

Biogeographic Affinity Helps Explain Productivity-Richness Relationships at Regional and Local Scales

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ABSTRACT: The unresolved question of what causes the observed positive relationship between large-scale productivity and species richness has long interested ecologists and evolutionists. Here we examine a potential explanation that we call the biogeographic affinity hypothesis, which proposes that the productivity-richness relationship is a function of species' climatic tolerances that in turn are shaped by the earth's climatic history combined with evolutionary niche conservatism. Using botanical data from regions and sites across California, we find support for a key prediction of this hypothesis, namely, that the productivity-species richness relationship differs strongly and predictably among groups of higher taxa on the basis of their biogeographic affinities (i.e., between families or genera primarily associated with north-temperate, semiarid, or desert zones). We also show that a consideration of biogeographic affinity can yield new insights on how productivity-richness patterns at large geographic scales filter down to affect patterns of species richness and composition within local communities.

Keywords: species diversity, species richness, productivity, niche conservatism, regional and local richness, serpentine, plants.

Productivity is the strongest and most consistent predictor of regional-scale patterns in terrestrial species richness (Wright et al. 1993; Francis and Currie 2003; Hawkins et al. 2003; Currie et al. 2004). Terrestrial productivity is, in turn, globally controlled by solar energy and water availability, with greater control by water at lower latitudes and by energy at higher latitudes. The reason for its strongly positive effect on regional species richness is still unknown. Because productivity decreases strongly from the equator to the poles, this question is also closely linked to one of

the oldest questions in ecology and evolution: what causes the powerful relationship between latitude and species richness (Hillebrand 2004)? Currie et al. (2004) proposed three hypotheses for the productivity-richness relationship, which are applicable to the latitudinal gradient as well: (1) more individuals can coexist at higher levels of productivity, which translates into more species (the "more individuals" hypothesis); (2) rates of evolutionary diversification increase with productivity because of faster speciation or slower extinction or both (the "faster diversification" hypothesis); and (3) more species are physiologically capable of living in productive than in unproductive conditions (the "tolerance" hypothesis).

An important and little-recognized clue to the mechanism of the productivity-richness relationship is its strong dependence on spatial scale (Gross et al. 2000; Chase and Leibold 2002; Harrison et al. 2006a). Within local field plots, productivity-richness relationships are typically either weakly positive, negative, unimodal, or neutral (e.g., Grace 1999; Waide et al. 1999; Gross et al. 2000; Mittelbach et al. 2001) in contrast to the strong positive relationships that are seen at regional scales. In meta-analyses of the latitude-richness and productivity-richness relationships, respectively, Hillebrand (2004) and R. Field et al. (unpublished manuscript) found significantly stronger patterns at regional than at local scales. We suggest that this scale dependence casts doubt on purely ecological explanations, such as the more individuals hypothesis (Currie et al. 2004); because most ecological explanations propose that the relationship arises from local processes, they lead to the expectation that it should be at least as strong locally as it is regionally. In contrast, evolutionary or biogeographic explanations more readily predict strong regional patterns that filter down to create weaker local patterns.

A strong evolutionary and biogeographic framework is widely recognized as being necessary to improve our understanding of species richness patterns (Ricklefs 2004). As one example, Wiens and Donoghue (2004) recently proposed the "tropical conservatism" hypothesis for the latitudinal richness gradient. They argue that most modern families and other higher taxa originated under the trop-

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ical-like conditions that prevailed over most of the earth during the Tertiary period and that only a minority of these higher taxa have since evolved traits allowing them to inhabit the cooler and more arid climates of extratropical zones (for similar arguments, see also Farrell et al. 1992; Latham and Ricklefs 1993; Ricklefs and Renner 1994). Thus, Wiens and Donoghue (2004) argue that a key reason for the latitudinal richness gradient is niche conservatism, or the tendency of modern species to retain ancestral traits that govern niche boundaries. In support of this idea, it has been found that many temperate clades are relatively young and are nested within older tropical clades (Latham and Ricklefs 1993), that older clades show stronger climate-richness relationships than do younger ones (Hawkins et al. 2005, 2006), and that certain key traits such as frost tolerance may predictably distinguish temperate from tropical clades (Fine 2001).

We propose that Wiens and Donoghue's (2004) hypothesis, which was originally intended to explain the latitudinal richness gradient, can be linked to the tolerance hypothesis of Currie et al. (2004) and that the two together provide an evolutionary framework to explain the broader phenomenon of the productivity-richness relationship. Put simply, this combined hypothesis states that more species belong to higher taxa that evolved under mild and wet conditions than under either cold or dry conditions and that this is why we now find more species in mild and wet than in cold or dry regions. We will refer to this as the "biogeographic affinity" hypothesis because it predicts that the change in species richness along climatically driven productivity gradients will differ in predictable ways among higher taxa with different biogeographic affinities. It should be strongest among higher taxa that diversified under mild and wet historical climatic regimes, which is true of the majority, and weakest among the minority of higher taxa that diversified after adaptive breakthroughs permitted them to tolerate cooler or drier regimes.

As an example, we would predict that along a geographic gradient of decreasing productivity that is caused by decreasing temperature, such as ascending elevation in the tropics, the overall decline in species richness can be decomposed into a rapid decline in taxa that are primarily or entirely tropical and a slower decline—or even an increase over some range of elevations—in taxa that radiated in the temperate zone after acquiring traits that adapted them to cooler niches (for an example, see Wiens 2007). Where productivity is controlled mainly by rainfall rather than by temperature, such as along longitudinal gradients from wet coastal to dry interior environments, we would predict similar patterns with respect to rainfall (for examples, see Hawkins et al. 2007). That is, the overall decline in species richness with declining rainfall and productivity may mask a stronger decline among higher taxa

that diversified under wet climates and a weaker decline—or possibly even an increase—among higher taxa that diversified within drier climates after acquiring traits conferring drought tolerance. Such differences in the productivity-richness relationship at higher taxonomic levels would demonstrate that this relationship is not so much a universal ecological law as it is a function of the evolutionary history of taxa.

Alternatively, the biogeographic affinity hypothesis may be false even if the tolerance hypothesis is true. Independent of ancestry, there may simply be a greater number of trait combinations that permit organisms to survive under warm and moist than cold or arid conditions; a model by Kleidon and Mooney (2000) illustrates this argument and links it to global patterns in plant species richness. The predictions of the biogeographic affinity hypothesis also should not be supported under the other proposed explanations for the productivity-richness relationship, such as the more individuals or faster diversification hypotheses (Currie et al. 2004).

We tested the biogeographic affinity hypothesis with a data set previously used for relating regional and local plant species richness patterns to environmental gradients in California (Harrison et al. 2006a, 2006b, 2006c). As is the case in much of North America (Hawkins et al. 2003), productivity in California is broadly controlled by rainfall rather than by solar energy, and so we expect any productivity-richness patterns to be driven by rainfall rather than by temperature. Productivity was measured using the remotely sensed normalized difference vegetation index (NDVI; Hansen et al. 2004). Not surprisingly, NDVI in our data set was strongly related to mean annual rainfall but was unrelated to any measure of temperature. Our earlier analyses of these data supported the two major generalizations discussed above: first, the rainfall-associated productivity gradient was by far the strongest predictor of regional species richness, and second, there was no direct effect of rainfall or productivity on species richness at the local scale (Harrison et al. 2006c).

In this study we subdivide our Californian botanical data set into species belonging to families or genera of different biogeographic affinity: north-temperate (NT) or Arcto-Tertiary, semiarid or Madro-Tertiary (MT), Mediterranean or California Floristic Province (CFP), and warm temperate desert (WTD). It is believed that the higher taxa of Arcto-Tertiary affinity evolved under mesic conditions, while the taxa of MT and CFP affinities evolved under semiarid conditions and the WTD families evolved under arid conditions (see "Study System and Methods" for details). We test the biogeographic affinity hypothesis by asking whether contemporary species richness in these four groups shows the predicted differences in relationships to productivity (NDVI) across California. Specifi-

cally, we expect the strongest positive NDVI-richness relationship in the NT taxa and the least positive relationship in the WTD taxa, with intermediate relationships for the other two. (We have no *a priori* basis to predict whether the latter three relationships will be weakly positive, neutral, or negative; but see “Discussion.”) Conversely, we would predict no such differences among these four groups if the productivity-richness relationship is due to an effect of productivity *per se* on either the potential for ecological coexistence or the rate of evolutionary diversification (fig. 1).

Our primary concern in this analysis is at the regional scale, where a strong productivity-richness relationship is found, so we first asked (1) at the regional scale, is the relationship between species richness and NDVI more strongly positive for taxa of mesic (NT) affinity than for taxa of semiarid (MT and CFP) or arid (WTD) affinity? Because we would also like to know how any such regional pattern may filter down to affect local communities, we next asked (2) at the local scale, is NDVI associated with variation in community composition even though it is not directly associated with variation in total species richness? Or, more specifically, (3) in local communities, as NDVI increases, do NT species become increasingly dominant relative to MT, CFP, and WTD species? Finally, we asked (4) is our evidence consistent with competition as an additional factor shaping the trends in species composition at the local scale?

Study System and Methods

Serpentine Soils and Their Flora in California

The original purpose for which we assembled our database was to analyze the effects of the spatial configuration of a

naturally patchy habitat, serpentine soil, on the regional and local species richness of its flora. (For a map of our study regions and localities and for complete details on the assembly of our database, see Harrison et al. 2006c.) Serpentine or ultramafic rocks are derived from the oceanic crust and tend to be found in zones of convergence between tectonic plates. In California, serpentine is found in patchy outcrops throughout the Klamath Range, North and South Coast ranges, and Sierra Nevada foothills of California. Soils derived from these rocks contain high levels of magnesium and heavy metals and low concentrations of primary nutrients, leading to the exclusion of many species from the surrounding flora. In some parts of the world, serpentine soils may also support rich floras of edaphic endemics.

Of the more than 5,000 native species in California, about 1,100 are tolerant of serpentine, including roughly 250 that are restricted (endemic) to the substrate (Kruckeberg 1984; Safford et al. 2005; Harrison et al. 2006c). In this study we confine most of our analyses to native species capable of growing on serpentine, that is, the approximately 1,100 “tolerators,” but we found no evidence that these behaved substantially differently in terms of their productivity and richness patterns than did the >5,000 Californian species as a whole.

Regional and Local Databases

Our regional data consisted of plant species richness and multiple environmental variables measured for 86 contiguous areal units (regions) of California. Regional boundaries and regional species richness data were derived from two existing floristic databases as described by Viers et al. (2006). Regions ranged from 81 to 5,305 km² in area.

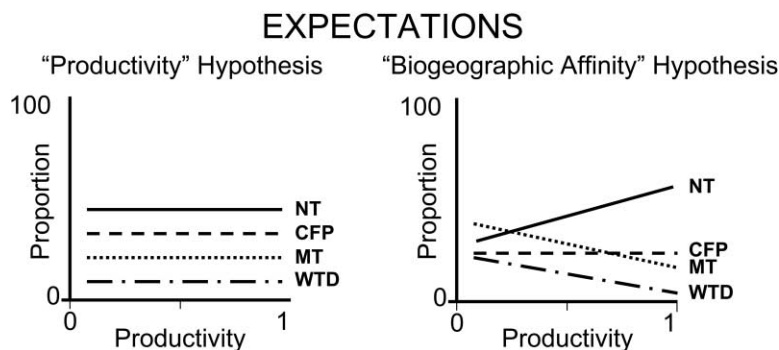


Figure 1: Expectations under the “productivity *per se*” and “biogeographic affinity” hypotheses. The affinity groups are north-temperate (NT), California Floristic Province (CFP), Madro-Tertiary (MT), and warm temperate desert (WTD). Under the biogeographic affinity hypothesis, we predict that the proportional contribution of these groups to total richness will vary predictably with productivity (normalized difference vegetation index) in the order NT > MT, CFP > WTD, while under the productivity *per se* hypothesis, the proportional representation of each affinity group will not vary with productivity.

Regional environmental variables, including precipitation and temperature (mean, minima, maxima, coefficients of variation), NDVI, soils, and topography, were obtained from multiple GIS data sources. The 86 regions in our study comprised only those parts of the state that contained serpentine. This included virtually the entire Mediterranean-climate portion of the state (i.e., the CFP; Dallman 1998) but excluded the deserts.

Our local data consist of species richness and environmental data from 109 1,000-m² field plots on serpentine soil, each of which was located in one of 78 (out of the total of 86) regions. We sampled plant species richness and associated variables (e.g., soil, rock, and litter cover; soil chemistry) at these 109 sites over a 4-year period.

Our measure of productivity was the remotely sensed NDVI, which measures the separation between energy reflectivity in the near-infrared and red wavelengths and indicates the density and vigor of the plant canopy (Hansen et al. 2004). We averaged NDVI values temporally for 2000–2004, using the same composite date and masking for yearly climatic conditions (i.e., clouds and snow) and water features. We then averaged these values spatially for each of the 86 regions and also for a circle of 250-m radius around each of the 109 study sites.

In our previous analyses, regional mean NDVI was the single strongest predictor of regional richness of both total species and serpentine endemics (standardized total effect size = 0.739). Regional mean annual rainfall was in turn a very strong predictor of NDVI, but NDVI was not related to any measures of temperature (this is expected in a water-limited climate). Neither regional nor local productivity had any significant direct effect on local total or endemic species richness, although we could have detected effects as small as 0.01. The weak positive correlation between regional NDVI and local richness was entirely mediated

through an indirect pathway in which NDVI affected regional richness, which affected local richness (Harrison et al. 2006c).

Classification of Species

By definition, all species found at our local sites were serpentine tolerators. Thus, to make valid comparisons of productivity-richness patterns between the regional and local scales, we focused our regional analyses on serpentine tolerators as well. We classified species as serpentine tolerators if we found them in any of our 109 serpentine study sites across the state. The total of 1,069 species we found in our study sites agrees well with Kruckeberg's (1984) estimate of 1,100 serpentine tolerators in California. For each region, we calculated both its total species richness and its serpentine tolerator species richness using species distributional information (Viers et al. 2006) that was independent of our field sampling. To ascertain whether plants tolerant of serpentine differed from other species in the patterns of interest, we performed several key analyses using regional total species richness and compared the results with those for regional serpentine tolerator species richness; we did not find any major differences (see "Results").

Thus, "regional total richness" is the number of species found in each of our 86 regions. "Regional tolerator richness" is the number of species capable of growing on serpentine found in each of our 86 regions. "Local richness" is the number of species (by definition, all tolerators) found in each of our 109 serpentine study sites distributed among the 86 regions.

To categorize our study species by biogeographic affinity, we used the classic monograph by Raven and Axelrod (1978) on the origin and relationships of the California

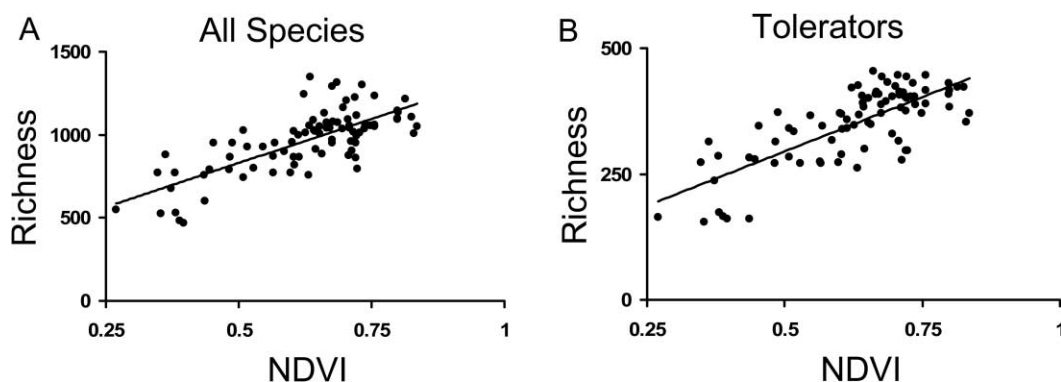


Figure 2: Changes in regional species richness (all four affinity groups combined) with increasing normalized difference vegetation index (NDVI) for all species and for serpentine tolerators. The standardized regression coefficient for the all-species regression = 0.74 ($P < .001$) and for tolerators = 0.76 ($P < .001$).

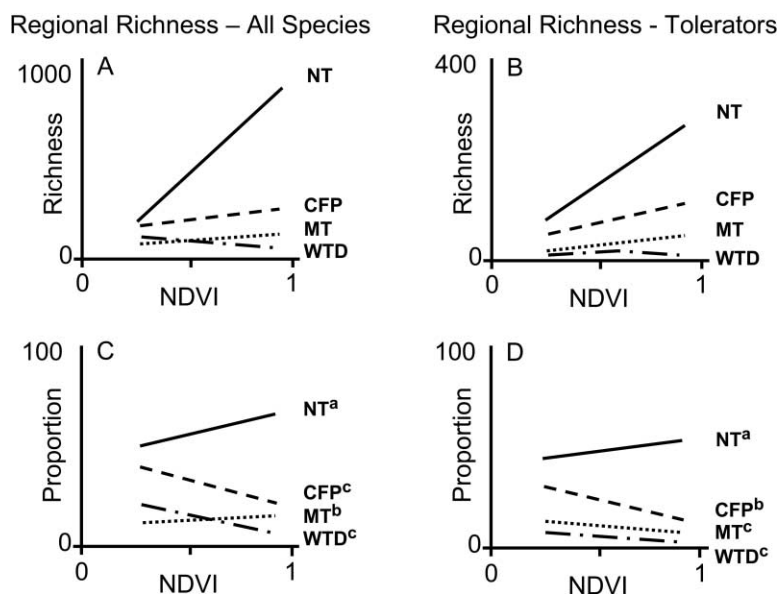


Figure 3: Changes in absolute and proportional regional species richness of the four affinity groups with normalized difference vegetation index (NDVI) for all species and for serpentine tolerators (data points not shown for simplicity). For absolute richness (A, B), all slopes were significantly different from 0. The plot for warm temperate desert (WTD) tolerators was significantly nonlinear. For proportional richness (C, D), groups with differing superscript letters were found to have different slopes from those of other groups. NT = north-temperate; CFP = California Floristic Province; MT = Madro-Tertiary.

flora. This provides the only comprehensive synthetic account of the history of this flora in sufficient detail that every species can be assigned to one of four groups. (1) Arcto-Tertiary or NT families and genera are those that are thought to have diversified in the mild and wet Eocene epoch when forests prevailed over much of the Northern Hemisphere. Their contemporary distributions tend to be centered in the NT zone. Raven and Axelrod (1978) describe this group of taxa as comprising 50% of present-day California species, including many that are now associated with mesic habitats, for example, *Aceraceae*, *Betulaceae*, *Iris*, and *Viola*. (2) Madrean or MT families and genera are believed to have diversified during the cooling and drying conditions of the late Eocene to Miocene; since then, they are thought to have expanded northward across California at the expense of the NT flora during drier periods and to have retreated southward during wetter periods. This historic flora was named “Madrean” because of Raven and Axelrod’s (1978) belief that the flora of the contemporary Sierra Madre mountains of northern Mexico resembles this historic flora. According to Raven and Axelrod (1978), this group comprises 33% of present-day Californian species (a figure that evidently includes the CFP species). This group includes many of California’s sclerophyllous shrubs, such as *Arctostaphylos*. (3) The CFP taxa are genera endemic to the region. These groups are believed to have diversified rapidly during the recent (Plio-

Pleistocene) development of the Mediterranean climate in California. Raven and Axelrod (1978) believed that most of these genera have their closest relatives in the Madrean flora, though they acknowledged some uncertainty about this. Like the MT group, the CFP taxa include sclerophyllous shrubs (e.g., *Ceanothus*) as well as many annual herbs (e.g., *Collinsia*, *Mimulus*). (4) The WTD families and genera, like MT taxa, are believed to have invaded California from the south and east during periods of warmer and drier climate. They comprise 14% of the present-day flora; examples are *Atriplex*, *Lepidium*, and *Solanum*.

The above interpretations by Raven and Axelrod (1978) were based on a combination of fossils, biogeographic evidence, and intuition. They have since been criticized on a number of grounds (e.g., Edwards 2004), notably Raven and Axelrod’s (1978) “Clementsian” notion of floras migrating in unison, their assumption that migration vastly outweighed adaptive evolution as a response to climate change, and the lack of rigorous evidence for many of their assertions. Nonetheless, several analyses of trait evolution in Californian plants have been consistent with their interpretive scheme (Ackerly 2003, 2004).

While modern phylogenetic analyses can provide much more definitive evidence on the “origins” of clades, that is, the geographic or ecological distributions of their most basal members, such analyses are not yet available for the vast majority of Californian families and genera. In ad-

Table 1: Standardized regression coefficients for relationships with regional NDVI shown in figures 3 and 6

	NT	CFP	MT	WTD
Figure 3:				
Regional richness (all species)	.75	.52	.29	.23
Regional richness (tolerator species)	.79	.66	.48	.15
Proportional regional richness (all species)	.70	.57	.50	.81
Proportional regional richness (tolerator species)	.69	.46	.46	.78
Figure 6:				
Proportional local richness (all species)	.62	.50	.34	.49
Proportional cover of local species (all species)	.28	.26	NS	.45

Note: All values shown were judged to be statistically significant on the basis of $P < .05$. NS = not significant. NDVI = normalized difference vegetation index; NT = north-temperate; CFP = California Floristic Province; MT = Madro-Tertiary; WTD = warm temperate desert.

dition, it is unclear how far back in the phylogeny one should go in assigning species to groups based on their origin. We have used the less specific term “affinity” to acknowledge these practical and conceptual problems with origins. Our essential proposition is that the response of species to productivity gradients should depend critically on the environments that the groups to which they belong have experienced over long periods of evolutionary time and especially the environments they occupied during critical periods of diversification. In spite of its weaknesses, Raven and Axelrod’s (1978) data provide the best available basis to test this proposition for the Californian flora.

Data Analysis

We used structural equations (Grace 2006) and the software Mplus (Muthen and Muthen 2006) to evaluate the equality of responses of the different affinity groups (NT, MT, CFP, and WTD) to productivity (NDVI) and thus to test the hypotheses represented in figure 1. Our model permitted unequal variances and correlated errors, which would be expected in comparisons of multiple responses from the same samples. Nonlinear relationships were allowed where needed, and examination of residuals confirmed appropriateness of the models. The analysis was based on a maximum likelihood solution procedure. Equality constraints were used in combination with model fit statistics to test whether slopes differed significantly.

We first examined richness at the regional scale. We conducted separate tests on regional total richness and regional serpentine tolerator richness; also, we conducted separate analyses of each of these two variables using the absolute and the proportional values of species richness of the four affinity groups. (We considered proportional richness to be the most conservative measure because it decouples trends in total richness from trends in representation of the four groups, but we also examined absolute richness.) Because the regional data came from spa-

tially contiguous units, we adjusted the degrees of freedom for spatial autocorrelation in the model residuals using the software program SAM (Rangel et al. 2005).

We next considered how local species composition changed across the study area in relation to regional productivity patterns. We began by using an ordination to describe the multidimensional patterns in overall community similarity and how they relate to NDVI. We used nonmetric multidimensional scaling (McCune and Grace 2002) because it is robust to high levels of β diversity, avoids 0 truncation errors, and can accommodate nonlinear relationships; our distance measure was the Sørensen metric. We used the autopilot mode in PCOrd (McCune and Medford 1999) to search for the optimal dimension reduction using 200 iterations of the analysis to compare stress reduction to that found in a random matrix. Monte Carlo tests permitted probability assessments of solutions of differing dimensions.

We then used the same structural equation model described above to test, at the local scale, whether the four groups responded equally or unequally to NDVI. There was negligible difference between analyses based on absolute and proportional local richness, so we report the results only for proportional local richness.

Finally, we used another structural equation model to ask whether the data were consistent with the hypothesis that at the local scale, increasing competitive dominance by the mesic-adapted (NT) group contributed to the proportional decline in richness of the other three groups (MT, CFP, and WTD) along the productivity gradient. This path model included both NDVI and the cover of the NT group as explanatory variables for the proportional representation of the other groups.

Results

The regional total richness of all four groups combined showed a significant linear increase ($P < .001$) across the

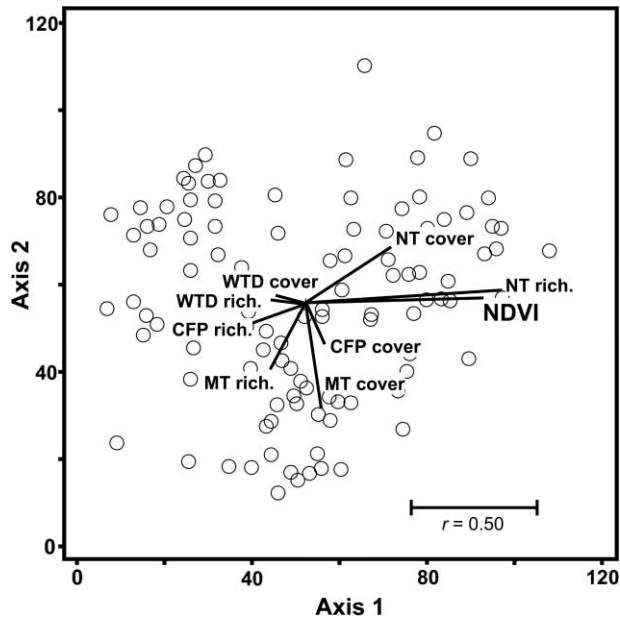


Figure 4: Ordination results showing two-dimensional separation of plots in species space and showing relationships to the number of species and cover of different affinity groups. For descriptive purposes, a vector length equivalent to a correlation strength of 0.50 is shown for reference. Abbreviations for affinity groups as in figure 1.

range of NDVI values (fig. 2A). We found no evidence for spatial autocorrelation in the regression residuals based on Moran's I ($P > .05$); thus, there was no need to adjust the effective sample size. For serpentine tolerators at the regional scale, the combined richness of all four groups also increased with regional NDVI (fig. 2B). In this case, we did find a slight degree of spatial autocorrelation at the highest and lowest degrees of lag, resulting in an estimated effective sample size of 66. Using this adjusted sample size, we found a significant relationship between regional tolerator richness and NDVI ($P < .01$).

In the analyses of absolute and proportional regional richness of the four groups across the NDVI gradient (fig. 3; table 1), spatial autocorrelation was significant in all cases, yielding effective sample size estimates ranging from 23 to 47. All four groups showed significant relationships of their regional total species richness to NDVI ($P < .05$), but the slopes differed significantly in sign and direction, with NT species showing the strongest positive relationship to NDVI in both absolute and proportional terms (fig. 3A, 3B). For a structural equation model with all slopes equal, $\chi^2 = 71.07$ ($P < .001$) was obtained, while $\chi^2 = 0.39$ ($P = .53$) was found for the final model with unequal slopes (indicating good fit of the final model). For regional richness of serpentine tolerators, the slopes for most groups again were significant but differed in sign and di-

rection, with NT species again showing the strongest positive relationship (fig. 3C, 3D). The structural equation model with all slopes equal yielded $\chi^2 = 39.69$ ($P < .001$), while the final model with unequal slopes had $\chi^2 = 2.45$ ($P = .12$).

Our ordination (fig. 4) is based on a two-dimensional solution with a stress value of 25.6, because only a 5.5-unit additional reduction was associated with a three-dimensional solution. To aid interpretation, we rotated the ordination so as to maximize the correlation between axis 1 and NDVI. Axis 1 was strongly associated with the proportion of NT species, indicating that variation in this set of community samples is associated with both productivity and NT dominance. However, the cover of NT species was oblique to axis 1, suggesting that NT richness and NT cover have somewhat different relationships to variation in community composition. The proportional richness and cover of MT species were both associated with axis 2, suggesting that MT species responded to local conditions that were uncorrelated with regional productivity. The CFP species were associated with conditions in which NT species were both less common and less abundant. The WTD species showed little correlation with either ordination axis. It is important to understand that these relationships between axis scores and overlay variables are complex, and their strengths are given solely for descriptive purposes (fig. 4).

Both local species richness (fig. 5A) and cover (fig. 5B) of all four groups combined showed significantly positive relationships to NDVI ($P < .05$). The proportional local richness of each group (fig. 6A; table 1) also varied significantly with NDVI, with the NT species showing the only positive relationship. The structural equation model with all slopes equal had $\chi^2 = 52.4$ and $df = 5$ ($P < .001$), while the final model with unequal slopes had $\chi^2 = 1.26$ and $df = 1$ ($P = .26$). For local cover (fig. 6B), NT increased, CFP and WTD decreased, and MT did not change significantly in proportional representation across the NDVI gradient. The structural equation model with all slopes equal yielded $\chi^2 = 8.32$ and $df = 2$ ($P = .01$), while the final model with unequal slopes had $\chi^2 = 0.002$ ($P = .96$).

The results of our second structural equation model were consistent with the hypothesis that NT cover might be suppressing the richness of MT and CFP species at the local scale (fig. 7). The final model had a model $\chi^2 = 8.89$ and $df = 5$ and an associated P value of 0.113 (indicating no significant deviation between model and data). The contributions of MT and CFP species to total species richness appeared to be sensitive to the amount of NT cover independently of the direct effect of NDVI. In contrast, WTD richness appeared to change independently of

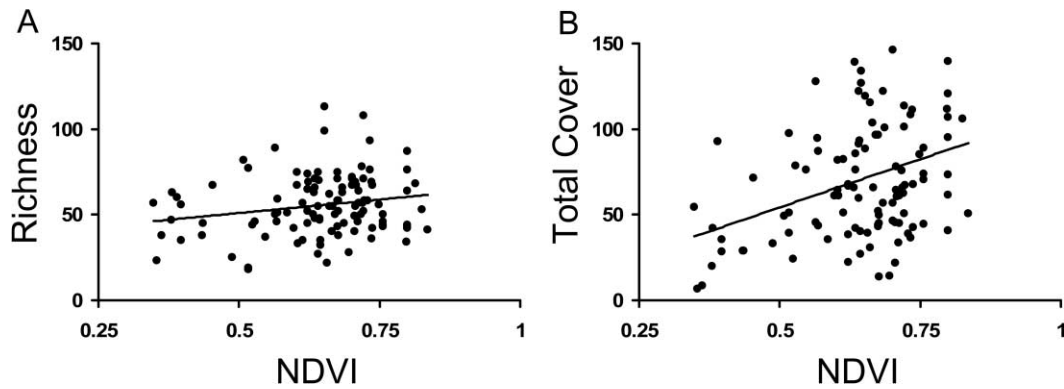


Figure 5: Changes in local species richness and total vegetative cover with increasing normalized difference vegetation index (NDVI). The standardized regression coefficient for the species richness regression = 0.20 ($P < .05$) and for tolerators = 0.34 ($P < .01$).

NT cover even though NT cover and WTD richness were negatively correlated via their opposite responses to NDVI.

Discussion

We found strong differences among the four groups in our regional analyses; the sign and strength of productivity-richness relationships varied in the direction predicted by the biogeographic affinity hypothesis (fig. 1B), whether all species or only serpentine tolerators were considered and whether absolute or proportional richness was analyzed. Only in families or genera of NT affinity did regional richness consistently increase strongly with productivity, while in families or genera of other affinities (semiarid or desert), regional richness either increased more weakly or decreased. The key message from this result is that the regional productivity-richness relationship is not an ecological law that applies equally to all species. Rather, our results support the idea that the positive relationship of

productivity to regional species richness can be viewed at least partly as a product of history and evolution, embodied in niche-determining traits that are conserved at higher taxonomic levels. We predict that in other cases where exceptions to the general positive productivity-richness relationship are found, the explanation may turn out to lie in the evolutionary history of the particular species pool in question (for an analogous result regarding the global pH-richness relationship, see Partel 2002).

The idea that key traits governing the climatic niches of species can be conserved over a long period of evolutionary time may seem strange, given the abundant evidence for rapid evolution in other traits affecting resource use (e.g., Carroll et al. 2005). However, there is no question that congeners and confamilials are more than randomly similar to one another, and growing evidence supports the idea of niche conservatism as an important influence on ecological and evolutionary phenomena (Webb et al. 2002; Ackerly 2004; Wiens and Graham 2005), including the

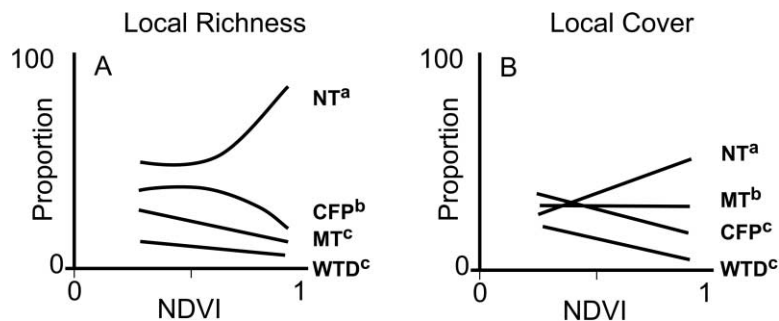


Figure 6: Changes in proportional contributions of the four affinity groups to local species richness and total cover with increasing normalized difference vegetation index (NDVI; data points not shown for simplicity). All slopes were found to be significantly different from 0. The lines for north-temperate (NT) and California Floristic Province (CFP) richness were found to be significantly nonlinear. Groups with differing superscript letters were found to have different slopes from those of other groups. MT = Madro-Tertiary; WTD = warm temperate desert.

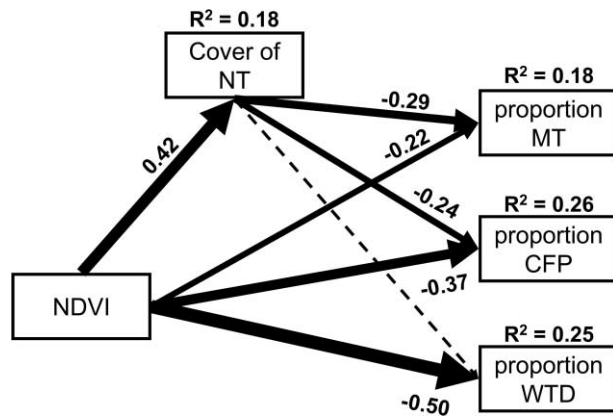


Figure 7: Relationships of the local richness of the three subordinate affinity groups (Madro-Tertiary [MT], California Floristic Province [CFP], warm temperate desert [WTD]) to normalized difference vegetation index (NDVI) and the local cover of north-temperate (NT) species. Standardized path coefficients are shown. The dashed line indicates that proportional representation of WTD species was unrelated to the cover of NT once the effect of NDVI was taken into account.

latitudinal gradient in species richness (Farrell et al. 1992; Latham and Ricklefs 1993; Wiens and Donoghue 2004; Hawkins et al. 2006). Although we do not know the full extent of the niche-determining trait differences between Raven and Axelrod's (1978) groups, Ackerly (2003) found that the NT species in California had significantly higher specific leaf area than the other groups, while the MT species had significantly higher seed sizes than the other groups. Our results add to the climatic niche conservatism hypothesis put forward by Wiens and Donoghue (2004) and others by extending it beyond the latitudinal gradient to other productivity-richness gradients and also by linking it to local community patterns, thus giving it even broader significance.

At the same time, we note that positive relationships of absolute richness to productivity were shown by three of our four biogeographic affinity groups even though these increases were strong in only one case (NT species) and considerably weaker in the other two (species of semiarid affinity). Only species belonging to taxa of desert affinity showed a decline in absolute regional richness with increasing productivity. The prevalence of positive relationships may indicate an intrinsic bias toward mesic conditions in plants, as illustrated in the physiologically based model of Kleidon and Mooney (2000). Our results do not contradict this idea so much as they suggest that evolutionary history may have a powerful influence on the strength of the bias toward mesic conditions.

Evolutionary diversification, that is, speciation minus extinction, may be faster at higher productivity; this is

another of the three alternative explanations for the global productivity-richness relationship proposed by Currie et al. (2004), in addition to the tolerance and more individuals hypotheses. In support of this, some evidence links environmental energy to rates of molecular evolution in plants (e.g., Davies et al. 2004). However, in our system, the productivity gradient is caused by variation in rainfall, not in environmental energy. Moreover, the Californian endemic (CFP) taxa represent the only group that underwent rapid and recent diversification under a near-modern Californian climate, yet CFP species show a much weaker productivity-richness relationship than do NT species, which largely diversified outside the context of the present Californian environment. Similarly, there are 45 NT genera that Raven and Axelrod (1978, p. 16) note as having speciated extensively in California, but the productivity-richness relationship is not stronger in this group than in the other NT families and genera. Thus, while the faster diversification hypothesis may be true, we consider it unlikely to explain the productivity-richness gradient for Californian plants.

Local community composition, as well as regional species richness, varied strongly with regional productivity in our analyses. With increasing productivity, the richness of NT species increased disproportionately at the local scale while local richness of the other three groups declined in both relative and absolute terms. These local changes were even more pronounced than the changes at the regional scale even though overall species richness (of all four groups combined) responded strongly and directly to productivity at the regional scale and only weakly and indirectly at the local scale. This apparent paradox can be reconciled by considering how competition can interact with regional species pools to shape the response of local communities to productivity gradients. We propose that as productivity increases, local communities are affected in two ways: there are more NT species available from the regional pool, and NT species become more competitively dominant, locally displacing species of at least some of the other groups. Together, these effects could produce the observed pattern just described. We found evidence consistent with this idea by showing that the decline of semiarid (MT and CFP) species richness at the local scale is associated not only with productivity itself but also with the increase in relative cover of NT species. Interestingly, local NT cover did not affect desert (WTD) species, the group that declined in richness with increasing NDVI at both the regional and local scales. Thus, we suggest that differences among groups in both fundamental and realized niches contribute to the patterns observed at the local scale.

Models have previously been proposed in which local community variation along a productivity gradient is

shaped by the regional species pool interacting with shifting competitive dominance (e.g., Grace 1999; Safford et al. 2001). We have taken these ideas a step further by quantifying how the different components of the regional species pool change in prevalence along a productivity gradient, which has not previously been examined. We note that altering the relative total richness of the four different biogeographic groups in our system might make it possible to obtain the full range of local productivity–richness relationships observed in other studies (Waide et al. 1999; Gross et al. 2000; Mittelbach et al. 2001), for example, positive if nearly all species were NT and negative if nearly all species were CFP and either unimodal or neutral if there were an equal mix of NT and CFP species, depending on the form of the nonlinearity caused by competition. Thus, we suggest that a consideration of biogeographic affinities may lend quantitative insights into the ways that local communities change along environmental gradients and may help reconcile differences among previous studies.

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