

## INVASION IN A DIVERSITY HOTSPOT: EXOTIC COVER AND NATIVE RICHNESS IN THE CALIFORNIAN SERPENTINE FLORA

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**Abstract.** Exotic species have been observed to be more prevalent in sites where the richness of native species is highest, possibly reflecting variation among sites in resources, propagule supply, heterogeneity, or disturbance. However, such a pattern leaves unclear whether natives at species-rich sites are subject to especially severe impacts from exotics as a result. We considered this question using path models in which relationships between exotic cover and native richness were evaluated in the presence of correlated environmental factors. At 109 sites on serpentine soils across California, USA, exotic cover was positively correlated with total native herbaceous richness and was negatively correlated with the richness of both serpentine-endemic and rare native herbs. However, in path models that accounted for the influences of soil chemistry, disturbance, overstory cover, and regional rainfall and elevation, we found no indication that exotic cover reduced any component of native herb richness. Rather, our results indicated similarities and differences in the conditions favoring exotic, native, endemic, and rare species. Our results suggest that, in spite of some localized impacts, exotic species are not exerting a detectable overall effect on the community richness of the unique native flora of Californian serpentine.

**Key words:** California; diversity hotspot; endemic plants; exotic richness; invasive species; native richness; path models; SEM; serpentine flora; serpentine soils; structural equation modeling.

### INTRODUCTION

Already considered one of the major threats to biodiversity, exotic species have become an even greater concern since recent studies have shown that more of them may tend to invade locations that are rich in native species (Lonsdale 1999, Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003, Bruno et al. 2004, Davies et al. 2005). Exotic and native species richness typically have been found to be positively correlated among sites at large scales, such as parks and other protected areas in the intermountain United States (Stohlgren et al. 1999). Such patterns have been interpreted to mean that resource availability (Stohlgren et al. 1999), propagule supply (Levine 2000), disturbance (Brown and Peet 2003), or internal heterogeneity (Davies et al. 2005) vary among sites in ways that affect exotic and native species similarly. Left unanswered is a key question: do such patterns mean that native species within diversity “hotspots,” especially the endemic or rare species that contribute most to global biodiversity, are under especially severe threat from the impacts of exotics? Alternatively, are the per-species impacts of invasion on natives equivalent across sites that vary in both resource levels and native species richness?

Questions about the impacts of exotic species are best answered through experiments (preferably remov-

als, not additions) or by detailed time-series analyses. However, managers do not always have the time or resources for such methods, especially when prioritizing exotic species control efforts over large geographic scales. Here we combine survey data with structural equation modeling (Shipley 1997, Grace and Pugsek 1998, Pugsek et al. 2003) to ask whether exotic plant cover has a direct relationship to several components of native species richness (total, endemic, and rare native herbs), in models that also take into account the indirect relationships generated by such factors as soils, disturbance, heterogeneity, and climate. We consider exotic cover rather than exotic richness because, although the two are highly correlated in our data, exotic cover should provide a more direct measure of impact. We consider only herbs for three reasons: there are no exotic trees or shrubs in our system; native woody species are unlikely to suffer from competition with exotic herbs; and woody species form a minor percentage (<10%) of total, endemic, and rare native species richness in our system.

Our study system is the flora of serpentine rocks and soils in California. Serpentine (or ultramafic) substrates are harsh environments for plants because of their low levels of calcium and nutrients and their excessive levels of magnesium and other metals (Kruckeberg 1984, Brooks 1987). In California, serpentine supports a rich flora of endemic (soil-restricted) plants that contribute disproportionately to the state’s status as a biodiversity hotspot (Myers et al. 2000, Stein et al. 2000). Over

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200 plant species, or >10% of those that are found only in California, are also found only on serpentine, although these soils form <2% of the state's surface area (Kruckeberg 1984, Safford et al. 2005). Serpentine is also botanically significant for a second reason: it harbors many native species that are soil generalists, but that have largely been displaced from more fertile substrates by the exotic species that now dominate much of lowland California (Kruckeberg 1984, Huenneke et al. 1990, Gram et al. 2004). Around the world, not only serpentine, but also other harsh and unusual soils, provide significant havens for native species richness and endemism (Anderson et al. 1999, Kruckeberg 2004).

Serpentine floras in California and elsewhere are not free from invasions, however, and threats from exotics appear to be increasing. Contributing factors include natural disturbance and rainfall variability (Hobbs and Mooney 1991, 1995), atmospheric N deposition (Weiss 1999), fire (Safford and Harrison 2004), the evolution of increased serpentine tolerance in exotics (Harrison et al. 2001), changes in microbial communities (Batten et al. 2005), propagule limitation in native species (Seabloom et al. 2003), and the spread of unusually serpentine-tolerant exotics such as barbed goatgrass (*Aegilops triuncialis*) (Meimberg et al. 2005). Several hundred plant species that are partly or wholly restricted to serpentine in California are officially considered rare (Skinner and Pavlik 1994, Safford et al. 2005). For at least some of these rare species, exotics are considered to be among the principal threats, together with habitat conversion and natural rarity (USFWS 1998).

The goal of our study was to ask whether, on a broad statewide basis, the serpentine environment is generally a secure refuge for its total, endemic, and/or rare native herb flora; or alternatively, whether there is a detectable negative influence of exotics on any of these components of native herb richness on serpentine. To answer this question, it is necessary to sample the flora widely and representatively, and to measure environmental predictors that enable the separation of direct relationships from those created by joint environmental influences. We sampled herb species richness and cover at 109 serpentine sites in a geographically stratified fashion across the state. We used field measurements and geographical information system (GIS) data to obtain >50 potential predictors of species richness and cover, including measures of soils, disturbance, spatial heterogeneity, landscape features, and climate. In a previous study, we used these data to ask questions about the effect of habitat spatial structure on endemic species richness (Harrison et al. 2006).

Here we used these data to ask, first, what are the simple correlations between exotic species cover and each component (total, endemic, rare) of native herb species richness on serpentine? Second, in structural equation models that include relevant environmental predictors, does exotic cover retain a direct negative

relationship to any component of native herb richness? A positive answer to this question would imply that exotics are an important factor in shaping the current distribution of native herb diversity on serpentine. Third, what specific environmental variables underlie the observed geographic patterns in exotic cover and native richness?

## METHODS

### *Sampling*

Serpentine in California is found in the Klamath-Siskiyou Mountains, the North and South Coast Ranges, and the Sierra Nevada. Its vegetation ranges from forest, woodland, and barrens at higher elevations and latitudes, through shrublands interspersed by barrens and grasslands, to primarily grasslands in lowland and southern situations.

To attain broad, representative coverage, we used a spatially referenced floristic database (Viers et al. 2005) combined with the state geologic map (Jennings 1977) to stratify the serpentine-containing parts of the state into 86 contiguous spatial units that we refer to as regions. Within each region, we examined geologic, road, and land ownership maps to identify accessible areas and approximate sampling sites without reference to the vegetation. Specific sites were chosen by using topographic maps to identify locations where a cool (N-NE) and a warm (S-SW) slope were in close proximity, generally 10–200 m apart. In the larger regions, we looked for >1 site, and in eight regions we could not find sites. We succeeded in sampling 109 sites in 78 regions, spanning 1200 km in north-south extent, and from sea level to 2750 m elevation. (for a map of serpentine outcrops, regions, and sampling sites, see Harrison et al. [2006: Fig. 1]).

At each site we established two 50 × 10 m plots, one on the cool and one on the warm slope, to measure the contribution of local topography to species richness. Plot origins were determined by blind tosses of a flag. We recorded overstory cover along a central 50-m transect. We recorded the identities of all species in the plots and in seven 1 × 1 m internal quadrats (five on the central transect and two at opposite corners of the plot). Plots were GPS-located and the plots and subplots were marked. Within the 1 × 1 m quadrats, we recorded percent cover by each species and by rocks, bare soil, litter, and animal disturbance (percent cover by trails, prints, burrowing), and the slope and aspect. We combined slope and aspect into a single measure of solar radiation using standard tables (Buffo et al. 1972). We calculated a mean and a coefficient of variation (cv) of each variable for each plot. We noted whether or not the site was grazed by livestock.

From five of the 1 × 1 m subplots we collected soil samples at 5–10 cm depth; these were kept in a cooler until analysis, and were analyzed for NO<sub>3</sub>-N, P, K, Ca, Mg, pH, texture, and trace elements (Cu, Zn, Co) by

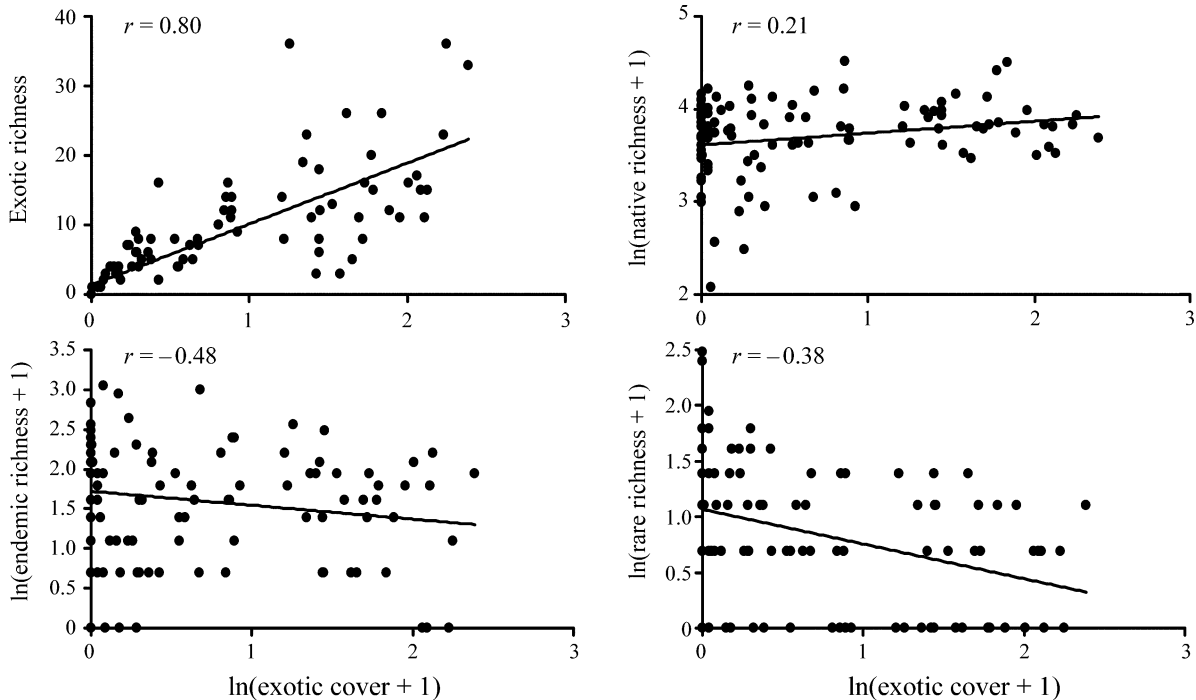


FIG. 1. Scatter plots showing bivariate relationships between various types of species richness and log-transformed exotic plant cover.

Western A&L Laboratories (Modesto, California, USA). In our analyses, we used the Ca/Mg ratio because previous work and preliminary analyses pointed to the key significance of this ratio in controlling plant responses to serpentine soil.

Species were identified using Hickman (1993), supplemented by county floras and local species lists. We identified taxa to subspecies in cases where the subspecies might be endemic to serpentine.

We conducted field sampling from April 2001 to July 2004. Our sampling schedule was timed to accommodate differences among sites in their peak flowering season based on their latitude and elevation. Our strategy was to sample each site at least three times in two years, with at least one visit early and one visit late in the site-specific peak flowering season. Our sampling was sufficiently complete that we almost always added <10% of the total species list on the final visit. Because our goal was to get a single representative sample for each of the 109 sites, we combined data across sampling dates and north-south plots to obtain one list of species for each site.

In addition to the field-collected data, we obtained measures of regional climate, including the mean, minimum, maximum, and standard deviation of annual rainfall and temperatures, from the state climate model (Daly et al. 1994). We obtained measures of regional topography, including the mean, minimum, and maximum elevation of serpentine in each region, from the state geologic map (Jennings 1977) and 30-m digital

elevation data (U.S. Geological Survey 2005). We measured the effects of roads at two scales. At the local scale, we obtained proximity of each site to the nearest highway, primary road, secondary road, or vehicular trail. At the regional scale, we calculated a measure of density (km/km<sup>2</sup>) for type of road and for all roads within the region. We used road vectors designated within a statewide transportation network created in 1996 (California Spatial Information Library 2002).

#### *Species information*

To characterize species as exotic or native, we used the state flora by Hickman (1993). To characterize species or subspecies as endemic to serpentine or not, we conducted an exhaustive survey of Californian botanical information (published literature, gray literature, expert information, and herbarium records), and found 669 species or subspecies that were reported by at least one source to have some degree of association to serpentine. We ranked each taxon from 1 to 6 for its degree of restriction as reported by each source (1, weakly positively associated with serpentine; 6, completely restricted to serpentine), and averaged these across sources to obtain one score for each species. To maximize consistency with previous literature (e.g., Kruckeberg 1984), we called a taxon "endemic" if its score was  $\geq 4.5$ , indicating that roughly >85% of its known occurrences were on serpentine. By this definition, there are 246 serpentine endemic species or subspecies in California, as compared with the 215 tabulated by

Kruckeberg (1984). For complete details, see Safford et al. (2005).

Our information on rarity came from the California Native Plant Society's rare plant inventory (Skinner and Pavlik 1994). Of our 246 endemics, 194 are rated by this source as "rare or uncommon," including 111 state and/or federally listed taxa.

We used these species lists to tabulate, for each of our sampling sites, the mean percent cover of exotic species and the total richness of exotic, native, serpentine-endemic, and rare herbaceous species.

### Analyses

Structural equation modeling (SEM; Bollen 1989) was used to examine the relationships between exotic cover and native species richness in the presence of environmental variables. This analysis was motivated by the fact that variables under common influence by environmental conditions can possess correlations that result from these influences rather than from any direct interaction. We constructed models in which we could partition the association between exotic cover and species richness into direct and indirect components. By indirect associations, we mean those that can be attributed to correlated influences (e.g., common habitat or soil associations). By direct associations, we refer to the residual relationships between exotic cover and richness once other variables have been statistically controlled, typically represented in SEM models by a simple or compound directed pathway. (In this application, indirect and direct associations should not be confused with direct and indirect "effects," which are commonly calculated in SEM analyses but which refer only to directed pathways between a predictor and response variable.)

We felt that, on theoretical grounds, it made most sense to model the effects of exotic cover on native richness, as it should be the abundance of exotics that causes an impact on natives. However, in order to be thorough in our analyses, we also examined models that included exotic richness. The inclusion of exotic richness yielded the same conclusions as when only cover was used; because these models were considerably more complex, but not more informative, we chose to present the results from models with exotic cover only. To further achieve clarity in presentation, separate models were used to represent the relationships of exotic cover to total native species and endemic and rare species. Endemic and rare species were included in a single model because the rare species in this study are a subset of the endemics.

Analyses were performed using the software M-plus (Muthén and Muthén 2005) and maximum likelihood procedures. Prior to SEM analyses, all variables were examined for distributional properties and the linearity of relationships. Logarithmic transformations yielded linear bivariate relations in the great majority of cases. Certain relationships required nonlinear specification

in the models. The adequacy of models was evaluated based on model chi-squares and associated  $P$  values, as well as whether residuals indicated omitted paths. The use of a chi-square assessment of model fit is generally considered to be conservative. Other fit indices examined (such as AIC, BIC, and RMSEA) were consistent with chi-square tests. Pathways retained in the model were also evaluated using  $t$  tests and single-degree-of-freedom chi-square tests. All results presented 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.

Our models included composite variables (Heise 1972, Edwards 2001, Grace, *in press*) as well as latent variables. In this case, latent variables (indicated in the figures by circles) represent the unmeasured true values of cover and richness components. Latent variables are included in this case simply to make the point that we are interested in the true values, although we only have imperfect measures by which to gauge them. Composite variables (indicated in the figures by hexagons) represent the combined effects of collections of variables, such as those related to soils, overstory, disturbance, and regional environmental features (precipitation and elevation). The specific variables described under *Sampling methods* were all examined for inclusion in these composites. Only those variables that contributed to explaining variance in exotic cover or any of the forms of richness (listed in Appendices A and B) were kept in the final models. Because models included composites, model evaluation was conducted using a two-stage procedure. In the first stage, models without composites (referred to as "reduced-form" models) were analyzed. This procedure was used because models containing composites do not permit tests of all parameters because some must be specified to construct the composites. In the second stage of the analysis, composite variables were included and estimations of the composite effects were obtained. Model fit was identical for the reduced form and composite models.

### RESULTS

Local species richness (mean  $\pm$  SD) in the 1000-m<sup>2</sup> plots averaged  $42.6 \pm 15.6$  species (total natives),  $5.3 \pm 4.1$  (endemics),  $1.8 \pm 1.9$  (rare species), and  $7.19 \pm 8.0$  (exotics). Cover values averaged  $36.3\% \pm 30.3\%$  (native herbs),  $20.1\% \pm 42.2\%$  (exotic herbs), and  $38.8\% \pm 26.1\%$  (overstory).

In simple bivariate analyses, exotic cover and exotic richness were strongly and positively correlated (Fig. 1A;  $r = 0.80$ ,  $P < 0.01$ ). Also, exotic cover and total native herb richness were positively correlated, although not strongly so (Fig. 1B;  $r = 0.21$ ,  $P < 0.05$ ). In contrast, exotic cover and endemic herb richness were negatively correlated (Fig. 1C;  $r = -0.48$ ,  $P < 0.01$ ), as were exotic cover and rare herb richness (Fig. 1D;  $r = -0.38$ ,  $P < 0.05$ ). The correlations between exotic richness and native richness were similar to

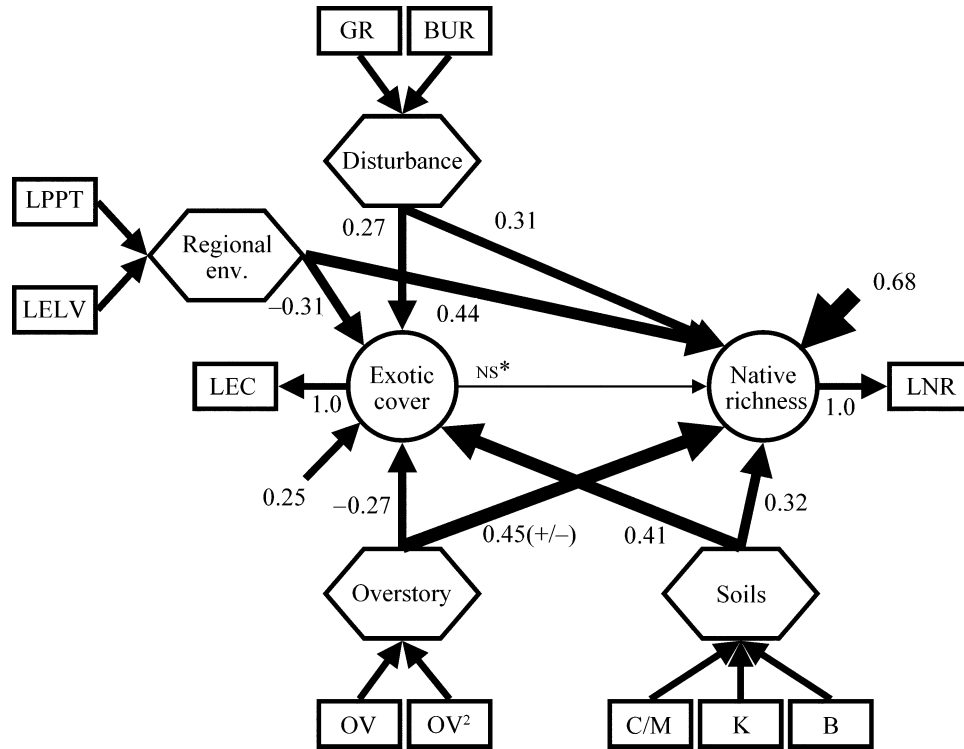


FIG. 2. SEM results for the model representing the relationship between exotic cover and native species richness. Abbreviations are: LNR, log(native richness); OV, overstory canopy cover; OV<sup>2</sup>, overstory canopy cover squared; BUR, density of animal burrows; LPPT, log(mean precipitation); K, soil potassium concentration; LEC, log(exotic plant cover); B, soil boron concentration; C/M, soil calcium to magnesium ratio; GR, whether the site was actively grazed or not; LELV, log(mean elevation). For the model fit,  $\chi^2 = 3.063$  (df = 6,  $P = 0.800$ ), indicating a close fit between model and data. Standardized parameters are shown. Codes for observed variables (in boxes) are given in Appendix A. Variables shown in hexagons are composites. Variables shown in circles are latent variables. Additional results related to this model are given in Appendix C. Note that “ns” refers to the fact that model results fail to support an effect of exotic cover on native richness. The asterisk indicates that there was a modest residual positive correlation between exotic cover and native richness ( $r = 0.16$ ). Also, note that (+/-) following path coefficients indicates nonlinear relationships.

those between exotic cover and native richness ( $r = 0.12$  for total,  $-0.50$  for endemic, and  $-0.42$  for rare herb richness). Various correlations were found among exotic cover, native richness, endemic and rare species richness, and the significant environmental variables that emerged from this analysis (Appendices A and B).

Our main goal in evaluating the structural equation models was to test for significant negative paths from exotic cover to total, endemic, or rare native herb richness, while statistically controlling for environmental variation. We were specifically interested in whether (1) a negative effect of exotic cover on total native richness would be revealed, and (2) the negative relationship of exotic cover to endemic and rare species richness would persist, once environmental influences were considered. For the models evaluated, we found good fits of model to data; see Figs. 2 and 3 for the structures of the models evaluated, as well as the results. The models explained 75% of the variance in exotic cover, 32% of the variance in total native herb richness, 49% of the variance in serpentine-endemic herb richness, and 53% of the variance in rare herb

richness (Figs. 2 and 3). The pathways from exotic cover to native, endemic, and rare species richness were not distinguishable from zero. This finding was confirmed by elimination of these paths from the models and reestimation, which again yielded a good fit between data and model.

Significant predictors of exotic cover were the same for both models and included soil potassium, boron, and Ca/Mg (all positive), overstory cover (negative), animal disturbance and the presence of livestock grazing (both positive), and mean regional elevation (negative) (Appendices C and D). For total native herb richness (Appendix C), significant predictors were soil potassium (positive), overstory cover (unimodal), animal disturbance (positive), and mean annual regional precipitation (positive). For endemic herb richness (Appendix D), the significant predictors were overstory cover (unimodal and modeled using a second-order polynomial), Ca/Mg (unimodal and modeled using a second-order polynomial), rock cover (positive), and mean annual regional precipitation (positive). For rare

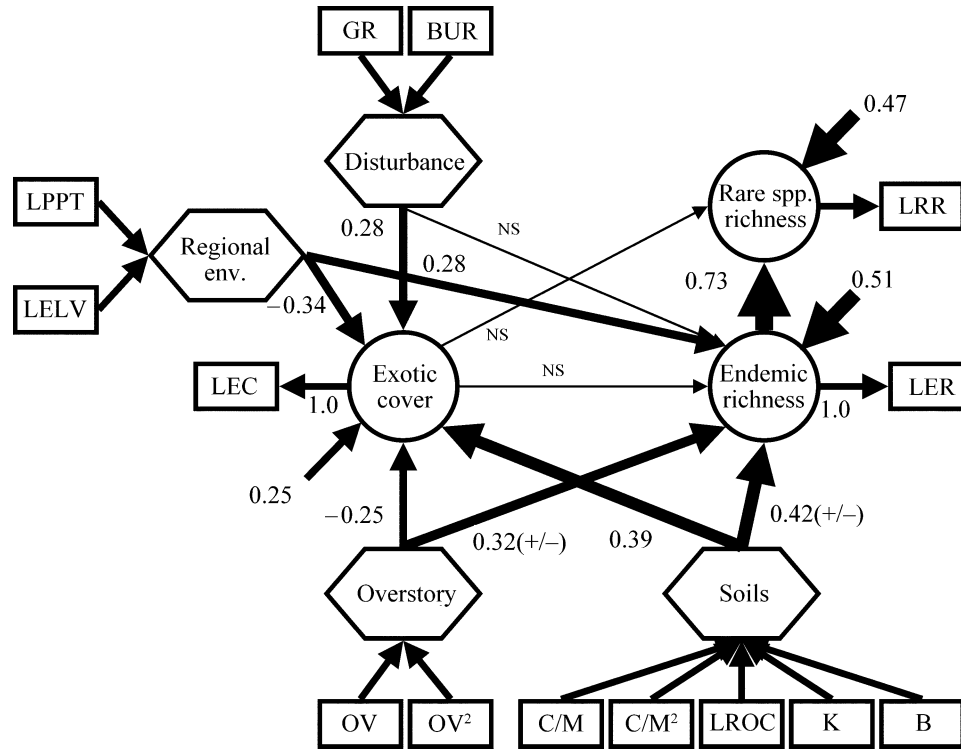


FIG. 3. SEM results for the model representing the relationship between exotic cover and both endemic and rare species richness. Variable abbreviations are as in Fig. 2, with the following additions: LRR, log(rare richness); LER, log(endemic richness); C/M<sup>2</sup>, calcium to magnesium ratio squared; LROC, log(rock cover). For the model fit,  $\chi^2 = 19.157$  (df = 22,  $P = 0.636$ ), indicating close fit between the model and data. See Fig. 2 for additional information about variable types. Standardized parameters are shown. Codes for observed variables (in boxes) are given in Appendix B. Additional results related to this model are given in Appendix D.

herb richness, the only significant relationship we found was to endemic herb richness.

It is important to understand that obtaining good model fits, as we achieved here, constitutes a robust validation of the nonsignificance of all omitted pathways. For example, in the model of endemic and rare richness (Fig. 3), not only were there explicit tests of the significance of pathways from exotic cover to endemic and rare richness, but also implicit tests for pathways from disturbance to endemics and from all environmental variables to rare species richness. Furthermore, the power of the maximum likelihood solution procedure allowed us to distinguish paths as weak as 0.10 (standardized metric) as different from zero. Such paths are biologically of little significance, with a maximum variance explanation capacity of only 1%.

Several other environmental predictors were tested to see if they could contribute to the explanation of either exotic cover or native richness. Categories of variables that did not contribute significantly to explaining native richness or exotic cover in our models included local road proximity, regional road density, and all measures of within-site heterogeneity (i.e., all

coefficients of variation of our environmental variables measured at the site scale).

#### DISCUSSION

We found that the degree of exotic species invasion, as measured by cover, tended to be higher in sites with a greater richness of native species. We also found a strong tendency for the sites with the highest cover or richness of exotics to have fewer endemic or rare species. A pessimistic interpretation of these correlations would be that exotics have preferentially invaded hot-spots of native diversity and have wrought havoc on the most vulnerable species, namely the endemic and rare ones. A more optimistic, but equally unjustified, interpretation would be that exotics are preferentially invading those sites with the fewest endemic and rare species, and are mildly beneficial to native species. To interpret the observed patterns correctly, it is necessary to consider the separate associations that contribute to the simple correlations: in this case, the joint effects of environmental variation on exotic cover and native richness, as well as the residual (direct) relationship that exotic cover may have on native species richness.

We found that exotic cover was highest in sites having little overstory cover, soils rich in potassium and

boron and in calcium relative to magnesium, and high levels of animal disturbance, within regions of low mean elevation. Native herbs, in partial contrast, were richest at sites with intermediate overstory cover, potassium-rich soils, and high levels of animal disturbance, in regions with high annual rainfall. When the association driven by the similarities in these responses was factored out, neither a positive nor a negative residual relationship remained between exotic cover and total native richness. Presumably, if exotics were actually exerting strong negative effects on natives, models that included these environmental variables could have revealed a remaining negative direct association between exotic cover and native richness, even though their simple correlation was positive.

For endemic and rare herbs, the case was somewhat more complex. These species were richest in rocky serpentine sites with intermediate levels of soil Ca/Mg and overstory cover, in regions of high rainfall. Their negative correlations with exotic cover were evidently due to their dissimilarities in environmental response, especially to Ca/Mg and overstory cover, as compared with exotics. Once again, there was no direct association from exotic cover to endemic or rare native richness in models that included the effects of the environment.

One could possibly argue that the contrasting environmental associations of exotic cover and endemic or rare richness represent the “ghost of invasion past,” in other words, that the present distributions of endemic and rare herbs along environmental gradients are the result of their displacement by exotics. However, for this to be true, invasion and displacement would have to reach a nearly complete equilibrium over a large geographic scale, leaving no residual variation in endemic or rare herb richness to be explained by variation in exotic cover. This possibility is contradicted by a range of evidence showing that, in California as a whole, exotics are much more prevalent where human densities and impacts are high, in turn suggesting that exotics are still spreading (Bossard et al. 1995, Gelbard and Harrison 2003, Marchetti et al. 2004, Williams et al. 2005).

We believe the most parsimonious explanation for our results is that the majority of endemic and rare herb species on serpentine have been spared the effects of invasion because they are naturally found in the particular environments where exotic species do not thrive. In the case of serpentine endemics, this is perhaps not surprising, because they are richest in the northern Coast Range and Klamath Mountains (Kruckeberg 1984, Harrison et al. 2000, 2006), whereas the most invaded serpentine sites are in the San Francisco Bay Area and southern California (S. P. Harrison and H. D. Safford, *personal observation*). This geographic gradient was reflected in our models by the significance of regional rainfall for endemic richness, and regional mean elevation for exotic cover; mean rainfall and el-

evation both decrease from northern to southern California.

It is also apparent that these edaphic and climatic gradients are stronger predictors of invasion in serpentine environments than are road-related disturbances. In general, coastal regions with urban centers are the most invaded regions of California; developed land uses such as urbanization and agriculture are strong predictors of invasion in the state's plant (Williams et al. 2005) and fish (Marchetti et al. 2004) communities, and road proximity exerts a significant influence on exotic invasion and native richness in grasslands (Gelbard and Harrison 2003). Our inability to detect effects of road densities on the invasion of our serpentine sites may reflect the unusually high resistance of many serpentine plant communities to invasion.

Overall, our results suggest that, at a broad, statewide scale, the prevalence of native herbs on Californian serpentine does not show a detectable direct relationship to the amount of exotic species cover. There are clearly important exceptions to this at a more local level, especially in the serpentine grasslands of the San Francisco Bay Area, where exotic species have been noted as a threat to several rare and endemic plants (USFWS 1998). Such severe, localized impacts should not be discounted based on our coarser analysis at a larger taxonomic, as well as spatial, scale. One must also consider other impacts of exotics besides reductions in plant species richness, such as the loss of butterfly and other arthropod populations (USFWS 1998, Weiss 1999), the reduction in attractive wildflower displays, and potential changes in ecosystem properties (Hooper and Vitousek 1998), in heavily invaded San Francisco Bay Area serpentine grasslands.

Our study was conducted at relatively large scales, both with respect to geographic extent (1200 km) and plot size (1000 m<sup>2</sup>). As other studies have noted, the correlation between exotic and native species richness is scale dependent (Levine 2000). It is likelier to be positive across larger total geographical extents, because greater environmental heterogeneity comes into play; and also at larger plot sizes, because space represents less of a constraint on coexistence than it does at small plot sizes (Davies et al. 2005). However, other studies have reported positive exotic-native correlations at scales smaller than (Levine 2000, Bruno et al. 2004, Davies et al. 2005), as well as similar to (Brown and Peet 2003) or larger than ours (Lonsdale 1999, Stohlgren et al. 1999). Thus, we believe that the principle illustrated by our study may apply to other cases as well: namely, that once relevant environmental information is used to explain patterns in exotic and native richness, there may not be a residual relationship between the two.

Our study reinforces the familiar cautionary note about not confusing correlation with causation. It also illustrates a method that may be generally useful for risk analyses in conservation biology, where there is

often a need to use observational data to draw working conclusions about cause and effect. It is typical that system properties of interest will be intercorrelated, and ignoring those relationships can lead to inferences that are not consistent with the data in hand. Careful use of structural equation modeling provides a means for considering the impact of known and suspected processes on our observations, and may prove useful in developing improved recommendations for conserving natural resources.

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#### LITERATURE CITED

- Anderson, R. C., J. S. Fralish, and J. M. Baskin. 1999. Savannas, barrens and rock outcrop communities of North America. Cambridge University Press, Cambridge, UK.
- Batten, K. M., K. M. Scow, K. F. Davies, and S. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biological Invasions*, *in press*.
- Bollen, K. A. 1989. Structural equations with latent variables. John Wiley, New York, New York, USA.
- Bossard, C. C., J. M. Randall, and M. C. Hoshovsky, editors. 1995. Invasive plants of California's wildlands. University of California Press, Berkeley, California, USA.
- Brooks, R. R. 1987. Serpentine and its vegetation: a multidisciplinary approach. Dioscorides Press, Portland, Oregon, USA.
- Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. *Ecology* **84**: 32–39.
- Bruno, J. F., C. W. Kennedy, T. A. Rand, and M. B. Grant. 2004. Exotic invasion of a marine plant community: a landscape-scale test of some predictions and paradigms of invasion biology. *Oikos* **107**:531–540.
- Buffo, J., L. Fritschen, and J. Murphy. 1972. Direct solar radiation on various slopes from 0° to 60° north latitude. USDA Forest Service Research Paper PNW-142, Pacific Northwest Forest and Range Experimental Station, Portland, Oregon, USA.
- California Spatial Information Library. 2002. Roads in Arc Info export format by the California Department of Fish and Game, Sacramento, California, USA. (<http://gis.ca.gov/casil/gis.ca.gov/teale/roads/>).
- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* **3**:140–158.
- Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology* **86**:1602–1610.
- Edwards, J. R. 2001. Multidimensional constructs in organizational behavior research: an integrative analytical framework. *Organizational Research Methods* **4**:144–192.
- Gelbard, J. L., and S. Harrison. 2003. Roadless habitats as refuges for native plant diversity in California grassland landscapes. *Ecological Applications* **13**:404–415.
- Grace, J. B. *In press*. Structural equation modeling and the study of natural systems. Cambridge University Press, Cambridge, UK.
- Grace, J. B., and B. H. Pugsek. 1998. On the use of path analysis and related procedures for the investigation of ecological problems. *American Naturalist* **152**:151–159.
- Gram, W. K., E. T. Borer, K. L. Cottingham, E. W. Seabloom, V. L. Boucher, L. Goldwasser, F. Micheli, B. E. Kendall, and R. S. Burton. 2004. Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? *Plant Ecology* **172**:159–171.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasions by alien grasses on serpentine soil. *Biological Conservation* **100**:45–53.
- Harrison, S., H. D. Safford, J. B. Grace, J. H. Viers, and K. F. Davies. 2006. Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs* **76**:41–56.
- Harrison, S., J. L. Viers, and J. F. Quinn. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. *Diversity and Distributions* **6**:153–161.
- Heise, D. R. 1972. Employing nominal variables, induced variables, and block variables in path analyses. *Sociological Methods and Research* **1**:147–173.
- Hickman, J. C. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.
- Hobbs, R. J., and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine grassland dynamics. *Ecology* **72**:59–68.
- Hobbs, R. J., and H. A. Mooney. 1995. Spatial and temporal variability in Californian annual grassland: results from a long-term study. *Journal of Vegetation Science* **6**:43–56.
- Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant competition and diversity on nutrient cycling. *Ecological Monographs* **68**:121–148.
- Huenneke, L., S. Hamburg, R. Koide, H. Mooney, and P. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478–491.
- Jennings, C. W. 1977. Geologic map of California. U.S. Geological Survey, Menlo Park, California, USA.
- Kruckeberg, A. R. 1984. California serpentes: flora, vegetation, geology, soils and management problems. University of California Press, Berkeley, California, USA.
- Kruckeberg, A. R. 2004. Geology and plant life. University of Washington Press, Seattle, Washington, USA.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Marchetti, M. P., T. Light, P. B. Moyle, and J. H. Viers. 2004. Invasion and extinction in California fish assemblages: testing hypotheses using landscape patterns. *Ecological Applications* **14**:1507–1525.
- Meimberg, H., J. I. Hammond, C. M. Jorgensen, T. W. Park, J. D. Gerlach, K. J. Rice, and J. K. McKay. 2005. Molecular evidence for an extreme bottleneck during the introduction of barbed goatgrass, *Aegilops triuncialis*, to California. *Biological Invasions*, *in press*.
- Muthén, L., and B. Muthén. 2005. M-Plus user's guide. Muthén and Muthén, Los Angeles, California, USA.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853–858.
- Pugsek, B., A. Tomer, and A. von Eye, editors. 2003. Structural equation modeling. Cambridge University Press, Cambridge, UK.
- Safford, H. D., and S. Harrison. 2004. Fire effects on plant diversity in serpentine versus sandstone chaparral. *Ecology* **85**:539–548.

- Safford, H. D., J. H. Viers, and S. Harrison. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño* **52**:222–257.
- Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications* **13**:575–592.
- Shipley, B. 1997. Exploratory path analysis with applications in ecology and evolution. *American Naturalist* **149**:1113–1138.
- Skinner, M. W., and B. A. Pavlik. 1994. California Native Plant Society's inventory of rare and endangered plants in California. Special Publication Number 1. Fifth edition. California Native Plant Society, Sacramento, California, USA.
- Stein, B. A., L. S. Kutner, and J. S. Adams. 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, Oxford, UK.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- USFWS (U.S. Fish and Wildlife Service). 1998. Recovery plan for serpentine soil species of the San Francisco Bay Area. USFWS, Portland, Oregon, USA.
- U.S. Geological Survey. 2005. National elevation dataset, 1 arc second. (<http://seamless.usgs.gov/website/seamless/products/1arc.asp>)
- Viers, J. H., J. H. Thorne, and J. F. Quinn. 2005. CalJep: a spatial distribution database of Calflora and Jepson. San Francisco Estuary and Watershed Science, *in press*.
- Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* **13**:1476–1486.
- Williams, J. W., E. W. Seabloom, D. Slayback, D. M. Stoms, and J. H. Viers. 2005. Anthropogenic impacts upon plant species richness and NPP in California. *Ecology Letters* **8**: 127–137.

#### APPENDIX A

A table showing bivariate correlations among predictors included in the model of native species richness (*Ecological Archives* E087-040-A1).

#### APPENDIX B

A table showing bivariate correlations among predictors included in the model of endemic and rare species richness (*Ecological Archives* E087-040-A2).

#### APPENDIX C

A table showing the results for the “reduced form” of the model of native richness presenting unstandardized estimates, test statistics, and standardized parameters (*Ecological Archives* E087-040-A3).

#### APPENDIX D

A table showing the results for the “reduced form” of the model of endemic and rare species richness (*Ecological Archives* E087-040-A4).