

Does the Age of Exposure of Serpentine Explain Variation in Endemic Plant Diversity in California?

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Abstract

We analyzed botanical, geologic, and climatic data in an effort to understand why there are many more serpentine endemics—i.e., plant species restricted to ultramafic substrates—in some regions of California than in others. We found that, in addition to elevational range (which subsumed the effect of serpentine area) and annual rainfall, the age of exposure of serpentine explained significant geographic variation in the diversity of endemic plant species. Estimated ages of subaerial exposure are generally higher in the Klamath and northern Coast Range serpentines than in Sierra Nevada and southern Coast Range analogues, paralleling the trends in endemic plant diversity. However, the fit of the relationship is weakened by the southern Sierran serpentines, which are apparently long-exposed yet poor in endemic plant species. These results have significance for understanding local ecological processes, because we have also found that the diversity of endemic species within 50 × 10 m field plots is best predicted by the diversity of endemics in the surrounding region, which in turn is a function of the age of subaerial exposure.

Introduction

THE CALIFORNIA FLORA is characterized by a remarkable number of plant species that are found nowhere else on earth (Myers et al., 2000; Stein et al., 2000). The state's rich flora is thought to be the product of rapid evolutionary diversification brought about by interactions between the Late Tertiary development of a Mediterranean-type climate along the southwest Pacific coast, active tectonism, and high levels of geologic and geomorphic complexity (Stebbins and Major, 1965; Raven and Axelrod, 1978). An important facet of California's geological and botanical diversity is the > 5,000 km² of ultramafic rocks found along ancient and modern tectonic margins. Ultramafic rocks generate soils that are poor in essential plant nutrients (N, P, K, Ca) and high in potential toxins (Mg, Ni, Cr). These conditions have led to the development of unique plant species and communities. California joins Cuba, New Caledonia, and Turkey as one of the world's richest locations for "serpentine endemics," or plant

species restricted to ultramafic substrates (Brooks, 1987).²

Serpentine endemics contribute disproportionately to the distinctiveness of the state's flora, comprising at least 10% of California's unique plant species, even though ultramafic rocks and soils cover only around 1–2% of the state's surface area (Kruckeberg, 1984). In his comprehensive treatise on this flora, Kruckeberg (1984) estimated that California has just over 200 strict serpentine endemics and another 200 serpentine "indicators," or plant species partially restricted to this rock type. The California serpentine flora has thus been a long-standing subject of study for those interested in the origins, distribution, and maintenance of biological diversity (e.g., Stebbins, 1942; Raven, 1964; Stebbins and Major, 1965; Raven and Axelrod, 1978; Kruckeberg, 1984; Coleman and Kruckeberg, 1999; Kruckeberg, 2002).

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² We here use the term "serpentine" in the broad ecological sense to refer to ultramafic rocks and soils derived from them.

Here we report part of an ongoing attempt to better understand variation in numbers of serpentine endemics *within* California, as a small step toward better understanding why some areas of the world are especially rich in unique biological diversity. Kruckeberg (1984) quantified the observation by earlier authors (e.g., Stebbins and Major, 1965; Raven and Axelrod, 1978) that the numbers of serpentine endemics decline sharply from the northwestern to the southern and eastern parts of the state. Kruckeberg estimated that there are about 80 total (50 restricted) endemics in the Klamath-Siskiyou region, about 100 total (40 restricted) in the northern Coast Ranges, 30 (20 restricted) in the San Francisco Bay Area, 60 (40 restricted) in the southern Coast Ranges, and 30 (15 restricted) in the Sierra Nevada. Kruckeberg surmised that these geographic trends were the evolutionary product of the greater area of serpentine in northwestern California (Fig. 1). In evolutionary biology, a larger area of islands or island-like habitats is well known to promote speciation by reducing the rate of extinction of new lineages (Rosenzweig, 1995).

To explore this and other explanations for variable levels of serpentine plant diversity in California, Harrison et al. (2000) assembled a geographic data base with the numbers of total plant species, numbers of serpentine endemics, and various geologic, topographic and climatic variables for each of the serpentine-containing spatial units ("subregions") of the state.³ The two most significant predictors of endemic diversity are the average annual rainfall and the elevational range (maximum minus minimum) of the ultramafic areas within a subregion. The area of ultramafic outcrops in a subregion, which is highly correlated with elevational range, is not statistically significant if elevational range is included in the model. Rainfall and elevational range are also positively correlated with the total number of plant species in a subregion, and with the percentage of plants that are serpentine endemics. Thus, there is a correlation between Californian plant diversity and climate, as others have found (Richerson and Lum, 1970), but it appears to be even stronger among serpentine endemics than plants as a whole.

In this paper we consider another possible influence, namely the length of time that serpentine has been available for plants to colonize. Species diver-

sity on old islands is widely observed to be higher than on younger islands (Rosenzweig, 1995). In Cuba, which has the world's richest known serpentine flora, with 920 endemic species and 24 endemic genera, the length of time that serpentine "islands" have been exposed is considered the primary reason for strong geographic patterns in serpentine endemism. Serpentine outcrops on the eastern and western ends of Cuba are believed to have been exposed above sea level for as much as 30 m.y., and these support 86% of the serpentine-endemic species and 100% of endemic genera. The serpentine in central Cuba are believed to have been exposed for only around 1 m.y., and although they comprise 36% of the serpentine area, they support only 19% of endemic species and 8% of endemic genera (Borhidi, 1996, pp. 129–130).

In their landmark monograph on the origin and relationships of the California flora, Raven and Axelrod (1978) considered the age of exposure as an influence on the distribution of Californian serpentine endemics. They concluded from map interpretation that most serpentine exposure ages in California were Late Pliocene to Early Quaternary. Because many shrub and tree species confined to serpentine (e.g., leather oak, *Quercus durata*; Sargent's cypress, *Cupressus sargentii*) were known to be older than this, Raven and Axelrod concluded that these species once occurred on other soils, and became restricted to serpentine following climate change.⁴ In contrast, these authors concluded that most herbs endemic to serpentine belonged to rapidly diversifying taxa—e.g. the genera *Navarretia*, *Streptanthus*, and *Hesperolinon*—and had originated recently on serpentine soils.⁵ However, Raven and Axelrod (1978) did not specifically address the relationship between age of exposure and the geographic variation in the numbers of serpentine endemics in California.

To explore this question, we generated a set of estimated ages of subaerial exposure to add to the database described above. We then examined the partial correlation of this variable with numbers of endemic plant species, employing statistical models that also included climate, elevational range, and serpentine area. We report our tentative conclusions

³ See the Methods section for more details.

⁴ Such old and relictually distributed species are called "paleoendemics."

⁵ Such newly evolved and narrowly distributed species are called "neoendemics."

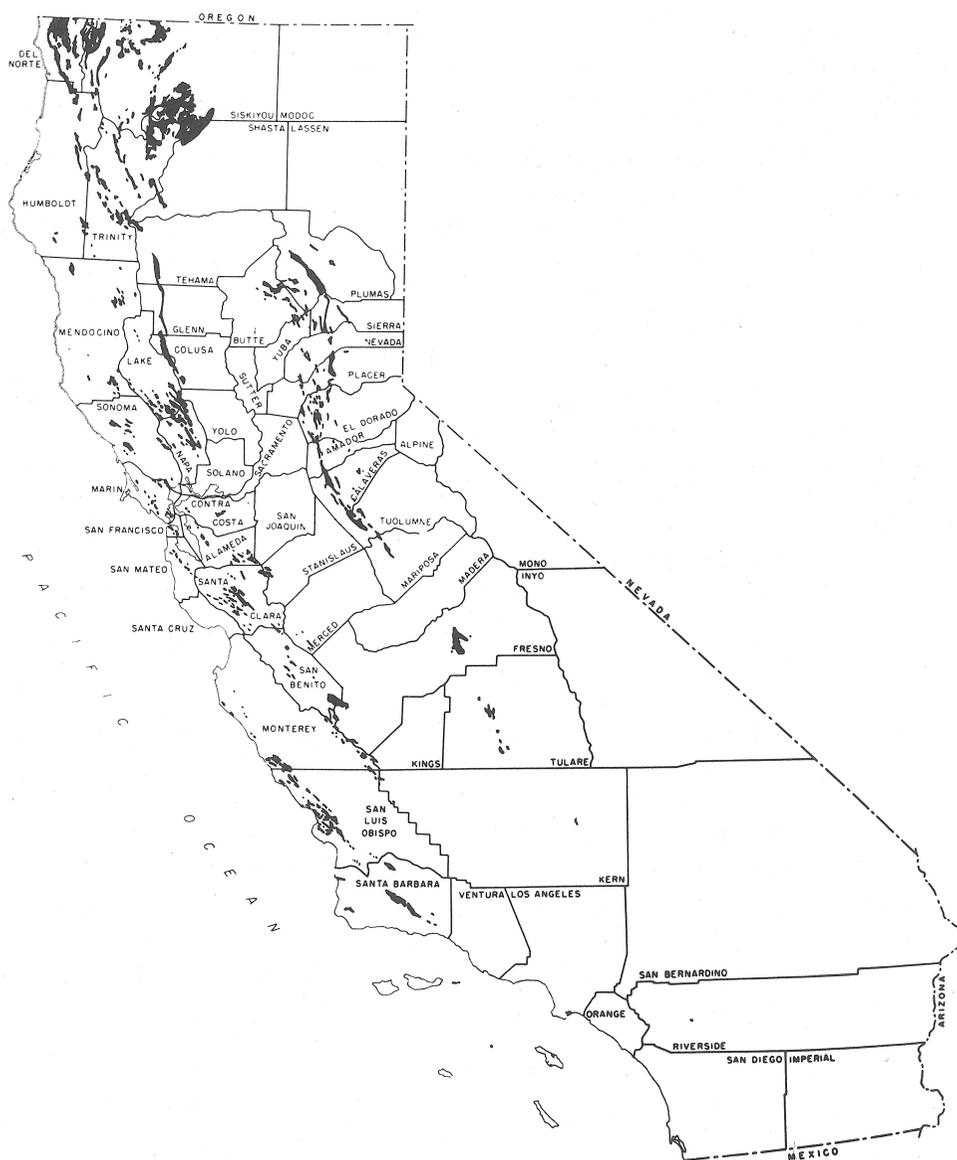


FIG. 1. Map of California showing counties and outcrop areas of serpentinized peridotite, after Jennings (1977).

here in the hope of generating discussion and perhaps filling gaps in the data.

In another part of our work, not discussed in detail here, we are conducting plant, soil, and rock sampling in 50×10 m field plots on serpentine outcrops at >100 sites well distributed across the 92 subregions. By combining our regional (GIS) and local (field) data, our ultimate goal is to understand

how biological diversity is shaped by the interaction between large-scale physical variables such as climate and geologic history, and smaller-scale ecological variables such as soil fertility, species interactions, disturbances, and the spatial distribution of available habitats (see Harrison, 1997, 1999; Harrison and Inouye, 2002; Safford and Harrison, 2004; Harrison and Safford, 2004).

Study System and Methods

Distribution and exposure of serpentine in California

Serpentine outcrops—i.e., outcrops of peridotite and serpentinite and the soils derived from them—are found in three regions of California: the Klamath-Siskiyou Mountains, the Coast Ranges, and the Sierra Nevada (Fig. 1). These outcrops total more than 5000 km², with individual exposures ranging in size from a few hundred square meters to hundreds of square kilometers. Ages of Californian ultramafic rocks generally range from Jurassic to Ordovician (Saleeby, 1992), but as noted by Raven and Axelrod (1978), this time scale has little relevance to plant evolution. Present-day ultramafic outcrops in the state are the products of considerably more recent processes of exposure by uplift and erosion, burial by sediments and volcanics, and subsequent re-exposure.

In the Coast Ranges, subaerial exposure of the Coast Range Ophiolite and other serpentines is believed to have occurred locally as early as the Eocene (Nilsen and McKee, 1979), with widespread exposure by the Miocene (Cole and Armentrout, 1979). The largest body of serpentine in the southern Coast Ranges, at New Idria in San Benito County, was first exposed in the Miocene (Coleman, 1996). However, the subsequent history of uplift and exposure in the Coast Ranges is highly complex. The northward migration of the Mendocino Triple Junction was associated with a migrating uplift welt, which may either have caused initial exposure of some rocks, or superimposed uplift on already exposed rocks (Furlong, 1984, Wakabayashi, 1999). This might have been expected to cause earlier uplift in the southern than northern Coast Ranges, which would be the wrong direction to explain plant diversity. However, extensive Neogene marine deposits indicate that many areas of the central and southern Coast Ranges were submerged until the late Miocene (Graham et al., 1984), whereas such deposits are scarce in the northern Coast Ranges (Cole and Armentrout, 1979). Hence it appears that the uplift and subaerial exposure of the Coast Ranges were generally earlier in the north, and that triple junction migration played a relatively minor role in this process. But complicating the picture further, triple-junction migration was also associated with Late Miocene to Pleistocene volcanism that buried substantial parts of serpentine-rich Napa, Sonoma, and Lake counties (Fox, 1983).

In the Sierra Nevada, major surface uplift of up to 2 km has taken place during the Late Cenozoic, superimposed on a range that already stood well above sea level (Wakabayashi and Sawyer, 2001). Except for the western margin of the range, which was submerged in the Tertiary, southern Sierran serpentines may have been exposed as early as the Late Cretaceous or Paleocene, when Upper Cretaceous arc volcanics were stripped off the metamorphic and plutonic basement rocks (Wakabayashi and Sawyer, 2001). This contrasts with the northern and central Sierra, much of which was blanketed with Miocene and Lower Pliocene volcanics, and only re-exposed when Late Cenozoic uplift led to removal of the volcanic cover by erosion. South of the Tuolumne River drainage, only scattered Cenozoic volcanic flows were present (Moore and Dodge, 1980). Thus the general pattern is one of considerably earlier exposure in the southern than the northern Sierra Nevada. However, some low-elevation serpentines on the western fringe of the southern Sierra were probably submerged during the Tertiary, as mentioned above. Conversely, some of the northern serpentine belts formed local topographic highs, so that islands of serpentine that were probably initially exposed in the Late Cretaceous or Paleocene remained exposed at elevations above the Cenozoic volcanic flows (Wakabayashi and Sawyer, 2001).

The Klamath Mountains as a whole have existed above sea level since at least the Paleocene and probably earlier (Nilsen and McKee, 1979; Schweickert and Irwin, 1989; Aalto et al., 1995, 1998), with the exception of the western margin of the range, which subsided below sea level by the Miocene. Elevations appear to have diminished from the Cretaceous/Paleocene until the Pleistocene, when major uplift began and raised the range to its present elevation (Aalto et al., 1998). The extensive ultramafics of the central Klamath block are considered to be part of a stable Oligocene surface, and the presence of laterite soils indicates that these ultramafics have been exposed since the subtropical climates of the Miocene (Coleman and Kruckeberg, 1999). Toward the western edge of the Klamath ultramafics, Miocene marine sediments of the Wimer Formation overlie the laterites, indicating that the ultramafics were submerged at that time and later re-exposed (Coleman and Kruckeberg, 1999). In contrast to the northern and central Sierra Nevada, the exposed serpentines of the Klamath Mountains were not covered by late Cenozoic volcanics.

Geographic data set

Our plant data came from two sources: the CalFlora database, which is a spatially referenced version of the state flora by Munz and Keck (1968), and the Jepson Manual (Hickman, 1993). CalFlora reports distributions by "subcounties," whereas the Jepson Manual reports distributions by "ecoregions." Intersecting the CalFlora subcounties with the Jepson ecoregions yields 300 spatial units, for each of which a plant species list can be generated. We overlaid these units with the state 1:1,000,000 geologic map (Jennings, 1977), selected those that contained serpentine, and lumped a few small slivers with their neighbors. The resulting 92 serpentine-containing spatial units, here called "subregions," form the basis for the analyses.

To obtain estimates of serpentine endemic richness by subregion, we compiled data from all available data sources, including the Jepson flora (Hickman, 1993), CalFlora, Kruckeberg (1984), numerous regional floras, and botanists with state, regional, and local expertise. For each data source, we listed the taxa (species and subspecies) that were reported to be positively associated with serpentine. We then gave each taxon a score of 1–6 based on each available data source (with 1 representing a tendency to be more common on than off serpentine and 6 being complete serpentine restriction) and averaged these scores across data sources. For our analyses, we defined "broad endemics" as all taxa reported to be associated with serpentine (i.e., a mean score of ≥ 1), and "narrow endemics" as taxa with mean scores > 4 . These are roughly equivalent to Kruckeberg (1984) "indicators plus endemics" and "endemics," respectively.

For each subregion we recorded the numbers of broadly and narrowly endemic species thus defined. From the geologic map, we obtained the total area of serpentine in each subregion, and from a state climate model (Daly et al., 1994), we obtained 30-year mean annual rainfall for each subregion (1961–1990). Other variables we have previously analyzed, but do not discuss here, are described in Harrison et al. (2000). To generate a consistent set of estimates of the ages of subaerial exposure of our subregions, we reviewed published geologic maps and the research described above.

Statistical analyses

To analyze the relationship between the richness of serpentine endemic plants and the estimated age of exposure, as well as other variables, we employed

multiple linear regressions. Independent variables included estimated age of exposure (either minimum or maximum), log area of serpentine, elevational range of serpentine, and mean annual rainfall. Dependent variables included the numbers of serpentine endemics per subregion, using either the broad or the narrow definition.

Because large uncertainties characterize some of the older estimated ages, and because it might be argued that beyond 5 m.y., ages of exposure become progressively less relevant to the diversification of the present-day flora, we also used either minimum or maximum ages of exposure transformed into a categorical variable (Pleistocene, Pliocene, or older, i.e., < 2 , 2–5, and > 5 m.y.).

Results

When endemic richness in the broad sense was regressed on maximum estimated age of exposure, log of serpentine area, annual rainfall, and elevational range, all of these variables were significant except for area, which as previously noted is subsumed by elevational range. In simple regressions, the proportion of the variation explained by estimated maximum age was relatively low ($r^2 = 0.09$) compared with other variables ($r^2 = 0.25$ for rainfall, 0.27 for area, and 0.41 for elevational range). The results were virtually unchanged when endemic richness in the narrow sense was used. When the minimum instead of the maximum estimated age of exposure was used, the age-diversity relationship was marginally significant ($p = 0.08$) and explained little variation ($r^2 = 0.04$). However, when either minimum or maximum estimated age of exposure was transformed into a categorical variable (< 2 , 2–5 or > 5 m.y.), then the relationship was highly significant ($p < 0.001$) and explained substantial variation in endemic diversity ($r^2 = 0.14$ – 0.18). The estimated age of exposure was not highly correlated with any of the other independent variables we examined (r always < 0.2).

These results were somewhat sensitive to our assumption that the Klamath serpentines have been exposed for a long time, about 50 m.y. When this estimate was lowered, the fit of the relationship deteriorated (e.g., 45 m.y.: $r^2 = 0.08$; 35 m.y.: $r^2 = 0.05$; 25 m.y.: $r^2 = 0.01$), and when it was increased the relationship improved (e.g., 70 m.y.: $r^2 = 0.13$). But when age was transformed to a categorical variable as described above, corresponding to the assumption that pre-Miocene age variation is largely

irrelevant, this issue disappeared. A bigger weakness in the age-diversity relationship characterizes the southern Sierra Nevada, which has very low endemic diversity despite estimated ages of exposure that could be as great as 50 m.y. If the maximum ages of exposure in this region were much less, then the age-diversity relationship would improve dramatically (e.g. 10 m.y.: $r^2 = 0.26$; 1 m.y.: $r^2 = 0.29$). Another problem involves the North Coast counties (Marin, Sonoma, Napa, Lake, Mendocino), where endemic diversity is high, and where the minimum age estimates range from 1 to 5 m.y. while the maximum estimates range from 16 to 40 m.y., depending in part on assumptions about the extent of Plio-Pleistocene volcanism. This region typifies the main reason that the maximum estimated age fits better than the minimum, although the transformation of age to a categorical variable once again largely negates this problem.

Discussion

Our analysis suggests that the age of exposure should be considered as a potential contributing factor to patterns in serpentine endemic diversity in California, together with other important variables such as climate and topography. The lack of strong correlations between age of exposure and the other significant predictor variables suggests that our results are not completely artefactual. The best support for the age hypothesis comes from the comparatively great age of exposure of the endemic-rich Klamaths, and from the north-to-south trends in age and endemic richness within the Coast Ranges. The main weakness of this hypothesis is the apparently high age yet low endemism of the southern Sierra Nevada. One possibility is that the area of serpentine in the southern Sierra that escaped marine submergence during the Tertiary was too small or fragmented to give rise to many endemic species. Clearly, our analysis could be improved by having much better estimates of the age of exposure of serpentine in certain key areas.

The plausibility of our results rests largely on the timing of evolutionary diversification in the lineages that include serpentine endemics. As described earlier, Raven and Axelrod (1978) argued that most serpentine-endemic herbs, which form about 80% of the state's serpentine endemics, are typical of the Californian "neoendemics" that diversified since the onset of the Mediterranean climate around 5 Ma. If it is true that the majority of serpentine endemics

diverged from their nonserpentine ancestors well within the past 5 m.y., perhaps even within the past 1-2 my, then the age estimates we have examined should have relatively little bearing on diversity. However, it has been argued that a proto-Mediterranean climate with drier summers than winters began to develop around 15 Ma (see Dallman, 1998). Some evidence suggests that extensive divergence began earlier than 5 Ma in certain herb lineages that include many serpentine endemics (B. Baldwin, pers. comm., 2003). More conclusive evidence on the timing of divergence in these lineages will undoubtedly arise as more molecular clock studies are conducted.

It is interesting to note that serpentine soils have been found to become less severe for plant life over time, as leaching of magnesium increases the calcium-magnesium ratio, and as biological processes cause nutrients to accumulate. For example, Alexander (1988) showed that older serpentine soils in the Trinity Ophiolite of northern California are more like "normal" soils in their productivity than are younger ones. This might lead to the opposite expectation than the one we tested here: that is, the diversity of serpentine endemics might *decrease* with age of serpentine exposure, if non-endemic vegetation takes over as the soils mellow. However, we found no evidence for this here, and it also does not fit the pattern observed in Cuba (Borhidi, 1991).

From the field part of our study, preliminary results suggest that the best predictor of the number of serpentine endemics within our 500 m² plots is the richness of the flora in the surrounding subregion (Harrison and Safford, 2004). Such positive correlations between local and regional diversity suggest that ecological communities are strongly shaped by the availability of species over evolutionary time (Ricklefs and Schluter, 1993; Cornell and Karlson, 1997). In turn, this means that ecologists studying contemporary processes such as competition, disturbance, or herbivory must be aware of the larger forces that shape and surround their study sites. In the case of serpentine plants in California, we suggest that a botanist wishing to observe a high concentration of endemic species may need to seek out a site within a region having dramatic topography, abundant rainfall, and serpentine that has been exposed for at least several million years. We hope that further elaborating such relationships between local diversity and regional processes will be of value in efforts to understand and conserve this rich and unique flora.

Acknowledgments

We thank B. G. Baldwin, E. M. Moores, and P. H. Raven for reviewing the manuscript, and P. S. Ward for valuable comments.

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