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Native and alien species diversity at the local and regional scales in a grazed California grassland

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Abstract Serpentine meadows in Northern California supported higher species richness at the 1-m² scale than adjacent nonserpentine meadows, and had a considerably higher proportion of native species. Within each soil type, total species richness (natives plus aliens) was unrelated to biomass, cover, soil depth, or soil characteristics (N, P, Ca⁺⁺, Mg⁺⁺, water-holding capacity). However, the proportion of native species on serpentine was higher in meadows with lower levels of phosphorus and a lower calcium/magnesium ratio; the proportion of native species in nonserpentine meadows was higher on cool (north to northeast facing) slopes. At a regional scale, some of these effects were partly reversed; the rate at which new species accumulated with the addition of new sites, or beta diversity, was highest for native plant species in nonserpentine meadows. All of the above effects were independent of whether grazing by cattle was absent (removed 13 years ago) or present. The status of low-productivity serpentine soils as a refuge for native grassland species appears to be the result of their abiotic resistance to alien species, but not of a negative relationship between productivity and total species richness.

Key words Plants · Diversity · Invasion · Serpentine · Grasslands

Introduction

Native species in California's remaining grasslands have been almost entirely displaced by Mediterranean grasses, with the notable exception of several environments: serpentine soils, mesic coastal regions, vernal pools, and

highly weathered soils on exposed slopes (Mooney et al. 1986; Wagner 1989; Murphy and Ehrlich 1989; Stromberg and Griffin 1996). This study focuses on serpentine or ultramafic substrates, which are characterized by a low ratio of calcium to magnesium and low levels of primary nutrients. Meadows on serpentine-derived soils support many native species that are not strictly endemic to serpentine, but are members of the native grassland community that were much more widely distributed prior to the invasion of Mediterranean species (Kruckeberg 1984; Huenneke et al. 1990). Compared with meadows on more productive soils, they show a markedly lower biomass, a higher diversity of native plants, and far less dominance by tall alien grasses such as *Avena*, *Bromus* and *Lolium* spp. (Poaceae). Understanding the ecological basis of this "refuge" for members of the highly endangered Californian grassland community is of obvious interest to conservation. Here I explore two hypotheses, both consistent with existing evidence, to explain the observed high diversity of native plants in serpentine meadows.

One hypothesis links the diversity of native species on serpentine to its low productivity, through the well-known ecological phenomenon of the diversity-productivity relationship. In grassland fertilization experiments, nutrient enrichment nearly always reduces diversity by promoting the dominance of a few highly competitive species (Tilman 1993, 1997; recent reviews in Foster and Gross, in press; L. Gough, C.W. Osenberg, K.L. Gross, and S.L. Collins, unpublished work; G.G. Mittelbach, C. Steiner, K.L. Gross, S.M. Scheiner, R.B. Waide, M.R. Willig, and S.I. Dodson, unpublished work). For example, Huenneke et al. (1990) found that fertilizing a Californian serpentine grassland with N and P led to reduced total (native plus alien) species richness, as well as increased biomass and increased dominance by alien grasses. Such results suggest that serpentine soils may permit a higher number of species to coexist because their lower productivity leads to reduced competitive dominance. This hypothesis implies that total species richness should not only be higher on serpentine soils

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than on neighboring nonserpentine soils, but should also increase with decreasing productivity within serpentine soils (for example, with decreasing nutrient levels or $\text{Ca}^{++}/\text{Mg}^{++}$ ratio). However, the negative diversity-productivity relationship is found less consistently on natural gradients of productivity than in experiments (Peltzer et al. 1998; K.L. Gross, M.R. Willig, L. Gough, R. Inouye, S.B. Cox, unpublished work; G.G. Mittelbach, C. Steiner, K.L. Gross, S.M. Scheiner, R.B. Waide, M.R. Willig, and S.I. Dodson, unpublished work), so its relevance to natural patterns of diversity remains uncertain.

An alternative hypothesis is that serpentine soils are exceptional not for the total diversity they maintain, but only for their high proportion of native species. In other words, the serpentine "refuge" for native species is a function of abiotic resistance to invasion, but not of an inverse diversity-productivity relationship. It is well known that many alien grasses grow poorly on serpentine, and nutrient amendment experiments have shown this may be due to either the low $\text{Ca}^{++}/\text{Mg}^{++}$ ratio or the low levels of primary nutrients (e.g., Gulmon 1979; Turitzin 1981; Kruckeberg 1984). However, it is less well known how this effect translates into patterns of native, alien and total plant species diversity along natural gradients of $\text{Ca}^{++}/\text{Mg}^{++}$ and nutrient levels. Under this second hypothesis, the proportion of native species will be higher on serpentine than nonserpentine, and will increase at lower levels of $\text{Ca}^{++}/\text{Mg}^{++}$ or nutrients. But within and between the two soil types, there will not be an inverse relationship between total species richness and productivity.

Grazing, like low productivity, has sometimes been shown to increase grassland diversity by reducing the dominance of highly competitive species (e.g., Collins et al. 1998), although this remains controversial (MacNaughton 1993; Fleischner 1994). In a recent review, Olff and Ritchie (1998) suggest that grazing tends to reduce diversity on nutrient-poor soils where plants are poorly defended against herbivory, but to increase diversity on richer soils where plants have been exposed to more herbivory and thus have evolved higher levels of grazing tolerance. Effects of livestock grazing on productivity tend to be strongest in grasslands lacking a long history of large ungulate herds (Milchunas and Lauenroth 1993), as is true in California. One recent study found lower diversity and a more alien-dominated species composition in grazed than ungrazed Californian grasslands (Stromberg and Griffin 1996). Clearly, grazing represents a possible complication to the questions posed above, since it may affect diversity, the diversity-productivity relationship, and the extent of invasion.

Spatial scale is another potentially important consideration when examining diversity patterns. Previous comparisons of plant communities on serpentine and nonserpentine soils have found they may differ not only in local (alpha) species richness, or the average number of species within a small sampling plot, but also in the number of new species gained by moving from one

sampling plot to the next (beta or differentiation diversity; Whittaker 1960; Harrison 1997, 1999). This relationship between species diversity and spatial scale could also be influenced by grazing; Olff and Ritchie (1998) suggest that grazing may promote coexistence and thus increase diversity at the local scale, yet also reduce diversity regionally by eliminating grazing-intolerant species. Interactions between grazing, scale and diversity were noted by Stohlgren et al. (1999), who found that grazing enhanced plant species richness at a small (1 m²) scale but not at a larger (1000 m²) scale.

In this study, I examined plant species richness and the proportion of native species in a complex of adjacent serpentine and nonserpentine meadows. Observations suggested that both soil types varied considerably in productivity within the study area. The plant community in the serpentine meadows consisted largely (>95%) of species not endemic to serpentine, and I avoided sampling rocky serpentine outcrops because these supported chaparral and a largely endemic herb flora. Thus, the meadows I studied were chosen to represent California lowland grassland, with high variation in composition and productivity owing to soil type. I also took advantage of an inadvertent grazing exclusion experiment. All grasslands in the study region were grazed historically and most still are, but in some areas cattle were removed 13 years ago when a mine was constructed. There is no reason to believe these currently ungrazed areas were previously different in any systematic way from the areas still grazed. At the scale of 1-m² quadrats, representing the scale at which local interactions take place, I measured the species richness of natives and aliens, above-ground net primary productivity (end-of-season biomass), and soil at 80 sites.

To test the above hypotheses, I asked the following questions:

1. Is species richness higher on serpentine than nonserpentine, and within either soil type, does species richness increase with decreasing biomass and/or vary with soil chemistry (N, P, Ca^{++} , Mg^{++} and water-holding capacity)?
2. Is the proportion of native versus alien species higher on serpentine than nonserpentine, and does this proportion vary with biomass and/or soil variables?
3. Do the answers to these questions depend on the presence or absence of grazing?
4. Do the answers to these questions depend on spatial scale; specifically, do serpentine and nonserpentine, or grazed and ungrazed sites, differ in the ratio of regional to local species richness ("beta diversity")?

Materials and methods

This study took place in northern Napa and southern Lake Counties, California, United States at the Homestake Mine/Donald and Sylvia McLaughlin University of California Natural Reserve. This 4200-ha site consists roughly half of serpentine and half of the sandstone and shale Knoxville formation (Wagner and Bortugno 1982). Soils, vegetation and flora of this site are described

by D'Appolonia (1982), and soil-vegetation relationships have been analyzed in the Knoxville formation by Evans and Young (1989) and in nearby serpentine sites by Koenigs et al. (1982). The serpentine supports two types of chaparral, with either leather oak (*Quercus durata*, Fagaceae) or cypress (*Cupressus macnabiana*, Cupressaceae) and their associated species (Sawyer and Keeler-Wolf 1995). Meadows on serpentine are infrequent, and tend to be found in depressions that trap alluvium. Nonserpentine at the site is roughly half blue oak woodland (*Q. douglassi*) and half open meadows; blue oak cover may have a strong influence on the plant community (Bartolome 1989), so sampling in this study was confined to open meadows.

In May 1998, I chose 80 sampling sites representing currently grazed or ungrazed, serpentine or nonserpentine meadows. The intended design included 20 sites for each of these four "treatments", but six serpentine sites I classified as grazed later were reclassified as ungrazed. Sites were selected for maximum interspersal of treatments, within the constraints imposed by the landscape; later analysis showed that the treatments did not differ in their mean latitude or longitude (multivariate analysis of variance, P always > 0.10). Using roads or trails that crossed meadows, I selected points at random distances > 100 m apart, then chose a random side of the road or trail (if possible), and a random distance 60–120 m from the road or trail. No more than three sampling sites were placed in any one contiguous area of meadow. At each site thus determined, I chose a random compass direction and established a 50-m transect along which five quadrats were placed at 10-m intervals.

The quadrats I used were 1 m^2 , and for most analyses, values from the five quadrats were averaged to get a single value of each variable for each site. Sampling at the 1-m^2 scale undoubtedly underestimates diversity in the sense that rare species are likely to be missed (Stohlgren et al. 1998); however, by comparing the average versus the total diversity of the five quadrats per site, I could at least examine the issue of scale dependence.

From 4 to 14 May 1998, I sampled plant species richness in each of the 400 quadrats. Because of an unusually rainy spring, the flowering season for vernal annuals was prolonged in 1998. Thus it was possible at a single time point to sample everything from the earliest-flowering species (e.g., *Claytonia exigua*, Portulacaceae; *Lepidium nitidum*, Brassicaceae) to the latest-flowering ones (e.g., *Hemizonia congesta* and *Holocarpha virgata*; Asteraceae), even if the plants were sometimes present in the post- or pre-flowering condition respectively. To my knowledge, in only two cases did this lead to identification problems; I could not distinguish pre-flowering individuals of *Calochortus luteus* and *C. superbus* (Liliaceae), or of *Clarkia purpurea* and *C. gracilis* (Onagraceae). However, later observations suggested that these congeners co-occurred so seldom at the 1-m^2 scale that this should have caused only minor underestimation of local richness. Plants were identified with the help of an expert regional botanist (J. Callizo, Wantrup Sanctuary and California Native Plant Society). For each site, I calculated average richness per square meter of all species, native species and alien species. Nomenclature follows Hickman (1993).

For each site I recorded its aspect, slope (on a four-level scale), and position (using a GPS receiver), and for each quadrat its soil depth using a steel probe and its approximate percentage cover. I combined aspect and slope into a three-level classification: warm (aspect south to southwest, slope moderate or steep), cool (aspect north to northeast, slope moderate or steep) and neutral (all others). Also at this time, I collected approximately 300 mg soil from > 1 cm below the surface at each site. Soil samples were oven-dried, ground, and analyzed by the Soil Analytic Laboratory of the Division of Agriculture and Natural Resources, University of California, Davis, California, United States. Analyses included exchangeable Ca^{++} and Mg^{++} , using ammonium acetate extraction and atomic absorption/emission spectrometry; total N and P; and soil water-holding capacity at 0.3 atm pressure using a pressure plate system.

At this time I also recorded the occurrence of gopher disturbance, which has been implicated in maintaining diversity in another California serpentine grassland (Hobbs and Mooney 1991).

However, since gopher mounds were found in $< 5\%$ of the quadrats I sampled, this variable was not examined further.

From 1 to 10 June 1998, I returned to each site to sample total above-ground plant biomass. At this time the growing season had ended for all but a very few forbs (e.g., *Hemizonia congesta* and *Holocarpha virgata*). All above-ground plant matter was removed within a 30×30 cm area randomly located within the sampling site. This material was oven-dried and weighed.

The resulting data were analyzed using general linear models (Systat, Wilkinson 1996), after first inspecting scatterplots for nonlinear patterns such as unimodal curves, which were not evident. All proportions were arcsin square root transformed. To test how total (native plus alien) species richness and the proportion of native species varied between soil types, and between grazed and ungrazed sites, I used multivariate analysis of variance, with data from both soil types combined.

To examine patterns of diversity and invasion within each soil type, I performed separate analyses on serpentine and nonserpentine data, since they showed quite different relationships. For each soil type, I performed an analysis of covariance in which the dependent variable was total (native plus alien) species richness and the independent variables were biomass, grazing, slope, cover, soil depth and soil chemistry measurements. I then repeated the above analyses using as the dependent variable the proportion of native species at each site, and the same independent variables. To analyze the possible roles of soil nutrients in causing biomass variation within each soil type, I used multiple regressions with biomass as the dependent variable and the soil chemistry measurements as the independent variables.

Finally, again combining data for both soil types, I used analysis of variance to ask whether beta diversity (the ratio of the total regional species richness to the average species richness at each site) varied with soil type or grazing. I repeated this analysis using natives and aliens separately.

From 5 to 10 May 1999, I returned to the 80 sites and repeated the sampling of native and alien herb diversity. Late spring rains in May 1998 led to an extremely abundant growth of annual grasses and late-season annual forbs (e.g., yellow star thistle, *Centaurea solstitialis*), especially on nonserpentine soils. In turn, ungrazed meadows in 1999 appeared to have an unusually high cover of dead plant material. Therefore, my expectation was that grazing would show stronger effects on diversity in 1999 than in 1998. I did not repeat the soil chemistry sampling, but rather assumed that the soil measurements taken in 1998 were still valid in 1999.

Results

In total, this study found 69 native and 20 alien species on serpentine, and 57 native and 34 alien species on nonserpentine. In 1998, serpentine meadows supported a significantly higher average species richness within 1-m^2 plots (12.3 ± 2.3 , mean \pm SD) than nonserpentine meadows (10.3 ± 2.2). However, species richness was not significantly affected by grazing or the grazing-soil interaction. The proportion of native species within each plot was also higher on serpentine (0.81 ± 0.10) than on nonserpentine (0.43 ± 0.11), and again grazing and the grazing-soil interaction had no effect (Table 1).

These patterns were quite similar in 1999. Serpentine meadows again supported significantly greater species richness in 1-m^2 plots (11.4 ± 2.5) than nonserpentine meadows (7.8 ± 2.0); species richness was not significantly affected by grazing or the grazing-soil interaction; the proportion of native species within each plot was higher on serpentine (0.78 ± 0.17) than on nonserpen-

tine (0.34 ± 0.15); and grazing and the grazing-soil interaction had no effect (Table 2).

Most of the other variables measured in this study differed between the two soil types. Serpentine meadows were significantly lower in biomass, cover, soil depth, N, P, and Ca^{++} , and higher in Mg^{++} than nonserpentine meadows (Table 3). However, none of these variables was affected by grazing or the grazing-soil interaction (multivariate analyses of variance, P always > 0.05).

Within each soil type, average species richness per square meter was not significantly related to biomass, nor in fact to any of the other variables measured (multivariate analyses of variance, P always > 0.10). However, the proportion of native species showed strong gradients within serpentine, declining strongly

with increasing P and increasing $\text{Ca}^{++}/\text{Mg}^{++}$ ratio, as well as less strongly with increasing soil depth and water-holding capacity (Table 4). Within nonserpentine, the proportion of native species was significantly affected only by slope, being higher on cool and neutral slopes (0.44 ± 0.17 and 0.46 ± 0.10 respectively) than on warm slopes (0.38 ± 0.09) (Table 4). The same patterns were found in 1999 as well (Table 5).

Within serpentine meadows, biomass in 1998 showed a significant positive relationship to the level of nitrogen, but was not significantly affected by the $\text{Ca}^{++}/\text{Mg}^{++}$ ratio or water-holding capacity. On nonserpentine, biomass showed a weak positive relationship with the level of phosphorus (Table 6).

Beta diversity, or the ratio of the total number of species found in each treatment to the average local richness at each site, differed significantly by soil type but not by grazing or the grazing-soil interaction in 1998 (analysis of variance with $df = 76, 1, 1, 1$; $P < 0.001$ for soil type, $P > 0.5$ for the other variables). It was

Table 1 Patterns of diversity in 1998: effects of soil type (serpentine versus nonserpentine), grazing, and their interaction on total species richness and the proportion (arcsin square root transformed) of native species. Overall significance of each independent variable is determined by a multivariate analysis of variance with $df = 2, 75$; this is followed by results of the associated univariate tests for each dependent variable

	SS	df	MS	F	P
a Soil type (Wilks' $\lambda = 0.254$, $P < 0.001$)					
Richness	74.386	1	74.386	14.758	0.000
Error	383.078	76	5.040		
Native %	3.299	1	3.299	223.703	0.000
Error	1.121	76	0.015		
b Grazing (Wilks' $\lambda = 0.98$, $P = 0.49$)					
Richness	2.570	1	2.570	0.510	0.477
Error	383.078	76	5.040		
Native %	0.019	1	0.019	1.273	0.263
Error	1.121	76	0.015		
c Soil type \times Grazing (Wilks' $\lambda = 0.98$, $P = 0.45$)					
Richness	6.036	1	6.036	1.198	0.277
Error	383.078	76	5.040		
Native %	0.013	1	0.013	0.851	0.359
Error	1.121	76	0.015		

Table 2 Patterns of diversity in 1999: effects of soil type (serpentine versus nonserpentine), grazing, and their interaction on total species richness and the proportion (arcsin square root transformed) of native species. Analysis as in Table 1

	SS	df	MS	F	P
a Soil type (Wilks' $\lambda = 0.347$, $P < 0.001$)					
Richness	246.992	1	246.992	46.390	0.000
Error	404.640	76	5.324		
Native %	3.452	1	3.452	142.660	0.000
Error	1.839	76	0.024		
b Grazing (Wilks' $\lambda = 0.997$, $P = 0.89$)					
Richness	1.242	1	1.242	0.233	0.630
Error	404.640	76	5.324		
Native %	0.001	1	0.001	0.060	0.807
Error	1.839	76	0.024		
c Soil type \times Grazing (Wilks' $\lambda = 0.970$, $P = 0.32$)					
Richness	3.061	1	3.061	0.575	0.451
Error	404.640	76	5.324		
Native %	0.055	1	0.055	2.266	0.136
Error	1.839	76	0.024		

Table 3 Plant and soil variables (mean \pm SD) measured in serpentine and nonserpentine meadows in 1998. The two soils differed overall in a multivariate analysis of variance (Wilks' $\lambda = 0.21$, $df = 8, 71$; $P < 0.001$). In the associated univariate analyses of variance, soil differences were significant at $P < 0.001$ for all variables except water capacity ($P = 0.35$)

	Serpentine	Nonserpentine
Biomass (g/900 cm ²)	9.81 \pm 7.89	23.03 \pm 7.42
Cover (%)	73.12 \pm 20.02	97.00 \pm 7.57
Soil depth (cm)	35.7 \pm 21.5	49.2 \pm 4.7
Nitrogen (%)	0.12 \pm 0.03	0.18 \pm 0.07
Phosphorus (ppm)	9.89 \pm 6.04	23.88 \pm 12.62
Calcium (meq/100 g)	4.12 \pm 2.33	11.73 \pm 4.24
Magnesium (meq/100 g)	18.18 \pm 6.09	8.67 \pm 5.96
Water capacity (%)	26.87 \pm 5.07	25.77 \pm 5.29

Table 4 Patterns in the proportion of native versus alien species in 1998; analysis of covariance on arcsin square root transformed proportions

	SS	df	MS	F-ratio	P
a Serpentine ($r^2 = 0.61$)					
Grazing	0.008	1	0.008	0.603	0.444
Slope	0.050	2	0.025	1.810	0.181
Cover	0.010	1	0.010	0.710	0.406
Soil depth	0.016	1	0.016	1.140	0.294
Nitrogen	0.002	1	0.002	0.147	0.704
Phosphorus	0.247	1	0.247	17.803	0.001
Ca/Mg ratio	0.199	1	0.199	14.377	0.001
Water capacity	0.062	1	0.062	4.487	0.043
Error	0.415	30	0.014		
b Nonserpentine ($r^2 = 0.44$)					
Grazing	0.019	1	0.019	1.086	0.306
Slope	0.173	2	0.086	5.056	0.013
Cover	0.057	1	0.057	3.334	0.078
Soil depth	0.109	1	0.109	6.387	0.017
Nitrogen	0.045	1	0.045	2.648	0.114
Phosphorus	0.001	1	0.001	0.029	0.866
Ca/Mg ratio	0.001	1	0.001	0.015	0.903
Water capacity	0.005	1	0.005	0.297	0.590
Error	0.512	30	0.017		

Table 5 Patterns in the proportion of native versus alien species in 1999; analysis as in Table 4

	SS	df	MS	F-ratio	P
a Serpentine ($r^2 = 0.56$)					
Biomass	0.000	1	0.000	0.001	0.974
Grazing	0.036	1	0.036	3.747	0.063
Slope	0.018	2	0.009	0.951	0.398
Cover	0.012	1	0.012	1.211	0.280
Soil depth	0.043	1	0.043	4.473	0.043
Nitrogen	0.006	1	0.006	0.605	0.443
Phosphorus	0.134	1	0.134	13.956	0.001
Ca/Mg ratio	0.077	1	0.077	8.032	0.008
Water capacity	0.051	1	0.051	5.298	0.029
Error	0.278	29	0.010		
b Nonserpentine ($r^2 = 0.42$)					
Biomass	0.016	1	0.016	1.548	0.223
Grazing	0.006	1	0.006	0.575	0.455
Slope	0.086	2	0.043	4.138	0.026
Cover	0.013	1	0.013	1.294	0.265
Soil depth	0.021	1	0.021	2.041	0.164
Nitrogen	0.028	1	0.028	2.716	0.110
Phosphorus	0.001	1	0.001	0.107	0.746
Ca/Mg ratio	0.002	1	0.002	0.231	0.634
Water capacity	0.001	1	0.001	0.091	0.766
Error	0.301	29	0.010		

Table 6 Multiple regressions of biomass on soil variables

	Coefficient	t	P
a Serpentine ($F = 3.04$; $df = 4,35$; $r^2 = 0.26$)			
Constant	0.46	0.06	0.95
Nitrogen	88.02	2.11	0.04
Phosphorus	0.11	0.43	0.66
Ca/Mg ratio	-4.88	-0.65	0.51
Water capacity	-0.04	-0.16	0.87
b Nonserpentine ($F = 1.47$; $df = 4,35$; $r^2 = 0.14$)			
Constant	24.663	3.433	0.002
Nitrogen	-41.483	-1.551	0.130
Phosphorus	0.368	2.276	0.029
Ca/Mg ratio	-1.904	-1.919	0.063
Water capacity	0.027	0.097	0.923

higher on nonserpentine (9.4 ± 2.5) than on serpentine (7.5 ± 1.6), and this overall difference masked an even more substantial one between native and alien species. For native species, beta diversity was higher for nonserpentine (15.3 ± 8.8) than serpentine (7.5 ± 3.5). For aliens, beta diversity was higher for serpentine (12.5 ± 15.0) than nonserpentine (6.3 ± 2.1). These differences between soils in native and alien beta diversity are significant (multivariate analysis of variance, Wilks' $\lambda = 0.72$, $F = 14.8$, $df = 2,75$; $P < 0.001$).

Discussion

Serpentine meadows supported higher local species richness than nonserpentine, but evidently not as a result of their lower productivity, since species richness within each soil type was independent of variation in biomass

and soil chemistry. Numerous other studies comparing different sites within a community type, as opposed to comparisons across community types or biomes, similarly find no relationship between natural levels of species richness and productivity (reviewed by K.L. Gross, M.R. Willig, L. Gough, R. Inouye, S.B. Cox, unpublished work; G.G. Mittelbach, C. Steiner, K.L. Gross, S.M. Scheiner, R.B. Waide, M.R. Willig, and S.I. Dodson, unpublished work). This contrasts sharply with the results of fertilization experiments, including one performed in a very similar setting (Huenneke et al. 1990). One explanation for this discrepancy is that diversity along natural productivity gradients is shaped by long-term ecological and biogeographic forces that are not encompassed by fertilization experiments (L. Gough, C.W. Osenberg, K.L. Gross, and S.L. Collins, unpublished work). For example, if poorer soils are less extensive within a region than richer ones, the pool of species available to colonize any given site may be smaller for poor soils. This would counteract the tendency for reduced competitive dominance to promote diversity on poorer soils.

Serpentine meadows had a far higher relative as well as absolute local richness of native species than nonserpentine meadows. Within serpentine meadows, the proportion of native species increased along a natural gradient of harshness, i.e. decreasing phosphorus and calcium-magnesium ratio. This result corroborates both schools of thought that have emerged from nutrient amendment studies of serpentine, attributing the poor performance of serpentine-intolerant plants such as alien grasses to low levels of either primary nutrients or the $\text{Ca}^{++}/\text{Mg}^{++}$ ratio (Turitzin 1981; Kruckeberg 1984; Huenneke et al. 1990). Few previous studies have examined changes in community composition along natural gradients within serpentine. However, Armstrong and Huenneke (1992) noted higher abundances of alien grasses on serpentine sites with higher $\text{Ca}^{++}/\text{Mg}^{++}$ ratios. Harrison (1999) found that among separate patches of serpentine, the number and proportion of alien species increased with higher Ca^{++} levels, while the number of serpentine-endemic species showed the opposite response. The present study also found that for nonserpentine meadows, native species were more prevalent on cooler slopes, in agreement with observations by Wagner (1989).

One striking result of this study was the near-constancy of species richness at around $10\text{--}15\text{ m}^{-2}$, even while species composition changed considerably across soil types and nutrient levels. Very similar patterns were noted by K.L. Gross, M.R. Willig, L. Gough, R. Inouye, S.B. Cox (unpublished work), who found that diversity ranged only from 9 to 13 species m^{-2} in four widely different midwestern United States grassland communities, despite a tenfold range of variation in productivity. These results suggest it would be interesting to perform species removal and addition experiments to test whether initial diversity affects invasibility, as has been found in other grasslands (Tilman 1997).

The lack of effects of grazing in this study is surprising, and suggests that the study site has experienced a low to moderate intensity of grazing. However, it is important to remember that nearly all sites in this study were once grazed. Previous studies in nonserpentine grasslands have shown that, while grazing promotes the spread of Mediterranean grasses such as medusa-head (*Elymus caput-medusae*) (Stromberg and Griffin 1996), the cessation of grazing for even 27 years may not lead to appreciable recovery in species composition (Bartolome 1989). It appears that once grasslands on favorable soils are invaded, they do not recover to a native-dominated condition despite the removal of grazing. But conversely, in contrast to evidence from some other systems (Collins et al. 1998; Olff and Ritchie 1998), it also does not appear that native plant diversity is harmed by the removal of grazing in this region.

Patterns of relative diversity in this system are not independent of spatial scale, as the results for beta diversity show. Although nonserpentine meadows were lower in species richness at the local scale than serpentine meadows, their higher beta diversity implies that they gained new species faster as more plots were added. Therefore, the two soil types differ less in their regional species richness than in their local species richness. This result hints that while local processes such as reduced competition may favor increased coexistence and higher diversity on serpentine, regional processes that determine the size of the species pool (Cornell 1993) work in the opposite direction. Total habitat area is one obvious factor that could lead to a larger regional pool of species on nonserpentine. Evolutionary age is less likely to be important, since both soils were exposed to plant colonization at the same time (c. 10 myear).

Like other grasslands on unproductive soils, serpentine meadows are important targets for the conservation of native species (Mooney et al. 1986; Murphy and Ehrlich 1989; Foster and Gross, in press). This study indicates that their status as a refuge is not attributable to higher total diversity at lower levels of productivity, as suggested by experimental studies, but rather to their abiotic resistance to invasion. However, an important unanswered question is whether poor soils are truly less invasible than richer ones as a rule, or whether they simply benefit from the fact that most introduced aliens happen to be species that require richer soils. If the latter is the case, there may be alien species capable of dominating communities on poor soil once they eventually arrive. In the region studied here, some serpentine meadows are becoming invaded by goat grass (*Aegilops triuncialis*), hinting that even harsh soils may not be permanent refuges for native species.

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Appendix 1 Species list

	Alien	Serpentine	Nonserpentine
APIACEAE			
<i>Anthriscus caucalis</i>	+		+
<i>Lomatium dasycarpum</i>		+	
<i>L. utriculatum</i>		+	
<i>Sanicula bipinnatifida</i>			+
<i>S. crassicaulis</i>			+
<i>Torilis arvensis</i>	+		+
ASTERACEAE			
<i>Achillea millefolium</i>		+	+
<i>Achyraea mollis</i>			+
<i>Agoseris grandiflora</i>		+	+
<i>A. heterophylla</i>		+	+
<i>Ancistrocarphus filagineus</i>		+	+
<i>Centaurea solstitialis</i>	+	+	+
<i>Filago gallica</i>	+	+	+
<i>Grindelia camporum</i>	+		
<i>Hemizonia congesta</i>			+
<i>Hesperex sparsiflora</i>		+	
<i>Hieracium albiflorum</i>		+	
<i>Holocarpa virgata</i>		+	+
<i>Hypochaeris glabra</i>	+	+	+
<i>Lactuca serriola</i>	+	+	
<i>Lagophylla minor</i>			+
<i>Lasthenia californica</i>		+	+
<i>Layia platyglossa</i>			+
<i>Lessingia ramulosissima</i>			+
<i>Madia elegans</i> ssp. <i>vernalis</i>		+	
<i>Rigiopappus leptocladus</i>			+
<i>Senecio vulgaris</i>	+	+	
<i>Wyethia glabra</i>			+
BORAGINACEAE			
<i>Amsinckia grandiflora</i>		+	
<i>Cryptantha hispidula</i>			+
<i>Pectocarya pusilla</i>			+
<i>Plagiobothrys nothofulvus</i>		+	+
BRASSICACEAE			
<i>Brassica nigra</i>	+	+	+
<i>Capsella bursa-pastoris</i>	+	+	+
<i>Lepidium nitidum</i>		+	+
CAMPANULACEAE			
<i>Githopsis specularioides</i>			+
CARYOPHYLLACEAE			
<i>Minuartia douglasii</i>			+
<i>Petrorhagia prolifera</i>	+	+	+
<i>Stellaria media</i>	+	+	
<i>S. nitens</i>			+
CRASSULACEAE			
<i>Crassula connata</i>			+
EUPHORBIACEAE			
<i>Euphorbia crenulata</i>		+	+
FABACEAE			
<i>Astragalus breweri</i>			+
<i>A. gambelianus</i>			+
<i>A. rattanii</i> var. <i>jepsonianus</i>			+
<i>Lotus micranthus</i>		+	
<i>L. wrangelianus</i>		+	+
<i>Lupinus bicolor</i>		+	+
<i>L. microcarpus</i>		+	
<i>L. nanus</i>		+	+
<i>Medicago polymorpha</i>	+	+	
<i>Trifolium albopurpureum</i>			+
<i>T. bifidum</i>		+	+
<i>T. ciliatum</i>		+	
<i>T. depauperatum</i>		+	
<i>T. fucatum</i>		+	+
<i>T. hirtum</i>	+	+	+
<i>T. obtusiflorum</i>		+	
<i>T. wildenowii</i>			+

Appendix 1 (Contd.)

	Alien	Serpentine	Nonserpentine
<i>Vicia villosa</i>	+	+	
GERANIACEAE			
<i>Erodium cicutarium</i>	+	+	+
<i>Geranium molle</i>	+	+	+
HYDROPHYLLACEAE			
<i>Nemophila menziesii</i>		+	
<i>Phacelia corymbosa</i>		+	
IRIDACEAE			
<i>Sisyrinchium bellum</i>		+	+
LILIACEAE			
<i>Allium fimbriatum</i>			+
<i>A. serra</i>			+
<i>Calochortus luteus</i>			+
<i>C. splendens</i>			+
<i>Chlorogalum pomeridianum</i>		+	+
<i>Dichelostemma capitatum</i>			+
<i>Fritillaria pluriflora</i>			+
<i>Triteleia laxa</i>		+	+
<i>Zigadenus fremontii</i>		+	+
MALVACEAE			
<i>Sidalcea diploscypha</i>			+
ONAGRACEAE			
<i>Camissonia ovata</i>			+
<i>Clarkia gracilis</i>		+	+
<i>C. purpurea</i>		+	+
<i>Epilobium brachycarpum</i>		+	+
PAPAVERACEAE			
<i>Escholtzia californica</i>		+	
PLANTAGINACEAE			
<i>Plantago erecta</i>		+	+
POACEAE			
<i>Aira caryophyllea</i>	+	+	
<i>A. elegantissima</i>	+	+	
<i>Avena barbata</i>	+	+	+
<i>A. fatua</i>	+	+	+
<i>Brachypodium distachyon</i>	+	+	+
<i>Briza minor</i>	+	+	
<i>Bromus diandrus</i>	+	+	
<i>B. hordeaceus</i>	+	+	+
<i>B. madritensis</i>	+	+	+
<i>Elymus caput-medusae</i>	+	+	+
<i>E. elymoides</i>			+
<i>Gastridium ventricosum</i>	+	+	
<i>Hordeum murinum</i>	+	+	+
<i>Lolium multiflorum</i>	+	+	+
<i>L. perenne</i>	+	+	+
<i>Melica imperfecta</i>			+
<i>Nassella lepida</i>		+	
<i>N. pulchra</i>		+	+
<i>Poa bulbosa</i>	+	+	
<i>P. secunda</i>			+
<i>Scribneria bolanderi</i>		+	
<i>Vulpia bromoides</i>	+	+	+
<i>V. microstachys</i>		+	+
<i>V. myuros</i>	+	+	
POLEMONIACEAE			
<i>Allophyllum gilioides</i>		+	
<i>Gilia tricolor</i>		+	+
<i>Linanthus bicolor</i>		+	+
<i>L. ciliatus</i>		+	
<i>L. jepsonii</i>			+
<i>L. latisectus</i>			+
<i>Navarretia pubescens</i>		+	+
<i>Phlox gracilis</i>			+
POLYGONACEAE			
<i>Chorizanthe membranacea</i>		+	
<i>Eriogonum nudum</i>			+

Appendix 1 (Contd.)

	Alien	Serpentine	Nonserpentine
PORTULACACEAE			
<i>Claytonia parviflora</i>			+
PRIMULACEAE			
<i>Anagallis arvensis</i>			+
RANUNCULACEAE			
<i>Delphinium hesperium</i>		+	
<i>D. uliginosum</i>			+
<i>D. variegatum</i>		+	+
<i>Ranunculus occidentalis</i>		+	+
RUBIACEAE			
<i>Galium aparine</i>		+	
SAXIFRAGACEAE			
<i>Lithophragma heterophyllum</i>		+	
SCROPHULARIACEAE			
<i>Castilleja attenuata</i>		+	+
<i>C. densiflora</i>		+	
<i>C. rubicundula</i>			+
<i>Collinsia heterophylla</i>		+	
<i>C. sparsiflora</i>		+	+
<i>Mimulus douglassii</i>			+
<i>M. guttatus</i>		+	+
<i>Triphysaria versicolor</i>		+	
VALERIANACEAE			
<i>Plectritis ciliosa</i>			+
<i>P. macrosera</i>		+	
VIOLACEAE			
<i>Viola douglasii</i>			+

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