentine soils at low and high elevation.

## RESULTS

Hypothesis 1 was fully supported. We found that pairs of environmental factors consistently had interactive effects on beta diversity. For all three pairwise combinations of environmental variables, PERMANOVA analyses revealed all main effects and interactions between the two variables to be highly significant ( $p < 0.001$ ; Appendix: Table A1).

Hypothesis 2 was partly supported. More productive lower elevations were associated with significantly higher levels of topographic beta diversity ( $\beta_{\text{TMG}}$ ) in all three analyses, and also with nonsignificant trends toward higher levels of soil beta diversity ( $\beta_{\text{soil}}$ ) (Fig. 1). Likewise, more productive topographic microclimates (north slopes and streambanks) were associated with significantly higher levels of soil beta diversity ( $\beta_{\text{soil}}$ ) and elevational beta diversity ( $\beta_{\text{elev}}$ ) (Fig. 1). There was no consistent relationship of soil fertility to beta diversity, however; intermediately fertile gabbro soils showed the lowest levels of topographic beta diversity ( $\beta_{\text{TMG}}$ ) in two of three analyses, and there was no trend toward an influence of soil fertility on elevational beta diversity ( $\beta_{\text{elev}}$ ) (Fig. 1). Results were qualitatively the same when Whittaker’s beta was used instead of the Bray-Curtis metric (Appendix: Fig. A1).

Hypothesis 3 was not supported. There were significant differences in multivariate dispersion (based on Bray-Curtis dissimilarities) among sets of plots in different environmental conditions for the first analysis on 16 combinations of elevation, TMG, and soil type ( $F = 4.43$ ,  $df = 15$ ,  $333$ ,  $p < 0.001$ ; Fig. 2), but not in the second analysis using 4 combinations of elevation and soil type ( $F = 2.13$ ,  $df = 3$ ,  $172$ ,  $p = 0.16$ ; Fig. 2). Many of the pairwise comparisons in Fig. 2 were statistically significant (Appendix: Table A2). There was a slight tendency for greater unstructured beta diversity at high TMG scores (dry, hot sites), regardless of elevation or soil type, but the direction of the effects of each factor depended idiosyncratically on the other environmental factors (Fig. 2, Appendix: Table A2). Results using multivariate dispersion based on Jaccard’s

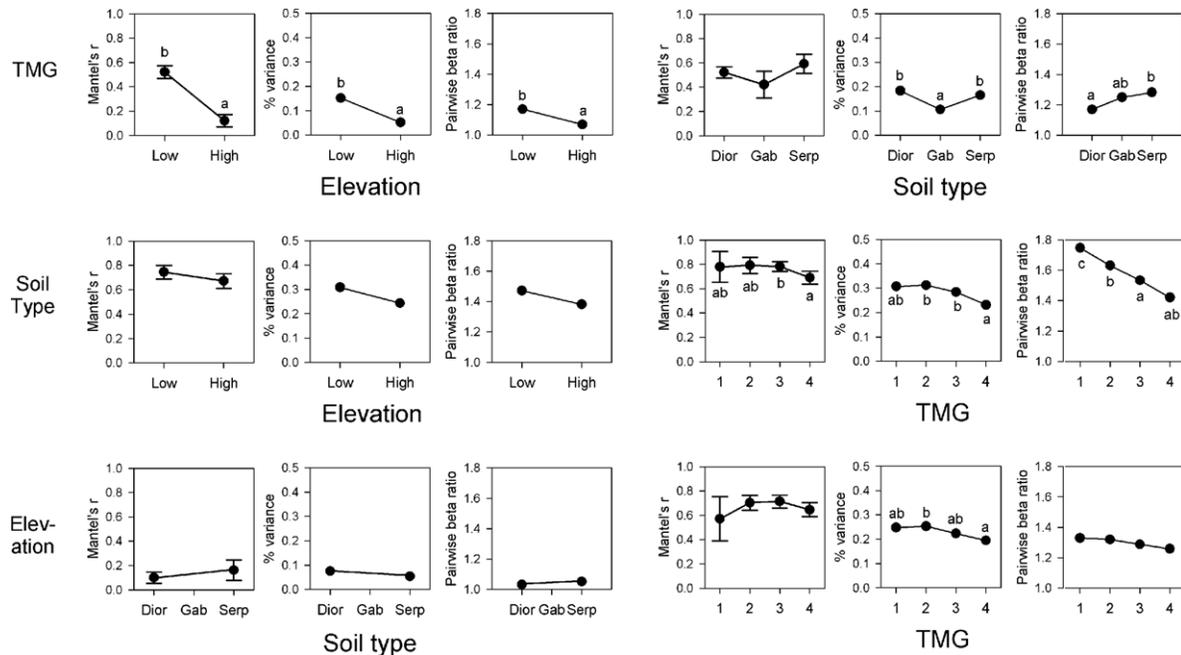


Fig. 1. Beta diversity along one environmental gradient (Env1, rows) at different levels of a second environmental factor (Env2, x-axes). Mantel's  $r$  is the correlation between pairwise Bray-Curtis dissimilarities and pairwise environmental differences, with 95% confidence intervals shown as error bars. “% variance” is the proportion of variance explained by Env1 in a constrained analysis of principal co-ordinates based on Bray-Curtis dissimilarities. “Pairwise beta ratio” is the mean Bray-Curtis dissimilarity across different levels of Env1 divided by the mean dissimilarity within levels of Env1. Different letters indicate statistically significant differences ( $p < 0.05$ ); note that these were calculated for each pair of levels separately, such that two relatively similar values can be significantly different while more dissimilar values may not be statistically different (depending on sample size in the two groups, see Table 1).

dissimilarities were closely comparable to those obtained using Bray-Curtis dissimilarities (results not shown).

## DISCUSSION

Our results suggest that beta diversity, and thus all geographic patterns in diversity, cannot be fully understood without considering the interactive effects of multiple environmental gradients on community composition. Thus, not only are “mountain passes higher in the tropics”, as Janzen (1967) suggested, but our study suggests that topography may be “steeper” at low elevations, while elevation may be “higher” and serpentine soil “harsher”, i.e., these variables exert stronger influences on community composition, in moist and productive topographic positions compared with hot and dry ones.

Likewise, previous observations on plant communities suggest that serpentine bedrock supports more distinctive floras in intermediately wet climates (Kruckeberg 1969, del Moral 1982, Stebbins and Hrusa 1995), topographic effects likewise are enhanced by a wet or intermediate climate (Stebbins and Hrusa 1995, Harrison et al. 2006), and climatic and topographic gradients are more influential at temperate than Arctic latitudes (Qian and Ricklefs 2007, Qian et al. 2009). Our results also agree with others that have found positive productivity-beta diversity relationships (Chase and Leibold 2002, Chalcraft et al. 2004, Chase 2010), except that our results emphasize the roles of deterministic rather than stochastic forces in community assembly. We found productivity to be associated with greater ‘structured’ beta diversity along environmental gradients, indicating that individual species

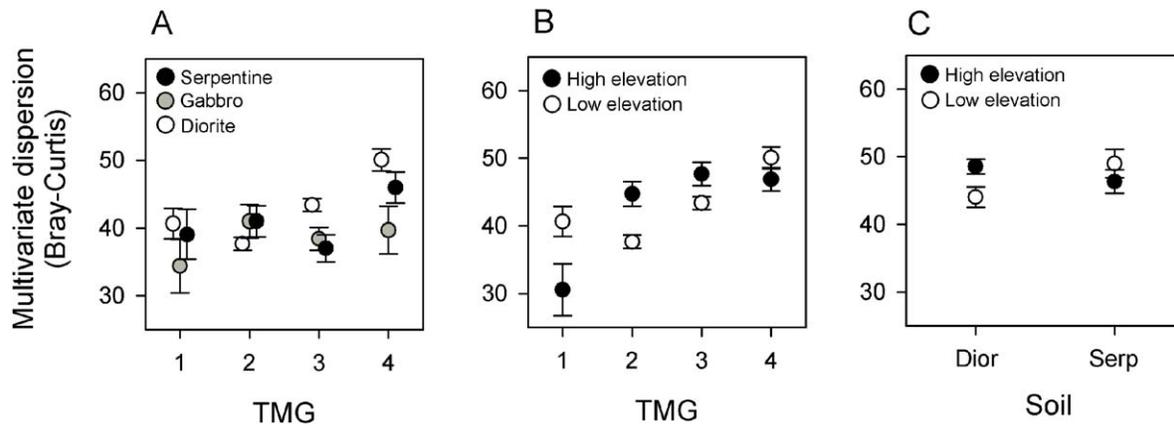


Fig. 2. Unstructured beta diversity, measured as multivariate dispersion (Anderson et al. 2006) based on Bray-Curtis dissimilarities within sets of plots defined by combinations of elevation, TMG, and soil type. Each pairwise comparison of the three environmental variables is shown in a separate panel. Panels A and B show the results for a single analysis (note that the results for low elevation, diorite plots appear on both panels), with significant overall differences ( $p < 0.001$ ) and many significant pairwise differences (Table A2); panel C shows the results of a second analysis, in which there were no overall significant differences ( $p = 0.16$ ).

occupied narrower portions of these gradients (i.e., their habitat specialization was greater) in productive microclimates. We did not find any consistent relationship of productivity to unstructured beta diversity (i.e., community divergence among environmentally similar plots).

Productivity is associated with increased numbers of individuals and hence with increased alpha (local) diversity, both in this study system (Grace et al., *in press*) and in many others (Stevens and Carson 1999, Gotelli and Colwell 2001). All else being equal, this should produce lower, rather than higher, beta diversity at higher levels of productivity. Together with the robustness of our results to presence-absence-based and abundance-based metrics, this consideration reinforces that our results genuinely reflect greater habitat specialization at high productivity rather than being an artifact of changes in species abundances.

It is noteworthy that we found increases in structured beta diversity along climate-related productivity gradients, i.e., topography and elevation, but not soil fertility. Productive climates, in which water is plentiful and growing-season temperatures are mild, are associated with high regional floristic diversity, both globally (Hawkins et al. 2003, Currie et al. 2004), and in the floristic province of which this study

system is part (Harrison and Grace 2007). Conversely, there is no general tendency for regional diversity to be high on fertile soils, and the opposite is readily observed in regions where fertile soils are rare (Pärtel 2002). Along our soil gradient, the lowest beta diversity was observed on the intermediately fertile soil, gabbro, which is very rare regionally and also supports the lowest alpha diversity (Grace et al., *in press*). In fact, our results combined with those of Grace et al. (*in press*) generally support the observation of Whittaker (1960: p. 322) that alpha and beta diversities tend to covary positively in the communities he sampled.

These considerations suggest that high beta diversity may be associated not with productivity per se, but with the richness of the regional species pool, which may spill over to enhance richness both within (alpha) and among (beta) communities. MacArthur (1965) proposed that competitive pressure from a larger regional species pool would lead to greater habitat specialization, so that “as the fauna increases, there will be more and more between-habitat diversity, and eventually all new diversity will be between-habitat” (p. 523). He argued that not only his own data for birds on islands and mainlands, but also Whittaker’s (1960) study, supported such an interpretation (we note that he

did not, however, elaborate on his brief remark about Whittaker's study). Because it is intrinsically macroevolutionary, this 'top-down' view of variation in beta diversity is harder to test than the 'bottom-up' view that best suits the scale of ecological experiments (Loreau 2000). However, it may be more consistent with the historical explanations that have been proposed for the existences of the Earth's biodiversity hotspots (e.g., Stebbins and Hrusa 1995, Qian et al. 2005). Indeed, Whittaker (1961) maintained that the extraordinary botanical richness of the Siskiyou was ultimately due to long-term climatic stability and an intermediate location between major biogeographic provinces, while the role of abiotic environmental gradients lay in spatially organizing, rather than generating, this diversity.

We conclude by proposing that in cases where independent and replicated estimates of regional species diversity are available, it may be worthwhile to reevaluate the productivity-beta diversity relationship under the hypothesis that regional species pools are a driving force, similar to the reexamination that has taken place for our understanding of diversity in general (Ricklefs 2004, Harrison and Cornell 2008). We have demonstrated that environmental gradients interact in their effects on species composition, and that beta diversity may increase with productivity. However, productivity might simply be a correlate of underlying causes rooted in historical biogeography rather than an ecological cause in itself.

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APPENDIX

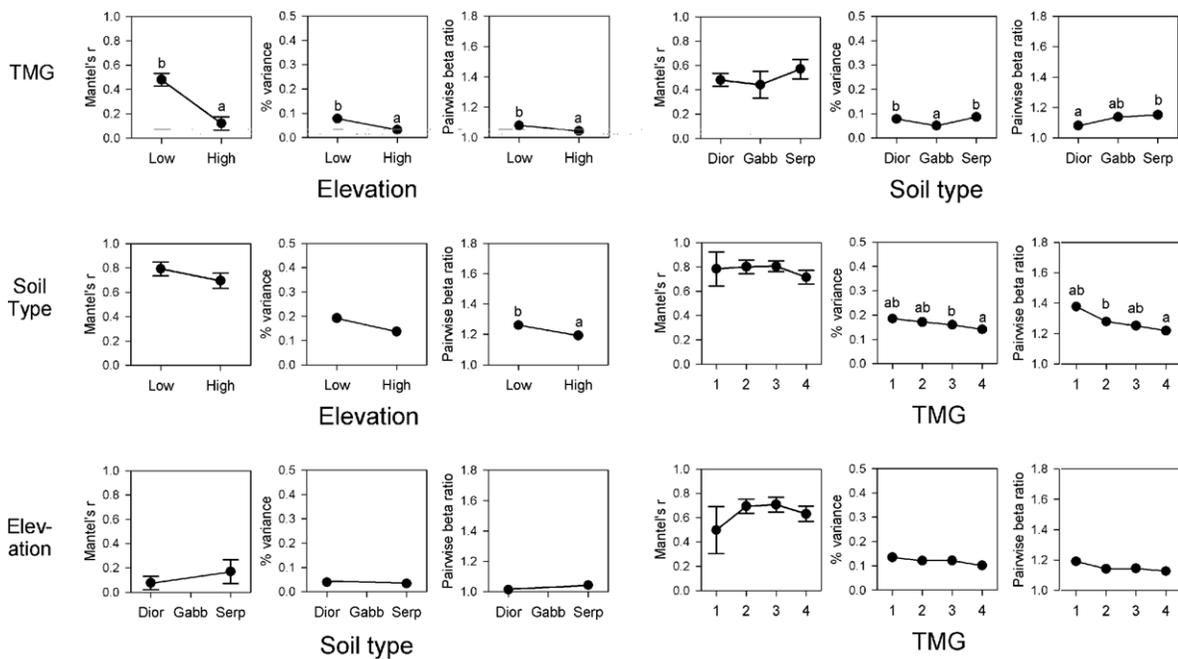


Fig. A1. Results as in Fig. 1, except using Whittaker's (1960) metric of beta diversity as the pairwise measure of community dissimilarity.

Table A1. PERMANOVA models testing for interactions between pairs of environmental factors on species composition: (a) elevation and topographic moisture gradient, (b) topographic moisture gradient and soil; (c) soil and elevation.

Source	df	SS	MS	F†	p
a)					
Elev	1	64299	64299	29.562	0.0002
TMG	3	50111	16704	7.6797	0.0002
<b>Elev × TMG</b>	<b>3</b>	<b>31888</b>	<b>10629</b>	<b>4.8869</b>	<b>0.0002</b>
Residual	235	511130	2175		
Total	242	707560			
b)					
TMG	3	42365	14122	7.2833	0.0002
Soil	2	178530	89264	46.038	0.0002
<b>TMG × Soil</b>	<b>6</b>	<b>66096</b>	<b>11016</b>	<b>5.6816</b>	<b>0.0002</b>
Residual	210	407170	1939		
Total	221	764680			
c)					
TMG‡	1	44669	44669	20.854	0.0002
Soil	1	134890	134890	62.975	0.0002
Elev	1	6769	6769	3.1603	0.0004
<b>Soil × Elev</b>	<b>1</b>	<b>6273</b>	<b>6273</b>	<b>2.9287</b>	<b>0.0004</b>
Residual	171	366280	2142		
Total	175	571930			

Note: Results are based on Bray-Curtis pairwise site similarities with raw abundances ( $\log_{10} + 1$ )-transformed, type III sums of squares, and 4999 permutations of residuals under a reduced model. The interaction term of interest in each model is highlighted in bold text. Subsets of data used in each model explained in text.

† These are pseudo-F statistics sensu Anderson et al. (2008).

‡ TMG was used as a continuous covariate in this analysis.

Table A2. Pairwise comparisons for multivariate dispersion in species composition (based on Bray-Curtis dissimilarities) between 16 sets of plots defined by combinations of elevation, TMG, and soil type.

Group 1			Group 2			t	p
Elevation	TMG	Soil type	Elevation	TMG	Soil type		
Low	1	Dior	Low	3	Dior	1.27	0.315
Low	1	Dior	Low	4	Dior	3.02	<b>0.015</b>
Low	1	Dior	Low	2	Dior	1.40	0.244
Low	1	Dior	High	4	Dior	1.73	0.169
Low	1	Dior	High	3	Dior	1.99	0.120
Low	1	Dior	High	2	Dior	1.13	0.338
Low	1	Dior	High	1	Dior	2.43	0.056
Low	1	Dior	Low	3	Serp	1.19	0.281
Low	1	Dior	Low	1	Serp	0.39	0.757
Low	1	Dior	Low	2	Serp	0.10	0.921
Low	1	Dior	Low	4	Serp	1.59	0.162
Low	1	Dior	Low	4	Gab	0.22	0.853
Low	1	Dior	Low	2	Gab	0.10	0.924
Low	1	Dior	Low	3	Gab	0.78	0.493
Low	1	Dior	Low	1	Gab	1.49	0.239
Low	3	Dior	Low	4	Dior	3.63	<b>0.001</b>
Low	3	Dior	Low	2	Dior	4.13	<b>0.001</b>
Low	3	Dior	High	4	Dior	1.71	0.129
Low	3	Dior	High	3	Dior	2.12	0.062
Low	3	Dior	High	2	Dior	0.65	0.554
Low	3	Dior	High	1	Dior	4.34	<b>0.005</b>
Low	3	Dior	Low	3	Serp	3.22	<b>0.002</b>
Low	3	Dior	Low	1	Serp	1.47	0.458
Low	3	Dior	Low	2	Serp	1.13	0.300
Low	3	Dior	Low	4	Serp	1.24	0.273
Low	3	Dior	Low	4	Gab	1.41	0.212
Low	3	Dior	Low	2	Gab	1.08	0.390
Low	3	Dior	Low	3	Gab	2.75	<b>0.011</b>
Low	3	Dior	Low	1	Gab	3.02	0.063

Table A2. Continued.

Group 1			Group 2			t	p
Elevation	TMG	Soil type	Elevation	TMG	Soil type		
Low	4	Dior	Low	2	Dior	6.51	<b>0.000</b>
Low	4	Dior	High	4	Dior	1.32	0.229
Low	4	Dior	High	3	Dior	1.00	0.361
Low	4	Dior	High	2	Dior	2.20	<b>0.044</b>
Low	4	Dior	High	1	Dior	4.35	<b>0.002</b>
Low	4	Dior	Low	3	Serp	4.77	<b>0.000</b>
Low	4	Dior	Low	1	Serp	2.47	0.105
Low	4	Dior	Low	2	Serp	3.28	<b>0.004</b>
Low	4	Dior	Low	4	Serp	1.45	0.197
Low	4	Dior	Low	4	Gab	3.08	<b>0.009</b>
Low	4	Dior	Low	2	Gab	2.86	<b>0.022</b>
Low	4	Dior	Low	3	Gab	4.81	<b>0.000</b>
Low	4	Dior	Low	1	Gab	3.49	<b>0.015</b>
Low	2	Dior	High	4	Dior	4.28	<b>0.000</b>
Low	2	Dior	High	3	Dior	4.73	<b>0.000</b>
Low	2	Dior	High	2	Dior	3.26	<b>0.004</b>
Low	2	Dior	High	1	Dior	2.47	0.114
Low	2	Dior	Low	3	Serp	0.33	0.771
Low	2	Dior	Low	1	Serp	0.48	0.807
Low	2	Dior	Low	2	Serp	1.55	0.153
Low	2	Dior	Low	4	Serp	3.90	<b>0.000</b>
Low	2	Dior	Low	4	Gab	0.75	0.513
Low	2	Dior	Low	2	Gab	1.50	0.211
Low	2	Dior	Low	3	Gab	0.40	0.702
Low	2	Dior	Low	1	Gab	1.13	0.537
High	4	Dior	High	3	Dior	0.32	0.785
High	4	Dior	High	2	Dior	0.87	0.464
High	4	Dior	High	1	Dior	3.11	<b>0.021</b>
High	4	Dior	Low	3	Serp	3.19	<b>0.006</b>
High	4	Dior	Low	1	Serp	1.49	0.280
High	4	Dior	Low	2	Serp	1.93	0.099
High	4	Dior	Low	4	Serp	0.30	0.792
High	4	Dior	Low	4	Gab	1.96	0.102
High	4	Dior	Low	2	Gab	1.62	0.192
High	4	Dior	Low	3	Gab	3.13	<b>0.007</b>
High	4	Dior	Low	1	Gab	2.37	0.087
High	3	Dior	High	2	Dior	1.18	0.331
High	3	Dior	High	1	Dior	3.34	<b>0.031</b>
High	3	Dior	Low	3	Serp	3.51	<b>0.004</b>
High	3	Dior	Low	1	Serp	1.69	0.237
High	3	Dior	Low	2	Serp	2.22	0.060
High	3	Dior	Low	4	Serp	0.55	0.635
High	3	Dior	Low	4	Gab	2.20	0.072
High	3	Dior	Low	2	Gab	1.88	0.137
High	3	Dior	Low	3	Gab	3.48	<b>0.003</b>
High	3	Dior	Low	1	Gab	2.59	0.098
High	2	Dior	High	1	Dior	2.70	0.076
High	2	Dior	Low	3	Serp	2.48	<b>0.033</b>
High	2	Dior	Low	1	Serp	1.08	0.412
High	2	Dior	Low	2	Serp	1.21	0.284
High	2	Dior	Low	4	Serp	0.39	0.741
High	2	Dior	Low	4	Gab	1.35	0.248
High	2	Dior	Low	2	Gab	1.03	0.391
High	2	Dior	Low	3	Gab	2.32	<b>0.040</b>
High	2	Dior	Low	1	Gab	1.97	0.173
High	1	Dior	Low	3	Serp	1.55	0.251
High	1	Dior	Low	1	Serp	1.60	0.216
High	1	Dior	Low	2	Serp	2.18	0.085
High	1	Dior	Low	4	Serp	3.31	<b>0.007</b>
High	1	Dior	Low	4	Gab	1.48	0.265
High	1	Dior	Low	2	Gab	2.34	0.069
High	1	Dior	Low	3	Gab	1.97	0.162
High	1	Dior	Low	1	Gab	0.69	0.586
Low	3	Serp	Low	1	Serp	0.49	0.737
Low	3	Serp	Low	2	Serp	1.29	0.255
Low	3	Serp	Low	4	Serp	2.92	<b>0.010</b>

Table A2. Continued.

Group 1			Group 2			t	p
Elevation	TMG	Soil type	Elevation	TMG	Soil type		
Low	3	Serp	Low	4	Gab	0.69	0.548
Low	3	Serp	Low	2	Gab	1.25	0.255
Low	3	Serp	Low	3	Gab	0.53	0.631
Low	3	Serp	Low	1	Gab	0.63	0.678
Low	1	Serp	Low	2	Serp	0.41	0.752
Low	1	Serp	Low	4	Serp	1.49	0.300
Low	1	Serp	Low	4	Gab	0.10	0.942
Low	1	Serp	Low	2	Gab	0.44	0.729
Low	1	Serp	Low	3	Gab	0.16	0.906
Low	1	Serp	Low	1	Gab	0.86	0.468
Low	2	Serp	Low	4	Serp	1.53	0.174
Low	2	Serp	Low	4	Gab	0.33	0.776
Low	2	Serp	Low	2	Gab	0.00	0.997
Low	2	Serp	Low	3	Gab	0.93	0.398
Low	2	Serp	Low	1	Gab	1.37	0.296
Low	4	Serp	Low	4	Gab	1.55	0.174
Low	4	Serp	Low	2	Gab	1.44	0.214
Low	4	Serp	Low	3	Gab	2.71	<b>0.014</b>
Low	4	Serp	Low	1	Gab	2.47	<b>0.044</b>
Low	4	Gab	Low	2	Gab	0.29	0.814
Low	4	Gab	Low	3	Gab	0.37	0.744
Low	4	Gab	Low	1	Gab	0.86	0.500
Low	2	Gab	Low	3	Gab	0.87	0.447
Low	2	Gab	Low	1	Gab	1.46	0.258
Low	3	Gab	Low	1	Gab	1.01	0.451

*Note:* Means and standard errors for each combination listed in this table are shown in Fig. 1. P-values were calculated with 4999 permutations using the PERMDISP function in PERMANOVA+ for PRIMER v. 6 (Anderson et al. 2008), and significant differences ( $p < 0.05$ ) are shown in bold.