

REGIONAL AND LOCAL SPECIES RICHNESS IN AN INSULAR ENVIRONMENT: SERPENTINE PLANTS IN CALIFORNIA

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Abstract. We asked how the richness of the specialized (endemic) flora of serpentine rock outcrops in California varies at both the regional and local scales. Our study had two goals: first, to test whether endemic richness is affected by spatial habitat structure (e.g., regional serpentine area, local serpentine outcrop area, regional and local measures of outcrop isolation), and second, to conduct this test in the context of a broader assessment of environmental influences (e.g., climate, soils, vegetation, disturbance) and historical influences (e.g., geologic age, geographic province) on local and regional species richness. We measured endemic and total richness and environmental variables in 109 serpentine sites (1000-m² paired plots) in 78 serpentine-containing regions of the state. We used structural equation modeling (SEM) to simultaneously relate regional richness to regional-scale predictors, and local richness to both local-scale and regional-scale predictors.

Our model for serpentine endemics explained 66% of the variation in local endemic richness based on local environment (vegetation, soils, rock cover) and on regional endemic richness. It explained 73% of the variation in regional endemic richness based on regional environment (climate and productivity), historical factors (geologic age and geographic province), and spatial structure (regional total area of serpentine, the only significant spatial variable in our analysis). We did not find a strong influence of spatial structure on species richness. However, we were able to distinguish local vs. regional influences on species richness to a novel extent, despite the existence of correlations between local and regional conditions.

Key words: disturbance; geologic age; local richness; plant diversity; productivity–diversity; regional richness; serpentine; spatial habitat structure; species–area; species–energy; structural equation modeling.

INTRODUCTION

All ecological communities are the products of biogeographic history, the physical environment, and biotic interactions, but the relative roles of these factors in producing observed patterns in species richness remain incompletely integrated. Historical explanations are evidenced by relationships between species richness and such factors as time since glaciation, volcanic eruption, island emergence, and other major geologic events, or proximity to centers of species origin or persistence (e.g., Qian and Ricklefs 2000, Stephens and Wiens 2003, Hawkins et al. 2003b, Ricklefs 2004). Evidence for contemporary explanations often takes the form of correlations between species richness and climate, productivity, or other gradients in the physical environment (e.g., Adams and Woodward 1989, van Rensburg et al. 2002, Francis and Currie 2003, Hawkins et al. 2003a). Experimental and other evidence often support strong roles for species interactions and disturbance (e.g., Tilman 1982, Huston and DeAngelis

1994, Grace 1999, Grime 2001). A major challenge lies in building a conceptual framework that includes all of these elements, and within such a framework, evaluating hypotheses about specific factors while explicitly recognizing the influences of others.

One useful building block in such a framework is the idea that local communities, within which diversity responds to species interactions and disturbance, are embedded in regions whose species pools are relatively unchanging on an ecological timescale. In most communities that have been examined in this way, regional richness is a strong predictor of local richness, demonstrating that the regional availability of species is one key determinant of local richness (e.g., Cornell 1993, Partel 2002, Karlson et al. 2004, Ricklefs 2004). If regional richness provides a starting point for understanding local richness, however, the regional–local relationship also raises many further questions (Ricklefs 2004). For example, what determines the size of the regional species pool itself, and what additional factors lead to variation in local richness? Do environmental variables such as climate act primarily at the local or the regional scale, or could they affect richness in different ways at different scales? Is it possible to

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distinguish direct effects of the environment on local richness from indirect ones mediated by regional richness?

Another important element that has been missing from most previous work on local and regional richness is a consideration of spatial habitat structure. Many natural environments are insular at some scale, e.g., true islands, freshwater habitats, and rock outcrops. Spatial habitat structure could influence the ability of local sites to sample from their regional pools. For example, local communities on smaller or more isolated habitat patches might be expected to receive a smaller share of their regional pools than those on larger or less isolated patches (MacArthur and Wilson 1967, Harrison 1997, 1999), although isolation could also lead to slower competitive exclusion (Shurin and Allen 2001, Mouquet and Loreau 2003, Amarasekare et al. 2004). Habitat structure could also influence the size of the regional pool itself. For example, a region containing a larger total area of habitat is likely to support higher regional richness, both for evolutionary reasons such as enhanced speciation (Rosenzweig 1995), and ecological reasons such as habitat heterogeneity (Richerson and Lum 1980, Hawkins and Porter 2003). In addition, much theory suggests that the way that habitat is subdivided into patches of different sizes, shapes, and degrees of isolation could affect the regional richness of a community by influencing the ability of species to persist and coexist (e.g., Kolasa 1989, Case 1991, Caswell and Cohen 1993, Tilman 1994, Wiens 1995, Shurin and Allen 2001, Mouquet and Loreau 2003, Amarasekare et al. 2004).

Very little community-level empirical work has tested this body of spatial theory, except in microcosms and mesocosms where all other factors can be held constant. Observational studies at the single-species level have found mixed evidence for the proposition that the spatial configuration of habitat, as opposed to the total amount, affects population size and persistence (Flather and Bevers 1992, Fahrig 2002).

In this study we address these questions in the roughly 250 plant taxa endemic (restricted) to the >6000 km² of serpentine rock outcrops in California. The term "serpentine" as used by ecologists refers to ultramafic (Mg- and Fe-rich) rocks, principally serpentinite and peridotite, and the soils derived from them. Serpentine is a harsh environment for plants because of its low levels of Ca relative to Mg, exacerbated by low nutrient (NPK) levels and, in some cases, metal (Ni and Cr) toxicity and poor water-holding capacity. Throughout the world, vegetation on serpentine is more sparse, stunted, and xeromorphic than the vegetation of most other soils. Distinctive floras occur on serpentine, both because it excludes many plant species from the surrounding communities, and because it often supports substrate specialists ("serpentine endemics"). (For reviews of serpentine ecology, see Proctor and Woodell 1975, Brooks 1987, Kruckeberg 1992, and Roberts and

Proctor 1992.) Many serpentine endemics have narrow geographic distributions and are considered sensitive or rare taxa (Kruckeberg 1984, Brooks 1987, Skinner and Pavlik 1994).

The serpentine flora of California evolved in situ and is found nowhere else (Raven and Axelrod 1978), making it an unusually clearly defined group of habitat specialists. Evolutionists have long studied California's serpentine endemic flora as an example of the linkage between adaptation and speciation (Stebbins 1942, Raven 1964, Stebbins and Major 1965, Raven and Axelrod 1978). The floristics, distribution, and evolutionary ecology of this flora are well known (Kruckeberg 1954, 1984, 1992, Whittaker 1954), and considerable botanical, geological, and other large-scale data are available (e.g., Jennings 1977, Kruckeberg 1984, Hickman 1993, Skinner and Pavlik 1994, Jimerson et al. 1995). The regional richness of this flora is known to correlate broadly with climate (Kruckeberg 1984, 1992, Harrison et al. 2000). Within one region, very small outcrops are associated with lower local richness on a per-plot basis, as well as lower reproductive success in the endemic species *Calystegia collina*, than large outcrops (Harrison 1997, 1999, Wolf et al. 2000, Wolf and Harrison 2001). This history of prior studies sets the stage for our analysis of the role of habitat structure and other factors in shaping the local and regional richness of the entire serpentine flora of California.

Our hypotheses about spatial structure were: (1) for a given level of regional richness, local richness will be greater on larger and/or less isolated serpentine outcrops; (2) regional richness will be higher in regions with a greater total area of serpentine, and may also depend on the regional mean values of the area, isolation, shape, and/or number of serpentine outcrops; and (3) such spatial effects will be seen in habitat specialists, i.e., serpentine endemics, but not in the flora as a whole, which consists largely (>90%) of habitat generalists.

At the same time, we wished to evaluate these spatial hypotheses in the context of the fullest possible understanding of the environmental and historical influences on richness. By "environmental" we refer to variables describing current conditions at both the regional scale (e.g., regional climate) and the local scale (e.g., local soils, disturbance, vegetation, climate). By "historical" we refer to large-scale influences on richness that are not mediated by contemporary environmental conditions. One of these that we examined is "geological age," our term for the estimated time that serpentine has been available for plant colonization somewhere within a region. The age of oceanic islands (Rosenzweig 1995) and the age of exposure of serpentine in different regions of Cuba (Borhidi 1996) is positively correlated with endemic richness, presumably because of the availability of time for colonization and subsequent evolution. Our other historical variable was "geographic province," our term for the four major

TABLE 1. Variables used in this study, by category.

Variable, by category	Description
Local spatial	
Area	area of outcrop on which study site is located
Isolation	distance to nearest outcrop; area of serpentine within 1/10/100 km
Shape	circular ratio of outcrop; other FRAGSTAT metrics
Local environmental	
Cover	mean percent cover of woody species, herbs, rocks, bare soil, litter, animal disturbance
Slope and aspect	percentage of maximum solar radiation
Soil	texture, pH, total C and N, NO ₃ ⁻ , P, Ca ²⁺ /Mg ²⁺ , Ni ²⁺ , Cr ³⁺ , Co ²⁺
Climate	mean annual precipitation, temperature (January minimum, July maximum), productivity (NDVI†), in the 250 m radius circle surrounding the study site
Fire	presence or absence of recorded fire in past 100 years
Regional spatial	
Area	total area of serpentine in region
Isolation	distance between nearest-neighbor outcrops in region
Shape	number of outcrops, total perimeter, circular ratio, other FRAGSTATS
Regional environmental	
Climate	mean annual precipitation, temperature (January minimum, July maximum), productivity (NDVI), for whole region and for only its serpentine areas
Heterogeneity	spatial coefficients of variation of climate variables; elevational range; number of land cover types; all calculated both for whole region and for only its serpentine areas
Regional historical	
Geologic age	estimated time (Miocene or older; Pliocene; and Pleistocene or younger) that serpentine has been exposed to plant colonization somewhere in a region
Geographic province	four major serpentine-containing areas of the state (Klamath-Siskiyou Mountains, Sierra Nevada, North Coast Range, South Coast Range)

Notes: See *Methods* section for details.

† NDVI, normalized difference vegetation index.

serpentine-containing regions of the state; following Ricklefs (2004), we attribute variation in richness among provinces to their differing geologic and biogeographic histories.

What we have termed “spatial” factors might be considered either historical or contemporary, depending on whether their influences are thought to be ongoing or to have taken place primarily in the past. Since spatial factors are a major theoretical focus of our study, however, we retain them as a separate category. (See Table 1 for a list of variables by category, and the *Methods* section for further explanation.)

METHODS

Study system

Serpentine in California is found in four broad, geologically defined provinces: the Klamath-Siskiyou Mountains, the North Coast Range, the South Coast Range, and the Sierra Nevada (Kruckeberg 1984; R. G. Coleman, *unpublished data*; Fig. 1). Together it totals just over 6000 km², with individual outcrops ranging in size from a few square meters to hundreds of square kilometers. Serpentine vegetation ranges from conifer woodlands in the north, through chaparral in much of the state, to grasslands in the south. California has one of the temperate zone’s richest serpentine floras, with 200+ endemic taxa and another 200+ that show some degree of affinity to it (Kruckeberg 1984, Safford et al. 2005). Californian serpentine-endemic

plant richness is known to be highest in the Klamath-Siskiyou and North Coast Range and lowest in the Sierra Nevada and South Coast Range provinces, giving it a broad positive correlation with both rainfall and serpentine area (Kruckeberg 1984, Harrison et al. 2000).

Serpentine soils in California are unusable for farming, and logging has historically been rare, since trees tend to be small and sparse (Kruckeberg 1984). Watershed protection is one of the most common human “uses” of serpentine areas (Kruckeberg 1984). Where human disturbances such as mining, logging, and off-highway vehicle (OHV) use have occurred, they are generally easy to see, because vegetation and soil recovery are very slow. Fire has been much less noted as an influence on serpentine vegetation than on other vegetation in California (Whittaker 1960, Barbour and Major 1977). In earlier work, we found fire was less frequent in serpentine chaparral than in adjacent non-serpentine chaparral (73.7 ± 39 vs. 18.6 ± 3.1 yr since last fire; $N = 40, 40$; $P < 0.001$), and also less severe, because biomass is lower and patchier (Safford and Harrison 2004). We also found that both fire and livestock grazing had considerably less effect on plant richness in serpentine than in adjacent non-serpentine chaparral and grassland, probably because there is less light limitation in the more open serpentine vegetation (Harrison et al. 2003, Safford and Harrison 2004).

For the above reasons, most Californian serpentine vegetation, whether on public or private lands, is either

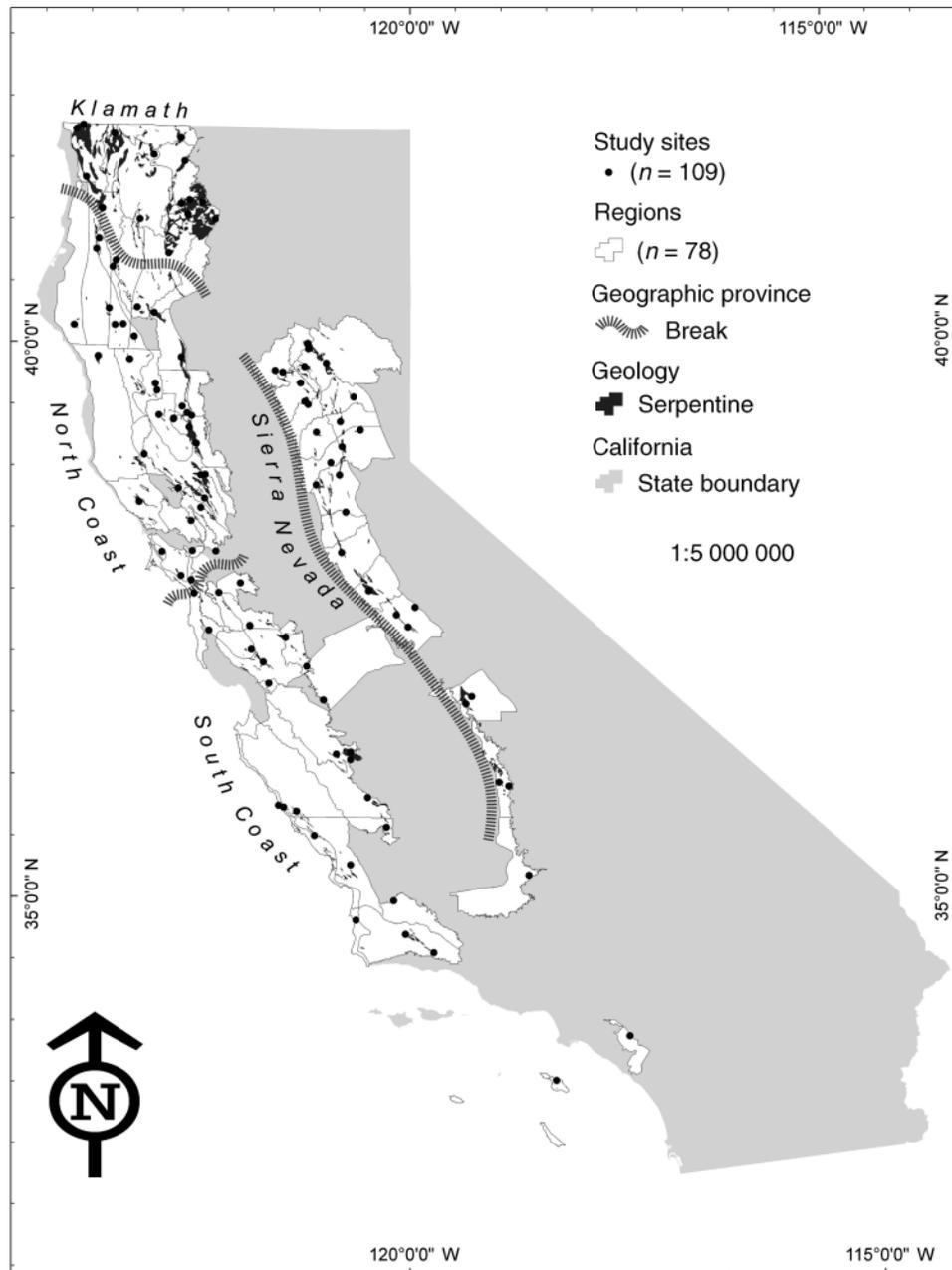


FIG. 1. Map of the study system in California, USA, showing provinces, serpentine outcrops, regions, and sampling sites.

relatively intact and late successional (the vast majority) or obviously disturbed. We dealt with disturbance in three ways: (1) avoiding sites with evidence of mining, logging, OHV damage, or recent fire, and sites <50 m from roads; (2) using a state database to ask whether each study site had been encompassed by a recorded fire in the past 100 years (this was true for only 13 of 109 sites, so we treated it as a binary variable); and (3) measuring at each study site the occurrence of disturbance by wild or domestic animals (hoofprints, trails, digging, scat). We also later examined

road density at the regional scale, and road proximity at the local scale, but found no significant effects on richness (J. H. Viers, *unpublished data*).

Local database assembly

We used unbiased multiscale sampling of richness (Stohlgren et al. 1997) in which “localities” or “sites” were pairs of 500-m² field plots on 109 serpentine outcrops around the state, and “regions” were 86 areal subunits into which we divided the serpentine-containing areas of the state. We sampled local plant richness

and environmental variables from April 2001 to July 2004. Our goals were to sample within as many as possible of the 86 regions, and to sample several sites within each of the larger regions. We succeeded in sampling 109 sites in 78 regions (Fig. 1); sites spanned 1200 km in latitude and from sea level to 2750 m elevation. We examined geologic, road, and ownership maps to identify accessible areas without reference to the vegetation. Specific sites were chosen by using topographic maps to identify locations where a cool (north-northeast) and a warm (south-southwest) slope were in close proximity, generally 10–200 m apart. We sampled on both public and accessible private lands.

At each site we established two 50×10 m plots, one on the north slope and one on the south slope, to capture the topographic component of local richness. Plot origins were determined by blind tosses of a flag. We recorded the identities of all plant taxa in the plots and in two 10×2 m and seven 1×1 m internal subplots (cf. Stohlgren et al. 1997). Plots were located by Global Positioning System, and the plots and subplots were marked. Species and subspecies were identified according to Hickman (1993), supplemented by county floras and local lists. Within the 1×1 m subplots, we recorded percent cover by each taxon and by rocks, bare soil, litter, and animal disturbance, and slope and aspect. We recorded woody species cover, height, and identity along a central 50-m transect.

From five of the 1×1 m subplots we collected soil samples at 5–15 cm depth; these were analyzed by Western A & L Laboratories (Modesto, California, USA) using the following methods: saturated paste pH (Rhoades and Miyamoto 1990); bicarbonate extractable phosphate (Olsen and Sommers 1982); ammonium acetate (1 M, neutral) extractable Ca^{2+} and Mg^{2+} (Thomas 1982); KCl (2 M) extractable NO_3^- (Keeney and Nelson 1982); diethylenetriaminepentaacetic acid (DTPA; 0.1 M) extraction of Ni^{2+} , Cr^{3+} , and Co^{2+} with measurement by inductively coupled plasma (ICP; Lindsay and Norvell 1978); micro-Dumas dry combustion using a Carlo Erba NA 1500 NC elemental analyzer for total C and total N (Fisons Instruments, Milan, Italy) (Dumas 1831).

In our analyses, we examined the Mg/Ca and Ca/Mg ratios because many studies have found that plant responses to serpentine are predicted by the relative amounts of these cations (see Proctor and Woodell 1975, Brooks 1987, Kruckeberg 1992, Roberts and Proctor 1992; also see Harrison 1999, Safford and Harrison 2004). We found no significant effects of Ca or Mg, and we used Mg/Ca because it yielded a better statistical fit than Ca/Mg. We combined our remaining soil variables, none of which showed significant bivariate relationships to endemic or total richness, into three principal component axes that explained 25.3%, 14.6%, and 12.2% of the variation. We combined slope and aspect into a single measure, percent of maximum solar radiation (Buffo et al. 1972).

Our sampling schedule was timed to accommodate differences among sites in peak flowering season based on latitude and elevation. Our general strategy was to sample each site at least three times in two years, with at least one visit early and one visit late in its site's peak flowering season. Our sampling was sufficiently complete that we almost always added <10% of the total list on the final visit.

To classify taxa as endemic to serpentine or not, we reviewed all available sources (Kruckeberg 1984, Hickman 1993, county floras). For the 669 taxa reported by any source as having some degree of affiliation with serpentine, we tabulated levels of serpentine restriction reported by each source. From this, we determined that 246 taxa met the criterion proposed by Kruckeberg (1984) for serpentine endemism, i.e., >85% of occurrences on serpentine (Safford et al. 2005). We used these 246 taxa as our list of serpentine endemics. In earlier analyses, results did not differ depending on whether we used a broader or a narrower definition of endemism (Harrison et al. 2000).

Because our goal was to get a single representative sample for each of the 109 sites, we combined the north and south plots at each site and accumulated across all sampling dates, and thus obtained one value of local serpentine endemic plant richness and one value of local total plant richness for each site. We averaged each environmental variable across the north and south plots and the 1×1 m subplots to obtain one value per site.

The field data were supplemented by several local-scale environmental variables from our Geographic Information System (GIS) analyses of published maps. These included the local spatial variables, i.e., area, isolation, and shape of the serpentine outcrop on which the sampling site was located. Isolation was measured in two ways: the distance to the next nearest outcrop, and the area of serpentine within radii of 1, 10, and 100 km of the sampling site. (The latter measures integrate area and isolation, and should be robust to small-scale map error.) Shape was measured using the circular ratio. Other GIS-derived local environmental variables included the mean rainfall, January minimum and July maximum temperature, productivity (normalized difference vegetation index, NDVI) of the 250-m radius circle surrounding the site, and whether a recorded fire in the past 100 years had encompassed the study site.

Regional database assembly

To define regions, we used the CalFlora database (*available online*)⁵ and the Jepson flora (Hickman 1993). CalFlora reports distributions in units called "subcounties," while Jepson uses "ecoregions." By intersecting the subcounties with the ecoregions, our database created smaller spatial units that are here

⁵ <http://www.calflora.org>

called “regions.” (A slightly modified version of our database, called “CalJep,” is available in Viers et al. [2005].) For each region, we generated a distributional species list; any species present in both a subcounty and an ecoregion was considered present in the region formed by their overlap. By intersecting these regions with the state geologic map (Jennings 1977), we obtained 98 regions containing serpentine; 12 were small slivers that we lumped with their neighbors. The resulting 86 regions formed the basis for our sampling, and the 78 regions in which we found sampling sites were used in our analyses. We constructed a database with the 78 regions as rows, and regional botanical, environmental, and spatial attributes as columns. Using our list of endemics, we calculated for each region one value of total richness and one value of endemic richness.

To quantify the regional species pool in a meaningful way, we constructed four elevational bands (500 m, 1000 m, 1500 m, and >1500 m), identified the corresponding band for each study site, and tabulated the corresponding number of species whose distributions intersected that band. On average, this was >85% of the total number of species in each entire region.

From the state climate model (Daly et al. 1994), we calculated for each region the 30-yr mean value of annual rainfall (1961–1990) and the mean January minimum and July maximum temperatures. To obtain the best possible predictive power, we calculated these climate variables in two ways: for each entire region, and for the serpentine areas within each region. For productivity, we used the remotely sensed index known as NDVI (normalized difference vegetation index), 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 spatially for each region and temporally for 2000–2004, using the same composite date (calendar day 129: ~8–23 May) and masking for yearly climatic conditions (i.e., clouds and snow) and water features.

To obtain measures of regional environmental heterogeneity, we calculated the spatial coefficients of variation (cv) for the rainfall, temperatures, and NDVI of each region. We calculated the elevational range (maximum minus minimum) of each region and of the serpentine within each region. We used the number of recognized land cover types in each region as another index of regional spatial heterogeneity (Vogelmann et al. 1988). We examined several measures of temporal environmental heterogeneity, but none approached significant correlations with richness (as also found by Richerson and Lum 1980) and so they are not further discussed.

Data on regional spatial habitat structure were obtained from the state geologic map (Jennings 1977), supplemented by more detailed measurements from local maps. Variables measured for each region included

the total area of serpentine; the number of outcrops; the total perimeter of outcrops; and the mean values of outcrop area, isolation (nearest neighbor distance), and shape. The shape metric we used was the circular ratio, i.e., the ratio of outcrop perimeter to the circumference of a circle with the same area as the outcrop; this is minimal for circular patches and increases as patches become complex in their shape (Forman and Godron 1986). We also tried a number of other spatial metrics from the program FRAGSTATS (McGarigal and Marks 1995), but they did not approach significance and are not further discussed.

“Geologic age” was a regional variable with three values (Miocene or older; Pliocene; and Pleistocene or younger). As we use this term, it represents the minimum time that we believe serpentine to have been available for plant colonization somewhere within each region. It was estimated through visual interpretation of 1:250 000 geologic maps by an expert in Californian tectonics and stratigraphy (J. Wakabayashi; see also Harrison et al. [2004] for details). “Geographic province” was a categorical variable with four values: Klamath Mountains, Sierra Nevada, North Coast Range, and South Coast Range. This variable is intended as a surrogate for large-scale aspects of biogeography that we could not otherwise measure.

Statistical analyses

Structural equation modeling.—We analyzed our data using structural equation modeling (SEM; see Mitchell 1992, 1993, Grace and Pugsek 1997, Shipley 1997, Pugsek et al. 2003). SEM is ideal for our purposes because it allows the testing of multivariate hypotheses in which some variables (e.g., regional richness) can simultaneously act as predictors and outcomes. In turn, SEM allows us to test whether a given effect is direct (e.g., rainfall influences local richness) vs. indirect (e.g., rainfall influences regional richness, which influences local richness). The SEM modeling process begins with the specification of a general model of relationships in the system under study, based on the investigator’s a priori and theoretical knowledge.

We created a general conceptual model of the relationships in our system (Fig. 2). We then constructed the best-fitting specific model that corresponded to the conceptual model, but in which general categories of variables were replaced by actual measured variables. Any specific predictor variable, to be considered significant and to remain in the final model, had to explain significant unique variance when the other variables were included in the model.

Our hypotheses about spatial structure are represented in the conceptual model (Fig. 2) by the relationships between local spatial influences and local richness (hypothesis 1) and between regional spatial influences and regional richness (hypothesis 2). Specific variables representing these concepts should remain in the final model for endemic richness, under hypotheses

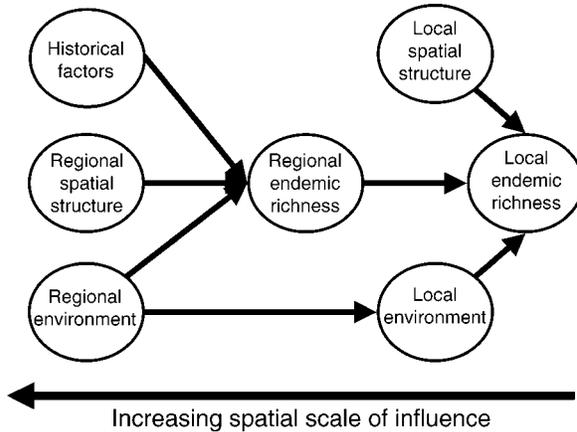


FIG. 2. Conceptual model of relationships in our study system. Variables in circles are general categories; specific variables corresponding to these categories are listed in Table 1.

1 and 2; however, they should not remain in the final model for total richness, under hypothesis 3.

The first step in the model-building process was to examine which local environmental variables (e.g., local rainfall, soil, vegetation, and disturbance) explained significant unique variance in local endemic richness. To this submodel, we then added the local spatial variables (e.g., area, isolation, and shape of the specific outcrops on which we sampled) and regional richness, which enabled us to evaluate hypothesis 1. To complete the model, we next added the regional environmental (e.g., climate, productivity) and regional spatial variables (e.g., regional total serpentine area, mean outcrop area, mean isolation, mean shape, perimeter) as predictors of regional richness, allowing us to evaluate hypothesis 2. Using parallel methods, we created a model of total (endemic plus nonendemic) plant richness to test hypothesis 3.

All variables were examined for distributional properties and transformed as necessary before analysis. We tested for linear relationships, and where justified by general theory (e.g., the humped relationship of richness to biomass, productivity, or fertility; Grace 1999, Grime 2001), we also examined quadratic relationships. Estimation was based on maximum likelihood. The adequacy of specific models was evaluated based on model chi-squares and associated *P* values, which is generally considered to be conservative; all other fit indices examined (e.g., Akaike's Information Criterion [AIC], Bayesian Information Criterion [BIC]) were consistent with the chi-square tests. Pathways included in the model were evaluated using *t* tests and by testing the consequences for model chi-square of omitting them from the model. The results are based on models found not to have a significant difference between expected and observed covariances based on a critical *P* value of 0.05. Path coefficients given in figures are standardized values, though analyses are based on actual covariances rather than correlations.

Spatial autocorrelation, or nonindependence in variables describing nearby spatial units, is ubiquitous in geographically based data. It can arise in either of two contexts, spatial pattern that is associated with predictor variables or spatial pattern in the error (residual) terms of statistical models. In the second case, though not the first case, it may compromise the robustness of significance tests (Legendre et al. 2002, Diniz-Filho et al. 2003, Hawkins and Porter 2003). To determine whether this was an issue in our study, we tested for spatial autocorrelation in the residuals of our models using semivariogram techniques (Rossi et al. 1992, Dale 1999, Mancera et al. 2005).

Multiple regression using generalized additive models.—Spatial effects could theoretically take a variety of nonlinear shapes, and SEM is limited in its ability to fit complex curves. As an additional way to test our hypotheses, we used generalized additive models (GAMs; Hastie and Tibshirani 1990), a special type of generalized linear model (GLM; McCullagh and Nelder 1989) that identifies highly nonlinear and nonmonotonic relationships even without prior specification. In four separate GAMs, we regressed local endemic, regional endemic, local total, and regional total richness on the same sets of local, regional, and spatial predictors that we used in our SEM modeling.

RESULTS

Overall richness

We found 1046 taxa in our field sampling, including 104 endemics (Appendix A). Local endemic richness averaged 5.27 ± 4.10 taxa (mean \pm SD), and local total richness averaged 63.16 ± 20.15 . Regional endemic richness averaged 37.28 ± 22.34 , and regional total richness averaged 1005.03 ± 156.05 . Endemics made up only $8.9 \pm 7.0\%$ of the local (per-site) total richness and $3.6 \pm 1.9\%$ of the regional total richness; thus the patterns we observed in total (i.e., endemic plus nonendemic) richness largely reflected nonendemics. Local total richness was not significantly correlated with local endemic richness ($r = 0.15$, $P > 0.05$). There was a significant correlation between regional total richness and regional endemic richness, however, suggesting (as our results later confirmed) that the endemic and nonendemic floras responded to common influences at the regional scale.

Endemic richness: SEM results

Local endemic richness and the local environment.—Our first submodel (Fig. 3) showed that 54% of the variation in local endemic richness can be explained by the combination of vegetation variables, rock cover, and Mg/Ca ratio. This supported the underlying assumption in our conceptual model that local richness is, in part, associated with local environmental gradients.

With respect to vegetation, local endemic richness was greatest at intermediate levels of overstory and

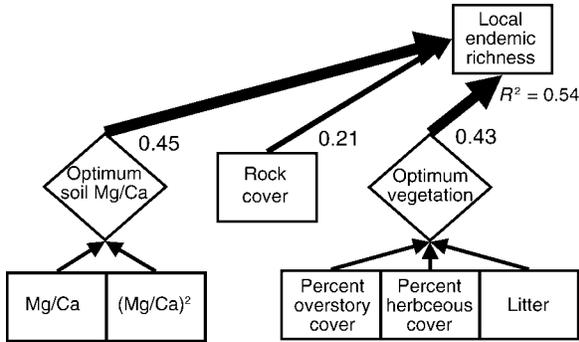


FIG. 3. Submodel relating local environmental variables to local endemic richness. Variables in boxes are observed variables, while those in diamonds represent composites. Numbers on arrows are standardized path coefficients.

litter cover, and declined at high levels of herb cover (Fig. 4). To simplify this set of relationships, least squares procedures were used to estimate a nonlinear predictor:

$$\hat{y} = \beta_{01}x_0 + \beta_{02}x_0^2 + \beta_{1H}x_H + \beta_{1L}x_L + \beta_{12}x_L^2 + \varepsilon$$

where \hat{y} is predicted local endemic richness, x_0 is overstory cover, x_H is herb cover, x_L is litter cover, β s are regression coefficients, and ε is random error. This predictor, termed "optimal vegetation," was substituted in place of the component variables in subsequent analyses. It represents the conditions of vegetation in which endemic richness was found to be highest.

Local endemic richness was low in plots with low rock cover, and peaked at intermediate values of the Mg/Ca ratio (Fig. 4). To capture the latter relationship, we modeled a nonlinear relationship between Mg/Ca and richness using an explicit second-order term and a composite of the influence of the two variables.

Adding local spatial influences and the regional pool.—In our next submodel, by adding the influences of local spatial variables and the regional species pool, we increased the variance explanation for local endemic richness to 62% (Fig. 5). However, we did not find that any local spatial variables contributed unique variance explanation for local endemic richness. Thus we found no evidence to support hypothesis 1.

Regional endemic richness was the sole contributor to the increase in R^2 from 0.54 to 0.62. This supported the assumption made by our conceptual model that local richness depends in part on the regional species pool.

Serpentine area within 100 km had a significant correlation with local endemic richness, but this could be explained entirely by its relationship to regional endemic richness (Fig. 5). In fact, the larger the scale of the spatial variable, the stronger was its correlation with local endemic richness: correlations were -0.17 (nonsignificant) for the area of the sampled outcrop, 0.18 (nonsignificant) for the area of serpentine within 1 km, and 0.34 ($P < 0.001$) and 0.53 ($P < 0.001$) for

the area of serpentine within 10 and 100 km, respectively. These results suggest that the effect of serpentine area on local endemic richness is entirely "top-down," i.e., it is mediated by regional effects.

Regional influences and the full model for endemic richness.—Our next step was to add regional influences on regional endemic richness. We found strong relationships with both regional productivity and regional precipitation, and a weaker relationship with regional serpentine area; in addition, regions of varying geological age and in different geographic provinces differed in their endemic richness (Fig. 6). These results supported the premise in our conceptual model that regional richness is shaped by both environmental (precipitation, productivity) and historical influences (age, province).

The significant effect of regional serpentine area provided support for our hypothesis 2 that regional spatial structure influences regional richness. The regional area of serpentine was strongly correlated with the area of serpentine within 100 km of our local study sites, which in turn was related (via regional endemic richness) to local endemic richness. Because the area effect on richness was entirely regional, our full model used the regional serpentine area instead of serpentine area within 100 km of the study sites.

No other variables contributed significant unique variance explanation for regional richness. Also, we did not find significant pathways from the regional variables that remained in the model to the local environmental variables that remained in the model, for example from regional rainfall or geologic age to local Mg/Ca ratio.

The full model (Fig. 7) explained 66% of the observed variation in local endemic richness and 73% of the variation in regional endemic richness. All variables in this model had unique variance explanation for either regional or local richness. The one exception is the total area of each region, which is included to show that its relation to regional endemic richness was explained entirely by the serpentine area within a region.

The correlations among all variables represented in the full model are a condensation of the full information matrix used to conduct the analysis (Appendix B). This matrix shows that both local and regional factors correlated significantly and fairly strongly with local and regional endemic richness, and that many of the predictors were intercorrelated.

We can summarize these results using "total effects" (Appendix C), which refers to the sum of direct and indirect pathways excluding undirected relations (i.e., correlations). In theory, total effects measure the net change that would occur in a response variable if a predicting factor were to change, allowing for changes in all associated pathways. We found that for local endemic richness, total effects were highest for geographic province, followed by soil Mg/Ca, vegetation,

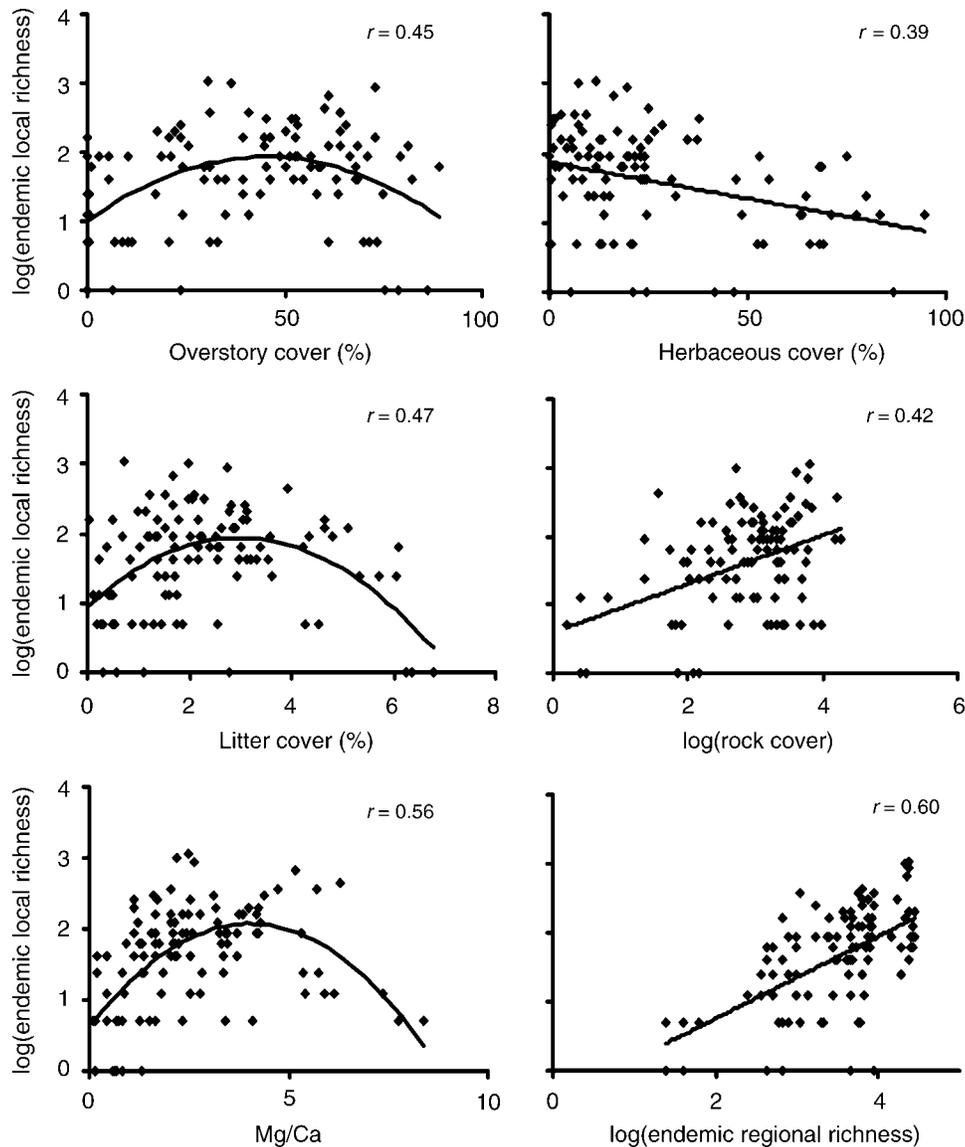


FIG. 4. Bivariate relationships of local endemic richness and local variables. The r values represent both nonlinear and linear relationships.

regional precipitation, regional productivity, and regional endemic richness. For regional endemic richness, total effects were strongest for productivity and geographic province, followed by geologic age, serpentine area, and precipitation.

Another way we can summarize the results is by comparing the unique variance explained by different groups of variables. This is done by removing groups of variables from the model and measuring the drop in variance explanation (i.e., semipartial regression). For local endemic richness, 20% of total variance was uniquely explained by local environment (soils, vegetation) and 10% by regional factors. Of the 10% explained by regional factors, 8% was due to regional

endemic richness and 2% to regional environment. The remaining 36% of explained variance was shared among these sets of variables. For regional endemic richness, 32% was uniquely explained by regional historical (geologic and geographic) conditions, 13% by regional environment (climate and productivity), and 4% by serpentine area. The remaining 24% of variance explanation was shared among these groups of variables.

Variograms demonstrated that there was no spatial autocorrelation in the residuals from the fitted models for either local or regional richness, and this was confirmed by a test of Moran's I statistic (local, $P = 0.20$; regional, $P = 1$).

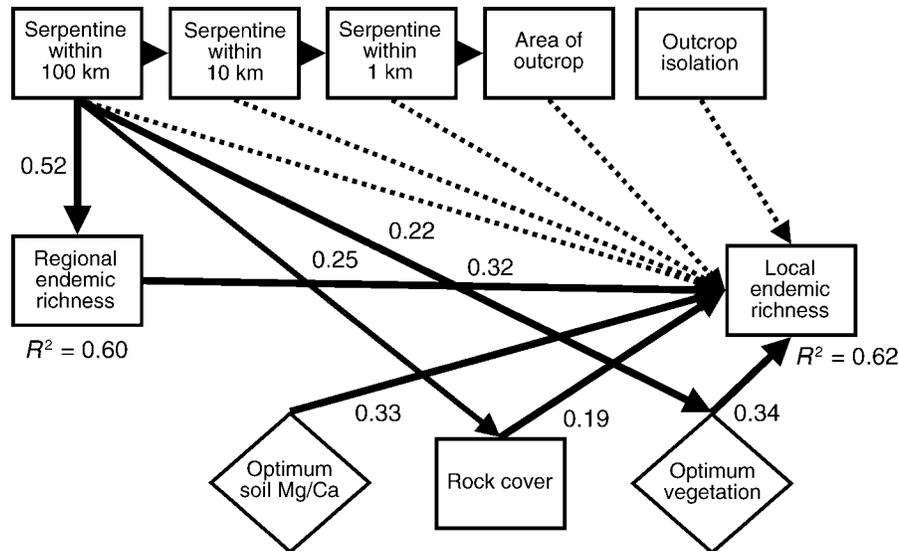


FIG. 5. Submodel relating local environmental variables, local spatial variables, and regional endemic richness to local endemic richness. Variables in boxes are observed variables, while those in diamonds represent composites. Numbers on arrows are standardized path coefficients. Dotted lines represent hypothesized pathways that were found to be nonsignificant.

Total richness: SEM results

Our SEM model for total richness explained 59% of the observed variation in local richness and 36% for regional richness (Fig. 8). There were no effects of any variables representing the spatial structure of serpentine, which supported our hypothesis 3. Local total richness was greatest in sites with high herb cover, moss cover, and animal disturbance, and with intermediate overstory cover. Regional richness did not explain any unique variance in local richness; all of the variance explained in local total richness was related to local environment.

Regional total richness was positively correlated with regional productivity, and thus indirectly to regional precipitation. Regional total richness was also positively correlated with the total area of the region. Finally, regional total richness was related to geographic province, mainly because it was lower than expected in the Sierra Nevada (Fig. 8).

Endemic and total richness: GAM results

Results from our generalized additive models (GAMs) supported our SEM inferences about spatial structure. Regional serpentine area was a significant predictor of regional endemic richness; regional total area was a significant predictor of regional total richness (both $P < 0.001$); and no spatial variables were significant predictors of local endemic or local total richness (P always > 0.10). These results were robust to the inclusion or exclusion of the suite of other environmental variables in the GAM models, and there were no substantive differences in the results from the GAM and SEM approaches.

DISCUSSION

We found little evidence for our first hypothesis, namely that outcrop area, isolation, or other aspects of spatial habitat structure exert direct influences on local richness. This contrasts with earlier studies that found lower endemic plant richness in plots on very small (0.5–3 ha) serpentine outcrops compared with equally spaced and sampled plots on large (>5 km²) outcrops within a region (Harrison 1997, 1999). However, the present study examined the full range of outcrop sizes, as well as the shape and isolation of outcrops, rather than the extremes of tiny vs. large. We conclude that spatial structure does have the potential to affect local endemic richness in our system, but that its effects are not strong enough to be evident across the study system as a whole, at least given the limitations of our approach. Although our first hypothesis was motivated to some extent by the MacArthur and Wilson (1967) theory of island biogeography, which was an important starting point for the subsequent development of spatial ecological theory, our results neither support nor refute the original MacArthur and Wilson model. Our system is inappropriate for such a test, both because it lacks a clearly defined mainland, and because serpentine “islands” are not truly insular, but exchange species with the surrounding matrix over ecological and evolutionary time (Kruckeberg 1991). Our results suggest that in systems with such features, local environmental variation has the potential to overshadow any influences of patch size and isolation on local richness.

We found that the richness of endemics at the local scale was strongly shaped by local environmental variation, a consideration that is often overlooked in spa-

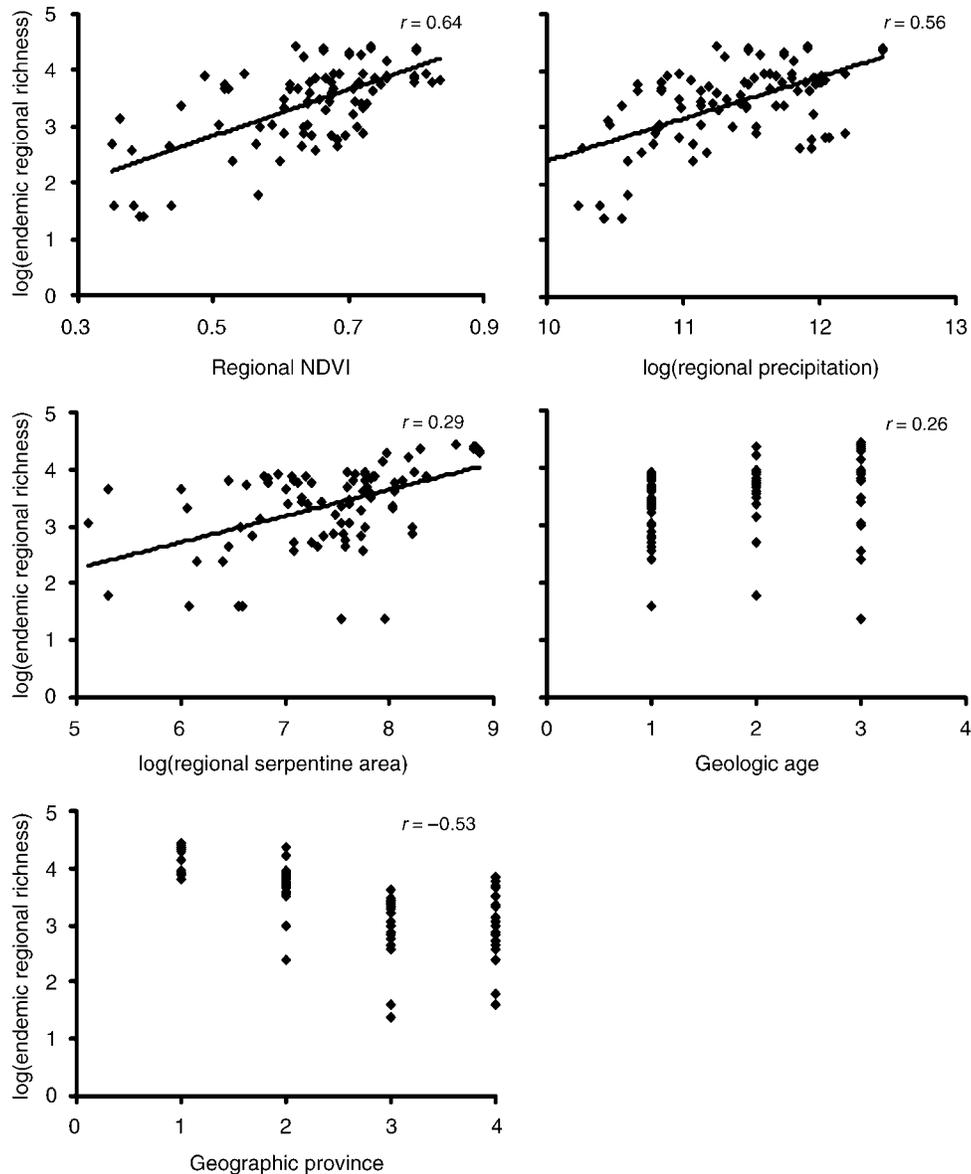


FIG. 6. Bivariate relationships of regional endemic richness and regional variables. Geologic age is defined as: 1, Miocene or older; 2, Pliocene; and 3, Pleistocene or younger. Geographic province is defined as: 1, Klamath Mountains; 2, Sierra Nevada; 3, North Coast Range; and 4, South Coast Range. The r values represent both nonlinear and linear relationships.

tial theory. The unimodal influences of the soil Mg/Ca ratio and vegetation (i.e., the combination of leaf litter and woody cover) may be an example of the hump-shaped relationship between productivity and local richness, where richness is reduced by abiotic stress at one end of the productivity gradient and by competition at the other; such a relationship is frequently observed, although it is often weak (Grace 1999, Grime 2001). Both these effects and the positive influence of rock cover are biologically reasonable, given that serpentine endemics have generally been found to be confined to serpentine because they require the reduced competition characteristic of harsh, open, rocky sites (Kruck-

eberg 1954, Brooks 1987). The two unimodal effects suggest that some serpentine sites are too harsh even for endemics, illustrating the role that local factors can play in filtering the species pool (Gough and Grace 1999).

Regional endemic richness was positively related to the total area of serpentine within a region, supporting our second hypothesis. Regional endemic richness was not affected by any measures of spatial structure other than total area, however. Thus our study did not provide support for the array of spatial ecological theory predicting that the spatial configuration of habitat should affect community structure (e.g., Kolasa 1989, Case

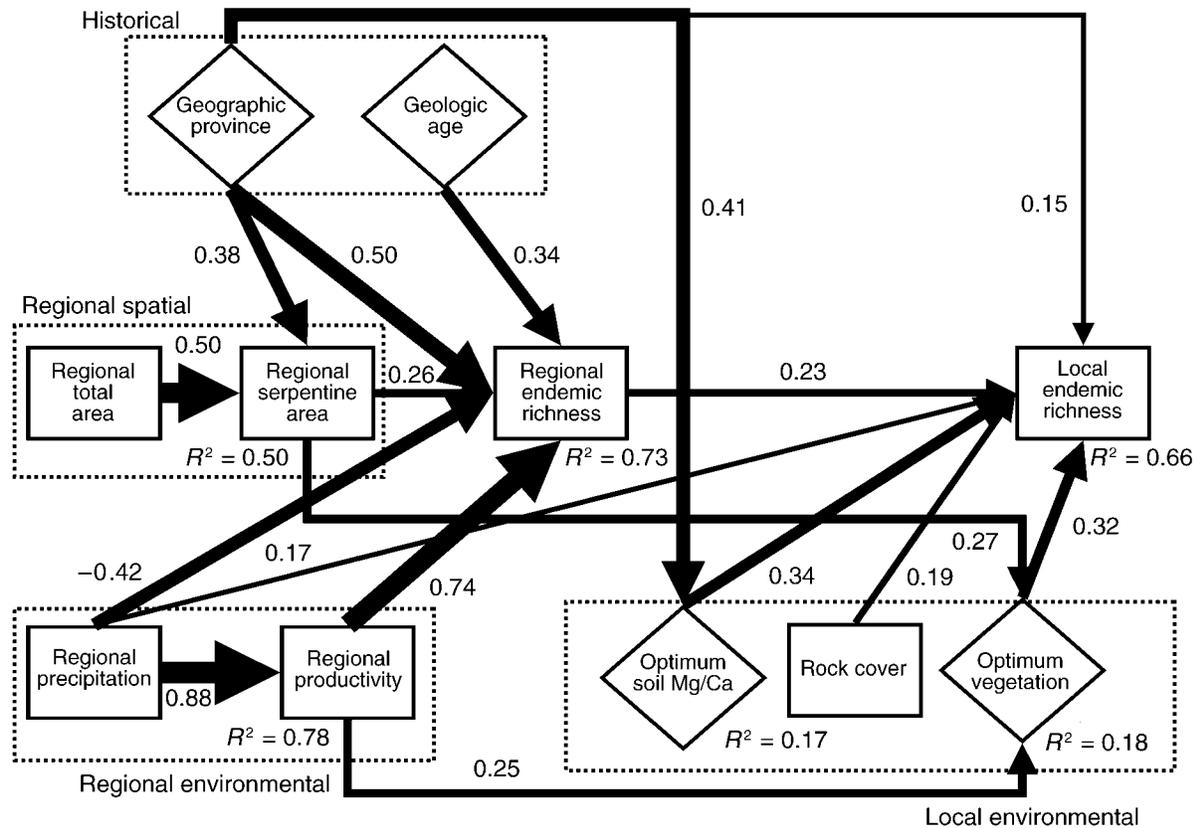


FIG. 7. Full model for endemic species richness. Variables in boxes are observed variables, while those in diamonds represent composites. Numbers on arrows are standardized path coefficients.

1991, Caswell and Cohen 1993, Wiens 1995, Shurin and Allen 2001, Mouquet and Loreau 2003, Amarasakare et al. 2004). Other authors, studying the population size and persistence of single species, have found that the effects of habitat configuration may be weak or nonexistent except within certain narrow ranges of other factors, such as total area, dispersal rates, and mortality rates (Fahrig 2002, Flather and Bevers 2002). Our results may be a community-level manifestation of the same phenomenon. For example, our regions may be too heterogeneous in their total serpentine area, or competition and extinction may be too slow relative to colonization, for spatial structure to have a strong impact on regional endemic richness.

Previous studies have found regional environmental heterogeneity to be a significant predictor of richness in Californian plants (Richerson and Lum 1980) and butterflies (Hawkins and Porter 2003). However, we examined many measures of regional heterogeneity, and none of them explained any unique variance in endemic or total richness. One possible explanation for this difference between our results and others is that serpentine is such a strong environmental “filter” that it makes regional heterogeneity less important to richness. In any case, because we found that the influence of regional serpentine area on regional endemic richness

was not mediated by heterogeneity, we speculate that it may instead have an evolutionary cause: i.e., as also suggested by Kruckeberg (1984, 1991), our result may be a case of the often-observed pattern that larger areas are more diverse because they provide greater opportunity for speciation (Rosenzweig 1995).

Regional endemic richness appeared to be strongly affected by rainfall via the effect of rainfall on productivity. This agrees with previous studies in California (Richerson and Lum 1980, Hawkins and Porter 2003), and also with species–energy theory, which finds a generally strong association between productivity and diversity at the regional scale (Francis and Currie 2003, Hawkins et al. 2003a). Interestingly, we found that once productivity was included in the model, the residual effect of rainfall on regional endemic richness was negative, meaning that regions with unusually high rainfall for their level of productivity (e.g., cold, high-elevation regions) were especially low in serpentine endemic richness.

Regional endemic richness was affected by both of our historical variables, geologic age and geographic province. As we used the term, “geologic age” is a coarse estimate of the length of time that some serpentine within a region has been exposed above oceans, inland seas, sediments, volcanic deposits, or other over-

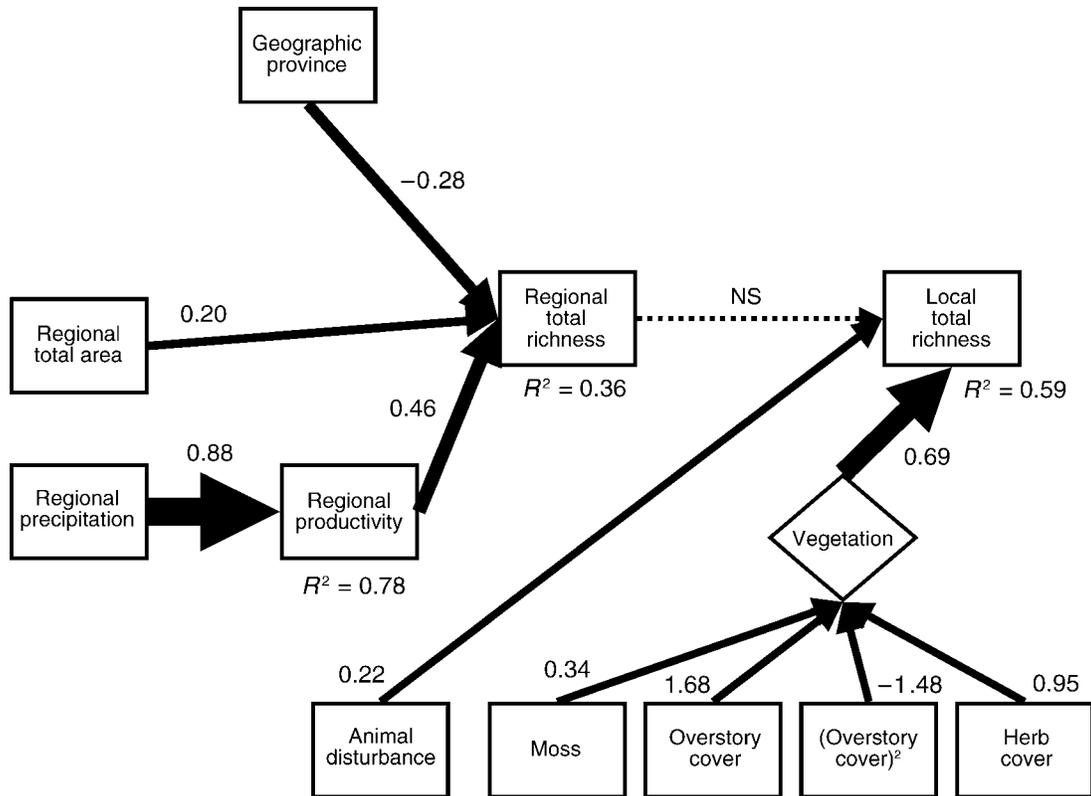


FIG. 8. Full model for total (endemic plus nonendemic) species richness. Variables in boxes are observed variables, while those in diamonds represent composites. Numbers on arrows are standardized path coefficients.

lying material; it is intended to indicate the time that has been available for plants to colonize serpentine in a region, and perhaps to subsequently evolve. Age in this sense is a good predictor of endemic richness on oceanic islands (Rosenzweig 1995) and Cuban serpentine (Borhidi 1996). We found that regions where serpentine has been exposed only since the Pleistocene or more recently ($<2 \times 10^6$ yr) were significantly less endemic rich than regions where serpentine has been exposed longer (see also Harrison et al. 2004). Our variable “geographic province” signifies that richness in the Klamaths, Sierra Nevada, and North and South Coast Ranges differed for reasons that we could not otherwise explain. While we speculate that this effect reflects biogeographic history (Ricklefs 2004), it could also reflect aspects of the environment for which we do not have good measures.

Our model for total plant richness showed no effects of the amount or spatial distribution of serpentine on either the local or the regional scale, supporting our third hypothesis. Over 95% of taxa at the regional scale, and over 90% at the local scale, were habitat generalists rather than serpentine endemics. Most theory about the effects of spatial habitat structure on community structure implicitly or explicitly concerns habitat specialists (although see Holt [1997]). If we had found effects of spatial structure on total richness, it would have sug-

gested problems in either our data set or our interpretations.

In many other ways, the models for total and endemic richness were similar, especially in the strong effects of local vegetation on local richness, and of rainfall, productivity, and geographic province on regional richness. One interesting difference was that animal disturbance had a significant effect on total richness but not serpentine-endemic richness. This is in good agreement with our previous work (Harrison et al. 2003, Safford and Harrison 2004) and with other studies showing that disturbance tends to promote habitat generalists rather than habitat specialists (e.g., Huntly and Inouye 1988, Stromberg and Griffin 1996).

Many previous studies have analyzed geographic patterns in regional richness, sometimes with the goal of testing historical vs. contemporary explanations (see Ricklefs 2004); a few have taken the approach that we did of trying to understand the relative contributions of both sets of factors (e.g., Hawkins and Porter 2003, Hawkins et al. 2003b). However, ours is the only study we know of that has come to grips with the fact that historical and contemporary variables may be partially correlated with one another, and thus not possible to completely disentangle. Our study demonstrates the ability of SEM to add clarity to the results in such cases, by explicitly quantifying the shared variance as well

as the variance that is uniquely attributable to each set of explanatory factors.

Another novel feature of our study is that it asked which influences on richness operated at the local vs. the regional scales. We found that climate, habitat area, geographic province, and geologic age act primarily to determine the size of the regional pool, which is consistent with the idea that “environmental determinism” as revealed by environment–diversity correlations may still have an evolutionary explanation (Ricklefs 2004). We found that local variation in soils and vegetation strongly influence local richness, but that regional richness has a measurable effect at this scale as well, even after correlations due to the environment are accounted for. We conclude that the combination of multiscale sampling and structural equation modeling allows us to make significant progress toward a more complete understanding of how environmental gradients and history interact to shape patterns in species richness.

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APPENDIX A

A species list from field surveys (*Ecological Archives* M076-003-A1).

APPENDIX B

Bivariate correlations (linear and nonlinear) among variables included in the full model (*Ecological Archives* M076-003-A2).

APPENDIX C

Standardized total effects of predictors on local and regional endemic richness (*Ecological Archives* M076-003-A3).