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GRAZING AND SUBSTRATE INTERACT TO AFFECT NATIVE VS. EXOTIC DIVERSITY IN ROADSIDE GRASSLANDS

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Abstract. We compared the native and exotic species composition of ungrazed roadside verges with that of adjacent grazed interiors in the grasslands of California's inner northern coast range (Napa and Lake Counties). We sampled 72 pairs of verge and interior quadrats at five sites representative of the region's grasslands, on both fertile (loam) and infertile (serpentine) soils, avoiding all obvious forms of roadside physical disturbance. We found that, on serpentine soils, ungrazed verges had a higher proportion of exotic species than grazed interiors; on nonserpentine soils, the reverse was true. Within serpentine soils, native species were more prevalent in quadrats with lower biomass; within nonserpentine, natives were more prevalent in quadrats receiving less radiation. Overall, the total species diversity was higher in grazed interiors than on ungrazed verges, regardless of the fertility of the substrate. Our results indicate that the ecological role of roadside verges depends on the interactive effects of community composition and history, environmental gradients, and land use practices that characterize a region.

Key words: California; exotic plants; exotic species richness; grazing; invasion; native species richness; nonnative plants; road verges; serpentine grassland.

INTRODUCTION

The ecological roles of roads and their adjacent plant communities have been little studied, relative to their ubiquity and potential importance (Forman and Alexander 1998, Forman 2000, Forman and Deblinger 2000, Trombulak and Frissell 2000). Roadside verges, where a relatively unmanaged strip of vegetation is bounded on one side by a road and on the other by a fence, are conspicuous features of many landscapes. In highly managed ecosystems, roadside verges are sometimes viewed as valuable refugia for the native flora and fauna (e.g., Perring 1967, Way 1977, Ullmann and Heindl 1989, Akbar 1997). In natural ecosystems, in contrast, roadside verges are more often considered as conduits or reservoirs for invasive species (e.g., Frenkel 1970, Schmidt 1989, Panetta and Hopkins 1991, Gelbard 1999, Parendes and Jones 2000). To understand the ecological role of roadside verges, it is essential to know how their floristic composition differs from that of interior communities, and how this difference varies across the variety of substrates and land uses that make up a landscape.

We analyzed the plant species composition of roadside verges, and of the immediately adjacent lands inside of fencelines, in the grazed oak woodland and grassland ecosystem of Northern California's Inner Coast Range. Our study region is lightly populated and little cultivated, but most of it has been grazed by cattle for much of the past century, making it neither totally natural nor intensively managed. In this region, roadside verges provide virtually the only places that have remained consistently ungrazed by livestock for decades. Consequently, we may expect that plant community responses to grazing or the lack of grazing will be a major determinant of the species composition of interiors vs. verges. We tested hypotheses about how the relative species diversity of the grassland community, just inside and outside of roadside fencelines, may be shaped by interactions between grazing, substrate, and invasion.

How grazing affects species diversity has been the subject of a large literature. Grazing may increase diversity by reducing the dominance of superior competitors (e.g., Grime 1973, Collins et al. 1998, Gough and Grace 1998), or it may reduce diversity by eliminating grazing-intolerant species (e.g., Waser and Price 1981). The outcome is likely to depend strongly on resource levels; in general, grazing is expected to affect diversity positively in resource-rich systems, and negatively in resource-poor ones (e.g., Olff and Ritchie 1998, Proulx and Mazumder 1998). The outcome is also likely to depend on the evolutionary history that shapes grazing tolerance in a particular community (Milchunas et al. 1988). Spatial scale is another important consideration (Olff and Ritchie 1998, Stohlgren et al. 1999); for example, grazing may increase diversity at a local scale by reducing competitive dominance, while decreasing it regionally by eliminating grazing-intolerant species.

In highly invaded ecosystems like California grassland however, it is questionable to what extent the effects of grazing on total species diversity should be central to considerations of conservation and management. In the four centuries since European arrival, California grasslands have been subject to an astonishingly

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thorough transformation by invasive species, with Mediterranean annual grasses largely replacing native perennials (Frenkel 1970, Baker 1978, Mooney et al. 1986, Mack 1989, Gerlach et al. 1998). Observations and experiments have shown that native and exotic species often respond differently to gradients of productivity, disturbance, and grazing (Evans and Young 1972, Hobbs et al. 1988, Huenneke et al. 1990, Armstrong and Huenneke 1992), but despite considerable effort, no simple regime of fire, grazing, or grazing exclusion has been found to restore the pre-European condition (Menke 1989, 1992, Heady 1995, Schierenbeck 1995). Today, poor soils and mesic microhabitats are among the few partial refugia remaining for the native Californian grassland flora (Wagner 1989, Huenneke et al. 1990). In this ecosystem, from a conservation perspective, it may be both more appropriate and of greater interest to analyze the relative diversities of native and exotic species than to exclusively test hypotheses about total species diversity.

Substrate is a major determinant of how relative native and exotic species diversities are likely to differ between ungrazed roadside verges and grazed interiors. Our study region includes large areas of serpentine soil, which is the most significant refuge for native grassland species in California (Kruckeberg 1984, Huenneke et al. 1990). Serpentine or ultramafic soils, found in areas of present or former tectonic activity throughout the world, contain high levels of iron and magnesium and low levels of calcium and primary nutrients (N, P, K). These characteristics lead to markedly lower productivity and a flora that includes many fewer exotics and more natives. In our study region, grasslands on serpentine were found to contain ~80% native species, compared with 40% natives on nonserpentine, at the scale of 1-m^2 plots (Harrison 1999*a*). The proportion of native species on serpentine in our region increases with the harshness of the soil, in particular the ratio of magnesium to calcium (Harrison 1999*a*, *b*). However, the experience of conservation managers in our area suggests that even on poor soils such as serpentine, moderate levels of grazing may be required to suppress the dominance of grasslands by exotic annuals (Edwards 1992, Menke 1992; C. Thomsen, *personal communication*).

The preceding observations motivated the hypotheses we tested here, concerning the species composition of ungrazed roadside verges in a grazed landscape. On rich (nonserpentine) soils, we predicted little difference in the proportion of native and exotic species found in ungrazed roadside verges vs. adjacent grazed interiors. Richer soils may be so dominated by exotics that there is little native flora to be "released" from competitive dominance by exotics by grazing. On infertile (serpentine) soils, we predicted that the proportion of natives would be higher in the grazed pastures just inside the fenceline, relative to the ungrazed verges just outside the fenceline, because of the hypothesized beneficial effect of grazing in releasing natives from suppression by exotics. Thus, we predicted that in this ecosystem, roadside verges may vary from playing a neutral role on exotic-dominated fertile soils, to acting as reservoirs of exotic species on native-dominated infertile soils.

METHODS

Study area

The study region encompassed ~360 km^2 of the Putah Creek and Napa River watersheds in the Inner Coast Ranges of Lake and Napa Counties, northern California (Fig. 1), with the center at 38°40′ N, 122°25′ W. The climate is mediterranean, with warm, dry summers and cool, moist winters. Depending on elevation, which ranges from 140 to 1324 m, the mean annual precipitation is 800–1500 mm, and mean temperatures range from 3.9–7.6°C in January to 17.8–21.3° in July (Major 1995). Regional vegetation is a mosaic of chaparral, grassland, and blue oak (*Quercus douglasii*) woodland, with valley oak (*Q. lobata*) groves in riparian zones, and mixed evergreen forest dominated by live oak (*Q. wislizenii* and *Q. agrifolia*) in the more mesic western and high-altitude areas.

Substrates in this region include large areas of relatively fertile soils, i.e., well-drained silt loams and loams derived from sandstone and shale substrates, supporting oaks, annual grasslands, and some cultivation, and also large areas of serpentine soils, i.e., shallow, well-drained gravelly loams or clays of low fertility derived from serpentine, supporting serpentine chaparral and grasslands (Lambert and Kashiwagi 1978, Smith and Broderson 1989). Thus, this region is well suited for examining the effects of ungrazed roadside verges on some of the best and worst soils of the Inner Coast Ranges.

Site selection

Our goal was to determine the ecological effects of having ungrazed roadside verges in an otherwise grazed landscape, across the natural range of variation in soils. Thus we avoided major roadside disturbances such as mowing, grading, and herbicide spraying, which are difficult to measure and may introduce confounding effects. We searched the region for sites at which we could sample plant communities in ungrazed but relatively undisturbed roadside verges and adjacent grazed interiors. We sought sites that contained both serpentine and nonserpentine soils within a single grazing management unit, so that we could control for the variation potentially introduced by grazing regimes. Only sites grazed by cattle on a rotational basis (spring and summer on, winter off) were considered. To further account for variation in grazing, we included site as a blocking variable in our analyses.

Using published soil surveys of Lake and Napa Counties (Lambert and Kashiwagi 1978, Smith and Broderson 1989), we mapped nonserpentine soils (de-

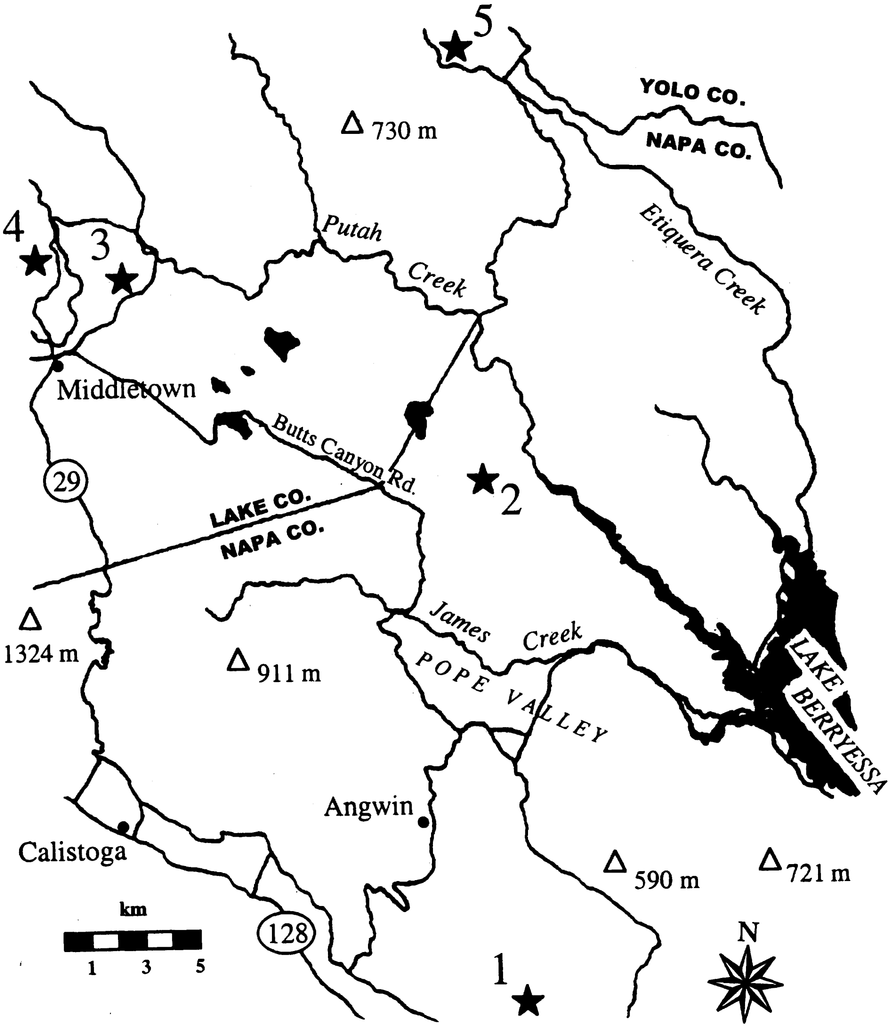

FIG. 1. Map of the study region in the Putah Creek and Napa River watersheds, northern California. Numbered stars correspond to the study sites: 1, Lake Hennessy; 2, Snell Valley; 3, Bar X Ranch; 4, Diamond D Ranch; 5, McLaughlin Reserve.

rived from sedimentary rocks) and serpentine soils onto topographic maps of the study region. We searched these maps for localities crossed by roads where both nonserpentine and serpentine soils were present. We then field checked the resulting 20–30 possible sites to determine whether both soil types were present within one grazing unit, whether suitable verges (see below) were present on both soils, whether grazing practices were appropriate, and whether permission to use the site was forthcoming. Five sites were obtained, two of them private ranches (Bar X Ranch, Diamond D Ranch), and the others owned by the City of Napa (Lake Hennessy), the Napa County Land Trust (Snell Valley), and the University of California and Homestake Mining Company (McLaughlin Reserve), respectively (Fig. 1, Table 1).

Although soil maps indicated that all five sites supported both soil types, problems with roadside disturbance prevented us from sampling nonserpentine soils at Snell Valley. In addition, analyses of soil chemistry and floristic composition later led us to determine that quadrats sampled at McLaughlin Reserve were best considered entirely serpentine. At the other three sites, we were able to sample on both soils; thus, our full data set allowed intra- and intersite comparisons of diversity patterns and grazing effects across varying substrates.

Sampling protocol

Across the five sampling sites, we chose a total of 72 points at which to sample matched pairs of 1-m^2 quadrats, one inside and one outside of roadside fencelines. Selection of these sampling points was based on the following criteria:

1) We strictly avoided sprayed or mowed areas. We consulted the Lake and Napa County road departments and the California Department of Transportation to confirm that sampling points were well beyond zones

TABLE 1. Attributes of sites sampled in this study.

Site	Mean elevation (m)	Relative grazing pressure†	No. of quadrat pairs		Total no. species (natives)
			Serpentine	Nonserpentine	
Lake Hennessy, Napa County	100	low	11	19 (+ 5 unpaired control plots)	83 (35)
Snell Valley, Napa County	170	low	6	0	63 (44)
Bar X Ranch, Lake County	320	high	7 (+ 3 unpaired control plots)	6	103 (70)
Diamond D Ranch, Lake County	350	high	7	5	104 (60)
McLaughlin Reserve, Lake County	635	moderate	11‡	0	83 (50)

† Based on interviews, personal observations, and comparisons of biomass, litter, cattle dung, and hoofprints between grazed and ungrazed quadrats.

‡ Published soil maps showed the McLaughlin site as split equally between sepentine and nonserpentine soils, but analyses of soil chemistry and floristic composition led to the locking of all quadrat pairs as serpentine.

subject to either disturbance. We chose points at which the distance between road edge (the road plus any obviously disturbed zone bordering it) and fence line was >5 m, such that a 1-m^2 quadrat could be sampled at a distance of 1 m outside the fence and >3 m from the road edge. Most of our verge quadrats were >5 m from the road edge (distance = 8.67 ± 0.35 m, mean ± 1 SE), that is, at least 2 m beyond maximum spray or mowing zones in either county (R. Akins, M. Dannenberg, and F. Riesenberg, *personal communication*). Late-season inspection confirmed that none of our quadrats were sprayed or mown in 1999.

2) We avoided areas with any sign of disturbance of the ground or vegetation, aside from grazing. This included borrow pits, roadcuts, roadbeds, runoff ditches, and any sites where vehicles had left the road or grading or burning had occurred. All sampling points were located where the natural slope of the landscape was clearly unmodified. Also, sampling points were located above road level (height above road = 1.37 ± 0.18 m, mean ± 1 SE), to avoid effects of road runoff.

3) We chose sampling points at least 5 m from one another within each of the five sites. Because of criteria (1) and (2), the actual distances between sampling points were much greater than 5 m (distance between nearest neighbors = 30.5 ± 2.9 m, mean ± 1 SE).

Subject to these criteria, we chose as many pairs of sampling points as possible at each of the five sites. At each point, we sampled pairs of 1-m^2 quadrats at equal distances (1–3 m) from the fence, with the external (verge) quadrat also at least 3 m from the road edge. Where possible, we also sampled 1-m^2 control quadrats in nearby ungrazed vegetation, to ascertain how typical our verge quadrats were of ungrazed grassland. We sampled five such control quadrats at Lake Hennessy (nonserpentine) and three at Bar X Ranch (serpentine).

Within each quadrat, we measured percent cover and height of all native and exotic vascular plant species (nomenclature follows Hickman 1993). We also recorded soil type (serpentine/nonserpentine), distance from road and fence, height above road, slope and aspect, altitude, and percent cover of: rock, bare ground, burrowing, thatch/litter, and overstory. We converted slope and aspect to a single measure, percentage of maximum potential radiation (hereafter radiation), by fitting polynomial regressions to tables of radiation input given in Buffo et al. (1972). From the center of each quadrat, we collected 200 g of soil at 5–10 cm depth. 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. Analyses included cation exchange capacity (CEC), organic matter, exchangeable Ca^{2+} and Mg^{2+}, total N and P (Olsen P method), and soil water-holding capacity at 1.5 MPa.

We used plant height and the cover of dung and hoofprints to assess apparent grazing pressure in each sampled quadrat. We estimated relative grazing intensity by dividing biomass of the ungrazed verge quadrat of each pair by biomass of the grazed interior quadrat. This method does not account for potential intrinsic differences in net productivity between verge and interior treatments, but quadrats of a pair were separated by only 2–3 m, so we believe differences in productivity were minimal.

We sampled the quadrats from 21 April–18 May 1999, beginning at the lowest site (Lake Hennessy) and following peak flowering along the elevational gradient. We sampled again in early June and in early July to obtain late flowering species. End-of-season biomass was measured in early July by removing all aboveground plant matter from a representative 30 × 30 cm area within each quadrat, and oven-drying and weighing this material.

Analyses

Data were analyzed in STATVIEW 4.5 (Roth et al. 1995), and SUPERANOVA 1.1 (Gagnon et al. 1991). All proportions were transformed by arcsine square root. Distributions of the data were tested for deviations from normality using the Shapiro-Wilks test in STATA 4.0 (StataCorp 1995); in no case could the null hypothesis of normality be rejected.

To test how total species richness (native plus exotic species) and the proportion of native vs. exotic species differed between verges and interiors, as well as between soil types (serpentine/nonserpentine) and sites, we used multivariate analysis of variance (MANOVA), with data from all soil types and sites. All interaction terms were included in the model.

To more fully understand differences in diversity between verges and interiors, we performed additional analyses in which we included such environmental covariates as biomass, radiation, cover, burrowing, soil variables, and other factors. We used stepwise multiple regressions to reduce the large number of continuous variables to a set of statistically significant ($P \leq 0.10$) predictors. We then entered these predictor variables into analyses of covariance (ANCOVAs), in which we again compared the proportional richness of native and exotic species between verges and interiors. We performed these analyses separately for serpentine and nonserpentine, because the variances differed between soils.

To determine how total and proportional native diversity varied with grazing intensity, we regressed species richness on our measure of relative grazing intensity (see above), using only the grazed interior quadrats of each pair. All other categorical and continuous variables were included in this analysis, including soil, site, and other variables.

To assess how species turnover (beta diversity) might contribute to observed patterns, we computed values of floristic dissimilarity among quadrats within treatments (verge/interior and soil type) for the total, exotic, and native flora, both within and across sites. We used two dissimilarity coefficients, the Marczewski-Steinhaus distance ($1 - J$, where J is the Jaccard coefficient, i.e., the number of species shared between two samples divided by the full species list of both samples; Colwell and Coddington 1994), and Whittaker's β-diversity measure (Whittaker 1972), the ratio of the total number of species in a treatment to the average richness of quadrats in that treatment. We used ANOVA to test whether dissimilarity in the total, exotic, or native flora varied between sites, between verges and interiors, or between soil types.

To investigate how verges and interiors differed in exotic and native species composition, not just richness, we used several methods. First, we calculated Marczewski-Steinhaus distances between verge and interior quadrat pairs, and examined how these varied between soil types. Second, we calculated values of percent cover for every species, and compared these between verges and interiors, using Bonferroni-adjusted t tests. Third, we totaled the number of native and exotic species found exclusively in each of the four primary treatment combinations (verge vs. interior, and serpentine vs. nonserpentine), and used a χ^2 test for independence to ascertain which treatment combinations supported more exclusive native or exotic species than expected by chance.

RESULTS

We sampled a total of 187 species, of which 123 were native and 64 exotic. On serpentine soils we found 106 native species and 54 exotics, and on nonserpentine we found 58 natives and 51 exotics. Total species richness per one square meter was significantly higher in grazed interiors (16.56 ± 0.61 species, mean ± 1 SE) than on ungrazed verges (13.63 ± 0.65 species), and was also higher on serpentine (15.35 ± 0.65 species) than nonserpentine (14.57 ± 0.65 species); there was not a significant interaction between these two variables. Richness varied significantly between sites, and there was an interaction between the effects of verge vs. interior and site (Table 2).

The proportion of native species did not differ between verges and interiors overall, but was higher on serpentine soils (0.52 ± 0.03 species) than on nonserpentine (0.28 ± 0.02 species), and also varied significantly among sites (Table 2). Moreover, as we hypothesized, there was a significant interaction between verge vs. interior and soil type. On serpentine, ungrazed verges had a lower percentage of natives than grazed interiors, while on nonserpentine, the reverse was true (Table 2, Fig. 2).

Examining the latter difference in terms of absolute numbers of species, nonserpentine soils showed substantially higher exotic richness in grazed interiors than ungrazed verges. Serpentine soils, in contrast, showed higher native richness in grazed interiors than ungrazed verges. But neither exotic richness on serpentine, nor native richness on nonserpentine, differed substantially between verges and interiors (Fig. 3).

When soil types were considered separately, and environmental covariates were included in the model, the proportion of native species again differed between verges and interiors on both soils (Table 3), although only marginally on nonserpentine. On serpentine, the proportion of natives was higher in the grazed interiors, declined with increasing biomass and soil organic matter, and increased in relation to overstory cover (i.e., shade). The proportion of natives on nonserpentine was higher in the ungrazed verges, and declined with increasing total soil nitrogen and radiation, and increased in relation to organic matter (Table 3).

Verge and interior quadrats did not differ significantly in any of the measured abiotic variables, including soil chemistry, water-holding capacity, slope and aspect, and there were no significant verge by site or verge by soil interactions (ANOVA, all $P > 0.23$). Neither species richness nor the proportion of native species varied significantly between ungrazed control quadrats and the ungrazed verge quadrats at either site where we were able to make such comparisons ($P(t) \geq 0.30$ in all cases).

When we considered variation in relative grazing intensity, using only the grazed interior quadrats at the

TABLE 2. Multiple analysis of variance for effects of soil type (serpentine vs. nonserpentine), site, verge (ungrazed verge vs. grazed interior), and their interactions, on total species richness and the proportion (arcsine square-root transformed) of native species.

Source	SS	df	MS	F	P
Soil type (Wilks' λ = 0.719, $P < 0.0001$)					
Richness	144.006	1	144.006	7.415	0.0073
Error	2641.244	136	19.421		
Proportion native	0.835	1	0.835	25.445	0.0001
Error	4.461	136	0.033		
Site (Wilks' λ = 0.372, $P < 0.0001$)					
Richness	1679.948	4	416.987	21.626	0.0001
Proportion native	4.471	4	1.118	34.081	0.0001
Verge (Wilks' λ = 0.932, $P < 0.01$)					
Richness	191.002	1	191.002	9.835	0.0021
Proportion native	0.033	1	0.033	0.994	0.3205
Soil × Site (Wilks' λ = 0.78, $P < 0.0001$)					
Richness	1.038	2	0.519	0.027	0.9736
Proportion native	1.03	2	0.515	15.705	0.0001
Soil × Verge (Wilks' λ = 0.946, $P < 0.05$)					
Richness	3.294	1	3.294	0.17	0.6811
Proportion native	0.179	1	0.179	5.452	0.021
Site × Verge (Wilks' λ = 0.901, $P = 0.08$)					
Richness	233.878	4	58.469	3.011	0.0204
Proportion native	0.08	4	0.02	0.614	0.6536
Soil × Site × Verge (Wilks' λ = 0.988, $P = 0.81$)					
Richness	11.264	2	5.632	0.29	0.7487
Proportion native	0.014	2	0.007	0.208	0.8125

three sites where both soil types were sampled, we found no effects of relative intensity (verge biomass divided by interior biomass) on either total species richness or the proportion of native species (Table 4). Within serpentine soils, species richness increased weakly with relative grazing intensity (r^2 = 0.21, $P < .05$).

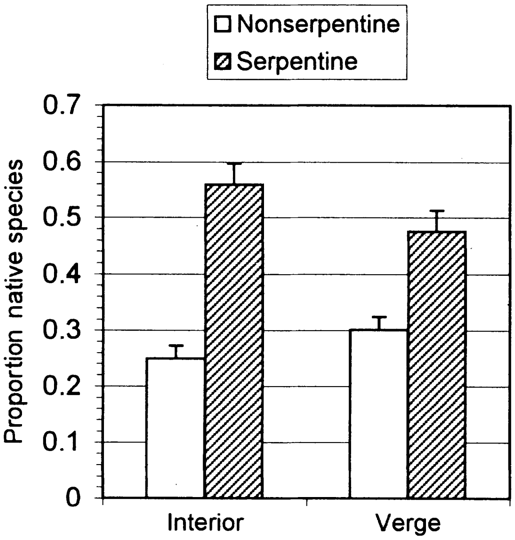

FIG. 2. Effects of road verge (ungrazed verge vs. grazed interior) and soil type (serpentine vs. nonserpentine) on the proportion of native species in 1-m^2 quadrats. Error bars indicate +1 SE.

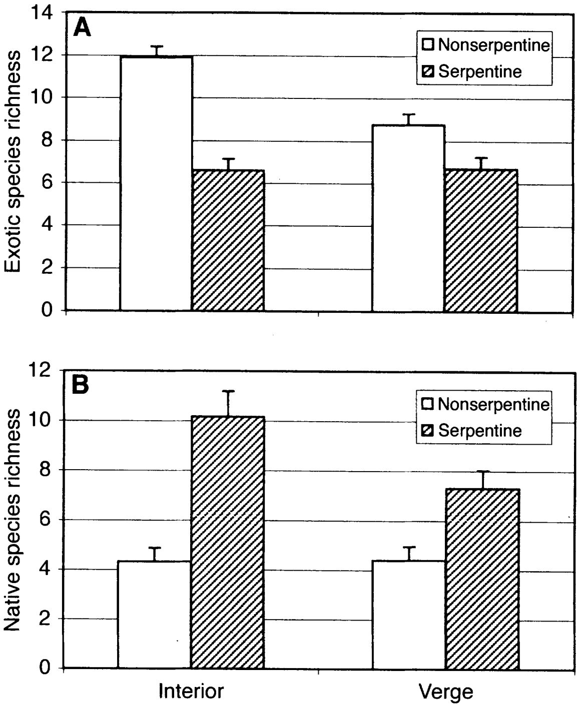

FIG. 3. Effects of road verge (ungrazed verge vs. grazed interior) and soil type (serpentine vs. nonserpentine) on (A) exotic species richness and (B) native species richness, in 1-m^2 quadrats. Error bars indicate +1 SE.

TABLE 3. Analyses of covariance on the proportion (arcsine square-root transformed) of native species: results from serpentine and nonserpentine soils.

Variable	SS	df	MS	*F*	*P*	Sign†
Serpentine (r^2 = 0.80)						
Verge	0.214	1	0.214	8.203	0.006	
Site	2.206	4	0.551	21.104	0.000	
Biomass	0.169	1	0.169	6.459	0.013	−
Distance from road	0.000	1	0.000	0.003	0.960	
Radiation	0.000	1	0.000	0.018	0.894	
Burrowing	0.026	1	0.026	1.006	0.320	
Overstory cover	0.118	1	0.118	4.508	0.038	+
Cover	0.063	1	0.063	2.405	0.126	
Cation exchange capacity	0.024	1	0.024	0.908	0.344	
Organic matter	0.126	1	0.126	4.826	0.032	−
Total N	0.049	1	0.049	1.880	0.175	
P	0.073	1	0.073	2.810	0.099	+
Water-holding capacity	0.095	1	0.095	3.617	0.062	−
Ca/Mg	0.089	1	0.089	3.420	0.069	−
Residual	1.698	65	0.026			
Nonserpentine (r^2 = 0.54)						
Verge	0.066	1	0.066	3.622	0.063	
Site	0.046	2	0.023	1.254	0.295	
Biomass	0.008	1	0.008	0.420	0.520	
Distance from road	0.004	1	0.004	0.214	0.646	
Radiation	0.112	1	0.112	6.150	0.017	−
Burrowing	0.014	1	0.014	0.749	0.391	
Overstory cover	0.001	1	0.001	0.053	0.819	
Cover	0.016	1	0.016	0.885	0.352	
Cation exchange capacity	0.015	1	0.015	0.822	0.369	
Organic matter	0.078	1	0.078	4.245	0.045	+
Total N	0.250	1	0.250	13.710	0.001	−
P	0.001	1	0.001	0.038	0.847	
Water-holding capacity	0.015	1	0.015	0.810	0.373	
Ca/Mg	0.012	1	0.012	0.665	0.419	
Residual	0.859	47	0.018			

† Sign of effect given only for regressors with $P \leq 0.10$.

However, within nonserpentine soils, species richness showed no relationship to relative grazing intensity.

The floristic dissimilarity among quadrats (measured as $1 - J$), differed significantly between verges and interiors, and between soil types. For all species, dissimilarity was significantly higher among ungrazed quadrats than among grazed quadrats (two-factor ANOVA, df = 135, $P = 0.006$), and it was higher on serpentine than on nonserpentine ($P = 0.001$). Exotic and native species showed the same patterns, but overall dissimilarity among quadrats was lower for exotics ($1 - J$: 0.817 ± 0.14 SD than for natives (0.934 ± 0.11) ($P < 0.001$). The overall dissimilarity ($1 - J$) of verge vs. interior communities was 0.304 for the exotic flora and 0.302 for the native flora; in other words, 70% of the exotic or native species found in ungrazed verges were also found in the adjacent grazed interiors.

With respect to their distribution on serpentine, eight exotic species were only encountered in ungrazed verges and four were only sampled in grazed interiors. Of these exotics, five were absolutely restricted to the serpentine-verge treatment (i.e., they were not encountered at all on nonserpentine), and one was absolutely restricted to the serpentine-interior treatment. The distribution of native species on serpentine showed a reversed pattern: eight natives were only encountered in ungrazed verges and 22 species were found only in grazed interiors. Of these native species, six were absolutely restricted to the serpentine-verge treatment (i.e., they were not encountered on nonserpentine), while 13 species were absolutely restricted to the serpentine-interior treatment (Table 5). Several species had significantly higher cover in verges than interiors on serpentine (the exotics *Avena barbata, A. fatua,* and *Lactuca serriola*), and several showed higher cover in interiors (the exotic *Hordeum marinum* and the natives *Triphysaria eriantha* and *Juncus bufonius*; $P(t) < 0.05$ in all cases). Three major exotic grasses were equally prevalent in verges and interiors on serpentine: *Bromus diandrus, Bromus hordeaceus,* and *Taeniatherum caput-medusae* (combined cover = 20 ± 1.73%, mean ± 1 SE on verges, 22 ± 1.77% in interiors).

With respect to their distribution on nonserpentine, three exotic species were only encountered in ungrazed verges and nine were only found in grazed interiors. Of these exotics, three were absolutely restricted to the nonserpentine-interior treatment (i.e., they did not occur on serpentine), while three others were absolutely restricted to the nonserpentine-verge treatment. On nonserpentine, 14 native species were exclusive to ungrazed verges and 13 were exclusive to grazed interiors. Of these natives, seven species were absolutely

TABLE 4. Analyses of covariance on (A) total species richness (per 1-m^2 quadrat) and (B) proportion (arcsine square-root transformed) of native species, for interior quadrats only.

Variable	SS	df	MS	F	P	Sign†
A) Total species richness ($r^2 = 0.66$)						
Soil type	0.500	1	0.500	0.035	0.852	
Site	100.106	2	50.053	3.509	0.041	
Relative grazing intensity‡	11.059	1	11.059	0.775	0.385	
Biomass	13.686	1	13.686	0.959	0.334	
Distance from road	47.936	1	47.936	3.361	0.075	−
Radiation	1.514	1	1.514	0.106	0.747	
Burrowing	45.468	1	45.468	3.188	0.083	−
Litter	36.854	1	36.854	2.584	0.117	
Overstory cover	3.613	1	3.613	0.253	0.618	
Cover	11.725	1	11.725	0.822	0.371	
Cation exchange capacity	4.990	1	4.990	0.350	0.558	
Organic matter	69.699	1	69.699	4.886	0.034	+
Total N	71.647	1	71.647	5.023	0.031	−
P	0.002	1	0.002	0.000	0.991	
Water-holding capacity	51.768	1	51.768	3.629	0.065	−
Ca/Mg	2.009	1	2.009	0.141	0.710	
Residual	499.245	35	14.264			
B) Proportion native species ($r^2 = 0.81$)						
Soil type	0.106	1	0.106	4.456	0.042	
Site	0.421	2	0.210	8.868	0.001	
Relative grazing intensity‡	0.000	1	0.000	0.010	0.921	
Biomass	0.075	1	0.075	3.178	0.083	−
Distance from road	0.011	1	0.011	0.480	0.493	
Radiation	0.049	1	0.049	2.063	0.160	
Burrowing	0.001	1	0.001	0.033	0.856	
Litter	0.053	1	0.053	2.241	0.143	
Overstory cover	0.000	1	0.000	0.010	0.922	
Cover	0.022	1	0.022	0.914	0.346	
Cation exchange capacity	0.003	1	0.003	0.108	0.745	
Organic matter	0.005	1	0.005	0.222	0.641	
Total N	0.005	1	0.005	0.232	0.633	
P	0.000	1	0.000	0.019	0.891	
Water hold. capacity	0.003	1	0.003	0.115	0.736	
Ca/Mg	0.001	1	0.001	0.059	0.809	
Soil type × Site	0.180	2	0.090	3.802	0.032	
Residual	0.830	35	0.024			

Note: Only three sites (Lake Hennessy, Bar X, and Diamond D) were used in this analysis.

† Sign of effect is given only for regressors with $P \leq 0.10$.

‡ Relative grazing intensity was determined by dividing biomass of the ungrazed quadrat of a quadrat pair by biomass of the grazed quadrat.

restricted to the nonserpentine-verge treatment, while three were absolutely restricted to the nonserpentine-interior treatment (Table 5). In addition, a large number of exotic species showed higher cover in interiors than on verges (e.g., the grasses *Briza minor*, *Hordeum marinum*, and *Lolium multiflorum*, and the forbs *Erodium botrys, E. cicutarium,* and *Medicago polymorpha*; $P(t) < 0.05$ in all cases). None of the native species found in both verges and interiors showed significant differences in cover.

The effects of verge vs. interior on species composition, like those on species richness, were in opposite directions on serpentine and nonserpentine. There were more native species exclusive to grazed interiors on serpentine, and more native species exclusive to ungrazed verges on nonserpentine, than expected under the χ^2 test for independence (Table 5).

DISCUSSION

In our study, roadside verges supported significantly fewer total species than did adjacent grazed interiors. Native and exotic species richness and composition also differed between verges and interiors, and the direction of the difference depended on the substrate. On infertile serpentine substrates, grazed interiors had considerably more native species than did ungrazed verges, while the number of exotics was roughly equal. On fertile nonserpentine soils, grazed interiors had higher exotic species richness than ungrazed verges, while the number of native species was equivalent. Strikingly, it thus appears that responses to altered disturbance regimes in this system are largely mediated through changes in the dominant portion of the flora, i.e., exotics on nonserpentine and natives on serpentine.

We must conclude, then, that ungrazed verges play a variable role in the distribution of exotic and native species in our region. However, we suggest that their overall effect on the remnant native grassland flora is a somewhat more negative than positive one. In our region, the only environment that strongly favors the survival of the native flora is serpentine soil, which

TABLE 5. Sampled native species exclusive to only one soil (serpentine or nonserpentine) by verge/interior treatment, with observed and expected n from χ^2 test for independence.

Species	Soil	Verge/Interior	n (observed)	n (expected)
Deschampsia danthonioides, Elymus trachycaulus trachy, Epilobium densiflorum, E. torreyi, Eriogonum nudum, Lepidium nitidum, Lotus humistratus, Lupinus luteolus, Navarretia jepsonii, Plagiobotrys stipitatus stipit., Polemonium californicum, Toxicodendron diversilobum, Trifolium willdenowii	Serpentine	interior	13	10.5
Angelica californica, Plagiobotrys nothofulvus, Sanicula bipinnata	Nonserpentine	interior	3	5.5
Juncus bolanderi, Linanthus latisectus, Lomatium dasyphyllum, Melica torreyana, Trifolium elegans, Wyethia augustifolia	Serpentine	verge	6	8.5
Amsinckia menziesii, Athysanus pusillus, Bromus laevipes, Clarkia unguiculata, Madia elegans, Osmorhiza chilensis, Trifolium barbigerum	Nonserpentine	verge	7	4.5

Note: $\chi^2 = 3.91$, $P < 0.05$, df = 1.

largely excludes nonnatives because of its infertility. Yet the uninvasibility of serpentine grasslands is not absolute, and ungrazed roadside verges on serpentine clearly tend to be overcome by exotic species. Our findings thus agree with the conclusion by other regional conservationists that the survival of native grassland communities is promoted by the combination of infertile soils and moderate levels of grazing (Edwards 1992, Menke 1992; C. Thomsen, *personal communication*).

This conclusion must be tempered with the caveat that our sampling sites were not intended to be representative of the entire landscape, but only of the zones along roadsides. Roadside zones are unusual in two major ways, even when most obvious forms of road-related disturbance are avoided as in our study. First, roadsides may be presumed to receive more exotic propagules than sites very distant from roads. Second, livestock grazing is not randomly distributed on the landscape, but is likely to be concentrated along roadside fencelines where slopes are usually more gentle. Thus, by comparing sites immediately inside and outside of roadside fencelines, we effectively asked how intensive grazing affects heavily invaded grasslands.

In a previous study within this region, Harrison (1999*a*) compared exotic and native species diversity in grasslands on serpentine and nonserpentine, grazed and ungrazed sites, many of which were >100 m from roads. The ungrazed sites in that study were pastures that had been grazed until 15 yr previously. These formerly grazed sites showed no differences in native or exotic diversity from the sites that were currently grazed. This lack of effect may have been because grazing was unusually light on this property, or because 15 years' cessation of grazing was not enough to allow appreciable change in the flora. But it also underscores the difference between studying roadsides and more isolated sites. Similarly to Harrison (1999*a*), in the present study we also found that on nonserpentine soils, less insolated sites tended to support a slightly more native-dominated flora. On serpentine soils we found that exotic species richness increased with biomass, suggesting that invasion of serpentine soils by exotic species is limited by the abiotic conditions that determine productivity.

When total species richness was considered, our analyses suggested a positive local effect of grazing on diversity (Collins et al. 1998). In contrast to some other studies, we found no obvious decrease in diversity with increasing grazing intensity in infertile environments (Milchunas et al. 1988, Proulx and Mazumder 1998). We found that grazed grassland was floristically more homogenous than ungrazed grasland, i.e., herbivory differentially affects the local and regional components of species diversity in the study system (Olff and Ritchie 1998), but mean floristic heterogeneity across the landscape was very different for exotic and native species. All in all, our results suggest that it may be difficult to apply general predictions about how grazing impacts vary across environmental gradients to the highly invaded California annual grassland, where the present-day flora is a mixture of groups that evolved under differing regimes of environment and disturbance.

We sampled in only one growing season. Although in mediterranean grasslands species cover and frequency often show great interannual variability (Hobbs and Mooney 1995), the community variables we investigated (species richness, proportion of native species) are fairly robust to these fluctuations. In a 20-yr study of grasslands in another northern California site, Stromberg and Griffin (1996) found that climatic variability did not alter community-level patterns caused by grazing, cultivation, and disturbance. In a five-year study of serpentine grasslands, Armstrong and Huenneke (1992) documented striking changes in species abundances, yet species richness and the proportion of native species varied by only a few percent. Similarly, Harrison (1999*a*), working in the same region as the present study, found that patterns in species richness and the proportion of native species did not vary significantly between a wet El Niño year and the subsequent cold and dry year.

Management implications

In summary, we found that the effects of ungrazed road verges on the species richness of native and exotic plants may vary with the extent of invasion and the environmental characteristics of the site in question. In the vicinity of roads, and possibly elsewhere where invasion pressure is high, our results support the use of moderate levels of grazing as a management tool for the maintenance of native-dominated grassland communities on infertile substrates like serpentine. On the other hand, our findings suggest that grazing on fertile soils in heavily invaded landscapes may abet further invasion rather than prevent it.

Our study was restricted to northern California; however most other highly seasonal, low productivity grasslands settled by European emigrants in the 17th and 18th centuries are also dominated by introduced Mediterranean forbs and grasses (Mack 1989, Rundel et al. 1998). These areas, including southern Australia, temperate South America, and the North American Great Basin, show strong parallels to northern California in terms of climate, vegetation structure, and histories of grazing and invasion (Mack and Thompson 1982, Mack 1989, Milchunas and Lauenroth 1993). Given these similarities, the implications of our results for grassland management may extend well beyond the immediate geographic scope of this study. We suggest that future studies of the effects of environmental gradients, grazing, and road verges on plant communities in these ecosystems take into account potentially reversed responses in native and exotic species.

In grazed landscapes such as our study region, ungrazed roadside verges form an important element of the plant community. To begin to understand the role of roadside verges in conservation it is necessary to examine the interactive effects of floristic composition, environmental variables, and land uses characteristic of a region. Carefully interpreted, roadside verges can serve as large-scale manipulative experiments to better understand the impacts of widespread human disturbances.

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