



High β diversity in the flora of Californian serpentine ‘islands’

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Abstract. Identification of global biodiversity hotspots is a leading conservation priority (Mittermayer et al. (1999) *Hotspots*. Conservation International, Washington, DC; Stein et al. (2000) *Precious Heritage: The Status of Biodiversity in the United States*. Oxford University Press, Oxford, UK), but we know little about the nature and structure of such hotspots. Botanical richness in one recently identified hotspot, the California Floristic Province, has long been attributed by evolutionists to edaphic and climatic heterogeneity. Here we demonstrate that the flora restricted (endemic) to serpentine soil, the state’s most botanically distinctive substrate, shows unusually high ‘ β diversity’ – i.e., spatial variation in species composition – among regions, although ‘ α ’ diversity within any given region is low. Conservation of an endemic-rich flora requires a network of sites to capture this among-region or spatial component of diversity.

Introduction

With even the tropical-temperate diversity gradient not yet fully explained, ecologists are unlikely to soon arrive at a mechanistic theory of species diversity that can be applied in conservation. However, novel insights can arise from careful analyses of diversity patterns that are grounded in insights from traditional biogeography (Brown 1988; Rosenzweig 1995). Serpentine soils in California are a classic system for understanding the origins and maintenance of plant diversity. Soils derived from serpentinite rock are critically low in Ca and primary nutrients, and high in Mg, Fe, Ni and other metals. Throughout the world, these harsh soils support a distinctive flora, and California is one of the world’s richest areas for plants restricted to serpentine (Brooks 1987). Serpentine is an important reason for California’s botanical richness; Kruckeberg (1984, 1991) estimates that it comprises only 1% of the state’s area, yet harbors 10% of the plants unique to the state. Serpentine endemic plants in California must have originated within about the past 10 million years (Kruckeberg 1954); most are thought to be neoendemic or ‘insular’ taxa that arose recently from ancestors on non-serpentine soils, while a minority may be paleoendemic or ‘relictual’ taxa whose once-widespread ancestors became extinct on other substrates. The insularity of serpentine outcrops has long been considered an important aspect of the origin and maintenance of serpentine endemic plants

(Stebbins 1942; Kruckeberg 1954, 1984, 1991; Raven 1964; Stebbins and Major 1965; Raven and Axelrod 1978; Mayer et al. 1994; Stebbins and Hrusa 1995).

We analyzed the statewide distribution of diversity in the serpentine endemic flora, focusing especially on the variation in species composition among regions of the state. We use the term ' β diversity' for this variation in species composition among regions, and ' α diversity' for the species richness within regions. Whittaker (1960) first proposed partitioning diversity into geographic components, where α or local diversity refers to the number of species within a single site; γ or total diversity is the number of species in a large collection of sites; and β or turnover (or differentiation) diversity, measured as $\gamma/(\text{average } \alpha)$, is a measure of the variation in species composition among sites. β Diversity is highest when each site contains different species, and lowest when the same species are found at every site. In contrast to Whittaker's original usage, however, our 'sites' in this study are large regions rather than small sampling plots.

We predicted that β diversity would be higher in plants endemic to serpentine, and would increase more rapidly with the geographic distances and environmental differences among regions, as compared with the flora as a whole. We expected this for two reasons. First, serpentine outcrops are insular, and their discontinuity presumably limits dispersal and biotic homogenization in ecological and evolutionary time. While this should lead to lower α diversity (MacArthur and Wilson 1967), it should also raise β , i.e. cause greater change in biotic communities over a given distance in comparison with the floras of more continuous habitats. Second, earlier work suggests a heightened sensitivity of plant distributions to climatic variation on serpentine, leading to greater change in community composition for a given degree of change in average elevation or rainfall, in comparison with floras on other soils (Whittaker 1954, 1960; Harrison et al. 2000).

Several lines of evidence suggest that both the spatial configuration of the substrate and climatic variation may influence the distribution of serpentine endemic diversity in California. In a field study in northern California, the spatial configuration of serpentine significantly influenced the distribution of endemic plant diversity in a 30×50 km region (Harrison 1997, 1999). Local (within-site) species richness was lower on 24 small isolated outcrops (< 5 ha) than on 24 equivalently spaced and similarly sampled sites within four large continuous outcrops (>1 km²). However, β (among-site) diversity was higher for the small isolated outcrops, leading to an equivalent total richness of serpentine-restricted plant species on the two sets of sites. In the present study, our goal was to extend this line of investigation to a larger scale, namely the entire serpentine flora of California.

The role of climatic variation was first noted by Whittaker (1954, 1960), who found a more rapid turnover in species composition along an elevational gradient in the serpentine compared to the non-serpentine flora of the Klamath-Siskiyou Mountains. Many authors have noted that the vegetation of serpentine is substantially more drought-adapted than that of neighboring soils (Kruckeberg 1984; Brooks 1987). Also, Kruckeberg (1984) described a strong north-to-south decrease in the richness of serpentine endemics across California. While he suggested that this seemingly anomalous, 'reverse' latitudinal gradient could be a product of the

north-to-south decrease in the area of serpentine, the pattern also appears to be related to variation in climate (Harrison et al. 2000). Thus, in the present study we compared (1) the overall β diversity of the serpentine and total floras, and (2) the strength of the responses of β diversity in these two floras to two explanatory factors, geographic distance and large-scale climatic variation.

Methods

The California Floristic Province comprises most of the state north of the Transverse Ranges and west of the Sierran crest, and contains nearly all (>95%) of the state's serpentine; for simplicity, therefore, the terms California and California Floristic Province are used interchangeably. A very small segment of the serpentine in the California Floristic Province is found in southern Oregon, but we lack botanical data for this area. To obtain spatially referenced plant diversity data, we combined the CalFlora and Jepson Manual databases (Richerson and Lum 1980; Walker 1992; Hickman 1993) to generate species lists for 284 separate regions. Only 92 of these regions contained serpentine, and seven were lumped with their neighbors because they contained small slivers of serpentine or lacked environmental data, leaving 85 regions in our analyses (Figure 1).

There is no precise definition of endemism, since most taxa restricted to serpentine can occasionally be found on other substrates, and since many taxa are restricted in only parts of their geographic ranges. Kruckeberg (1984) estimates that there are 215 serpentine endemics and 200 serpentine indicators in California. The Jepson Manual (Hickman 1993) lists serpentine as a major substrate for 369 taxa. We denoted these 369 taxa as endemics, and found that their diversity was significantly correlated with the area of serpentine in a region, but not with the total area of a region (Harrison et al. 2000). Non-endemics, including both serpentine avoiders and species that grow on and off on serpentine (Kruckeberg 1984), totalled 5587 taxa, of which 4566 occurred in our 85 regions.

We used a GIS database to calculate for each region its total area, distance from the coast, mean elevation, and distances from all other regions (Jennings 1977; Daly et al. 1994). For the serpentine in each region, we calculated area, number of outcrops, and mean isolation of outcrops (edge-to-edge nearest neighbor distance) from the electronic version of the California geologic map (Jennings 1977). Precipitation data from the California climate model (Daly et al. 1994) were used to calculate for each region its 30-year spatial and temporal average annual precipitation (1961–1990), both for the entire region and for the serpentine areas it contained. In analyses of total plant diversity, we used precipitation and elevation data for entire regions; in analyses of endemic diversity, we used precipitation and elevation data for serpentine areas only.

In the present analyses we focused on the variation in species composition among these regions, or β diversity. We calculated β diversity separately for each of the 3570 pairs of regions, using Whittaker's β diversity metric, $\beta = (s/\bar{\alpha}) - 1$, where s is the diversity of a collection of samples and $\bar{\alpha}$ is the mean diversity for each

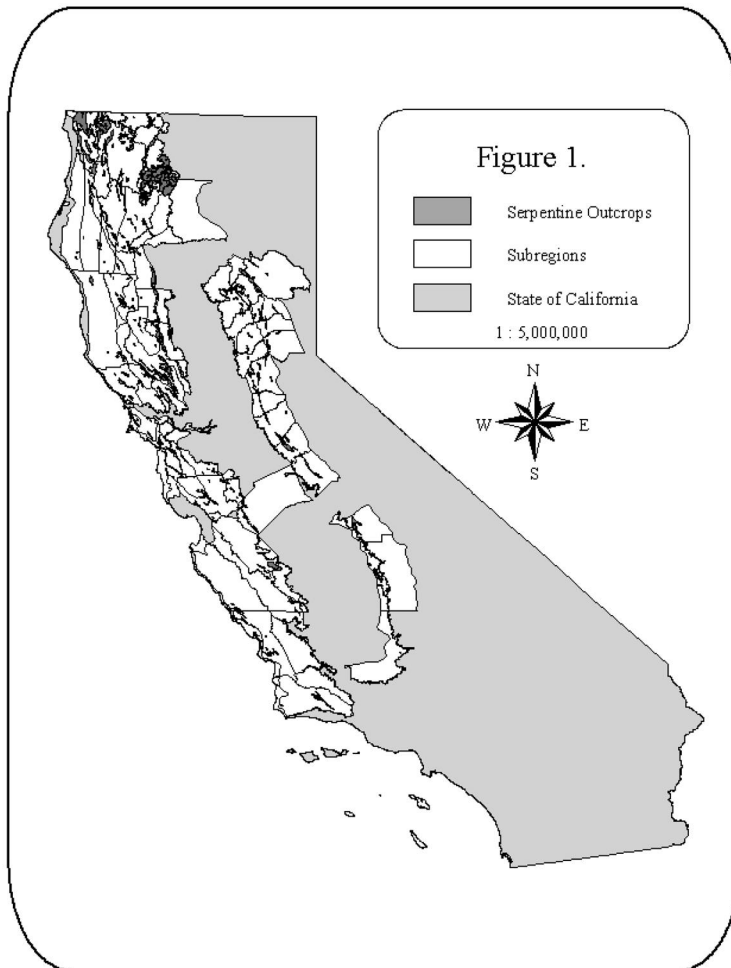


Figure 1. Serpentine outcrops in California, and regions analyzed in this study.

sample (Whittaker 1960). Values of β range from 0 for a pair of regions with identical species lists, to 1 for a pair of regions with no overlap in their species lists. Because the 3570 pairwise measures of β are not statistically independent, all of our analyses are non-parametric and are based on randomization methods. We calculated linear correlations between β and the geographic distances and environmental differences among regions, using single and multiple Mantel tests with P -values based on 10000 randomizations of the β matrix (Fortin and Gurevitch 1993; Manly 1997). Distance between regions was log-transformed because this provided a closer and more linear correlation with β than did untransformed distance. All statistical analyses were done using S+ 4.0 (Mathsoft Corporation 1997).

Results

Species–area plots show that the α or within-region diversity of serpentine endemics is considerably lower than that of non-endemics, even after controlling for the effect of serpentine area vs. total area (Figure 2). As predicted, β diversity was significantly higher in serpentine endemics (mean 0.55, range 0.03–0.90, $\sigma = 0.17$) compared to non-endemics (mean 0.44, range 0.02–0.74, $\sigma = 0.14$; $P = 0$, based on 10000 randomizations). Distributions of β for both sets of taxa were mildly left-skewed. There were many more narrowly distributed species among the serpentine endemics; only 4 (1.1%) endemics occurred in all 85 regions, whereas 52 (13.8%) were restricted to a single region. In contrast, 160 (4.0%) of the native non-endemics were found in all 85 regions, and only 396 (9.9%) occurred in a single region (Figure 3).

For both endemic and non-endemic plants, β diversity was strongly and significantly correlated with the distance between regions, as well as with differences between regions in mean precipitation, distance to the coast, and mean elevation (Table 1). The relative strength of each of these relationships for endemics vs. non-endemics was calculated by dividing the slope of a linear regression for endemics by the slope of a linear regression for non-endemics. For distance and precipitation, these relative slopes were substantially greater than one, indicating that the β diversity of endemics responded more strongly than that of non-endemics. For distance to the coast and mean elevation, relative slopes were close to one, indicating similar responses in the two sets of taxa (Table 1). Distances between regions were strongly correlated with the differences between regions in mean precipitation and other environmental variables; in multiple Mantel tests using all of

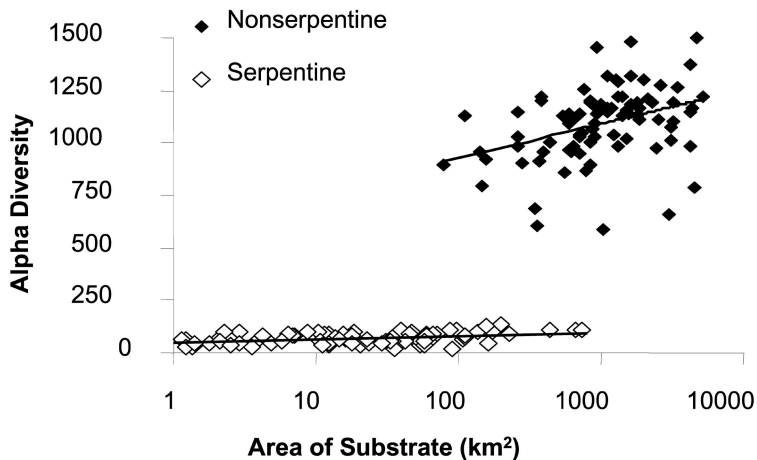


Figure 2. Species–area relationships: the diversity of serpentine endemics plotted against the area of serpentine in a region, and the diversity of non-endemics in a region plotted against the total area of the region. The y -intercepts, but not the slopes, are significantly different based on randomization tests.

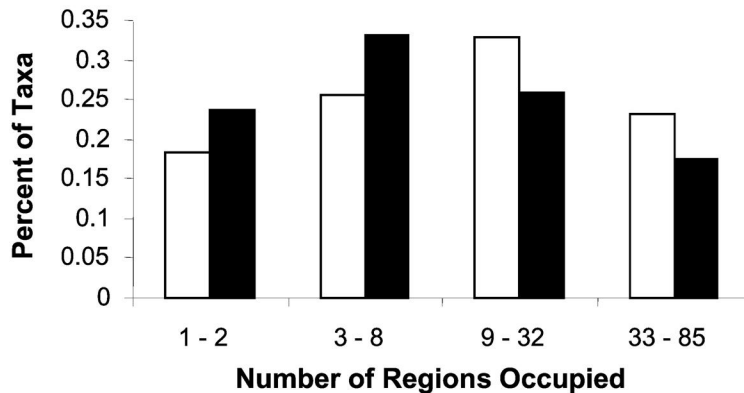


Figure 3. The percent of native serpentine endemics (solid bars) and non-endemics (open bars) that occur in different numbers of geographic regions. These distributions are significantly different (χ^2 test, $P < 0.001$), with serpentine endemics occurring on average in fewer geographic regions.

Table 1. Correlations between β diversity and the distances and environmental differences among all pairs of the 85 regions.

Attribute	Serpentine associated taxa		Non-serpentine associated taxa		Relative slopes
	<i>r</i>	<i>P</i> (two tailed)	<i>r</i>	<i>P</i> (two tailed)	
Distance	0.81	0	0.79	0	1.24
Mean precipitation	0.51	0	0.49	0	1.27
Distance to coast	0.42	0	0.50	0	0.99
Mean elevation	0.40	0	0.47	0	1.03
Total substrate area	0.13	0.0088	0.17	0.0010	0.85

The *P*-values are exact values from 10000 randomizations of the Mantel tests. Relative slopes are the slope of a linear regression for the serpentine endemic species divided by the slope for the non-endemic species.

the predictor variables, distance between regions was the only variable that was significantly correlated with β diversity for either endemic or non-endemic species ($P < 0.01$, all other *P*-values > 0.10).

Discussion

In a previous analysis of our GIS data set we focused on α diversity within the same 85 regions (Harrison et al. 2000). We showed, using linear regressions, that α species richness declined north-to-south and coast-to-inland, and that these patterns were interchangeable with a decline in species richness with decreasing precipitation. These patterns were seen in both serpentine endemic plants and the flora as a whole, but were stronger in serpentine endemics, as shown by the fact that endemics as a proportion of the total flora likewise declined with latitude, distance from coast

and precipitation. Area of serpentine was also a significant predictor of the α diversity of endemic plants, but this effect did not remove the significance of latitude, distance from coast or precipitation. α Diversity of serpentine endemics also decreased with increasing mean isolation of serpentine outcrops within regions (Harrison et al. 2000).

In the present study, our hypothesis that β or among-region diversity would be higher in the serpentine flora was clearly borne out by the results. The difference in species composition between pairs of regions was higher in serpentine endemics than for plants as a whole, and showed a much stronger increase with the geographic and environmental distances between the pairs of regions. In other words, the serpentine flora showed greater variation across geographic and environmental distance than did the non-serpentine flora, in proportion to its size. Our results are consistent with earlier suggestions that edaphic and climatic influences may interact in their effects on plant distributions and diversity (Whittaker 1954, 1960; Stebbins and Hrusa 1995). Our results are also strikingly consistent with the results of earlier field studies, which concluded that the patchiness of the serpentine substrate within a single region led to lower local (within-outcrop) diversity but enhanced among-site (among-outcrop) diversity (Harrison 1997, 1999).

These results illustrate the consequences of insular endemism at the level of the diversity of an entire floristic region. The species that have arisen on the state's many 'islands' of serpentine may add only modestly to the plant diversity of any one region, but these narrowly distributed species add disproportionately to the among-region component of diversity that is of such significance in producing California's botanical richness. Our results have important implications for conservation in a floristic province whose diversity arises in large part from its wealth of edaphic endemics. To conserve this flora, it is clearly futile to search for a few small 'hotspots' of high diversity. Rather, it will be necessary to protect a network of sites that represent a broad range of geographic, geologic and climatic variation.

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