Ecological Applications, 13(2), 2003, pp. 404–415

ROADLESS HABITATS AS REFUGES FOR NATIVE GRASSLANDS: INTERACTIONS WITH SOIL, ASPECT, AND GRAZING

JONATHAN L. GELBARD[1] and SUSAN HARRISON

Department of Environmental Science and Policy, University of California, Davis, California 95616 USA

Abstract. The idea that roadless habitats act as refuges for native-plant diversity against exotic-plant invasion has seldom been tested. We examined the effect of distance from roads and its interactions with soil type, aspect, and livestock grazing on native- and exotic-plant diversity in a 130 000-ha inland California (USA) foothill grassland landscape. During spring 2000 and 2001, we measured the numbers of and cover by native and exotic plant species in 92 sites stratified by distance from roads (10 m, 100 m, and >1000 m), soil type (nonserpentine and serpentine), and aspect (cool, warm, and neutral slopes). In nonserpentine grasslands, native cover was greatest in sites >1000 m from roads (23%) and least in sites 10 m from roads (9%), and the percentage of species that were native was significantly greatest in sites >1000 m from roads (44%) and least in those 10 m from roads (32%). In addition, the most distant sites had the largest number of native grass species and the fewest exotic forb species. In serpentine grasslands there was no significant effect of distance from roads on the numbers of and cover by native and exotic species. On both soils, two exotic species (*Centaurea solstitialis* and *Aegilops triuncialis*) were at their lowest frequencies, while a native bunchgrass, *Nassella pulchra*, was at its highest frequency, in sites >1000 m from roads. On nonserpentine soils only, the exotics, *Convolvulus arvensis* and *Polypogon monspeliensis*, were at their lowest frequency, while a native bunchgrass, *Poa secunda*, was at its highest frequency in the most distant sites. Native species were more abundant on serpentine than nonserpentine soils; on serpentine, natives were more abundant on slopes than flat sites, while on nonserpentine, natives were least abundant on warm, south-facing slopes.

Grazing, soil type, and aspect all significantly interacted in their effects on native and exotic richness and cover. Grazing negatively affected the number of native grass species, but not the number of native forb species on nonserpentine, and positively affected the number of native forb species, but not the number of native grass species on serpentine.

Roadless areas are significant refuges for native species. However, to protect these habitats from the continued threat of invasion, land managers should consider means of preventing construction of new roads, limiting off-highway vehicle access into grasslands with low road densities, identifying a regime of livestock grazing that favors the persistence of natives over the spread of exotics, and monitoring recreational trails and grazing allotments within roadless areas to detect and eradicate new infestations.

Key words: Aegilops triuncialis; *California grasslands;* Centaurea solstitialis; *exotic-plant invasions; grazing effect on species composition; habitat management;* Nassella pulchra; *native vs. exotic plant diversity; roadless habitats.*

INTRODUCTION

With increasing emphasis on land management measures aimed at protecting native diversity by controlling exotic-plant invasions (e.g., Noss and Cooperrider 1994, Soulé and Terborgh 1999), the need for a quantitative understanding of landscape-scale patterns of exotic invasion and native-species persistence has never been greater. Roads are a logical focus for a landscape-level examination of invasion, because they are the entry points for many or most human influences that affect the invasion process. Elevated concentrations of exotic species have been observed near roadsides in many ecosystems (Johnson et al. 1975, Forcella and Harvey 1983, Tyser and Worley 1992, Knops et al. 1995; Gelbard and Belnap, *in press*). Such patterns partly reflect the disturbed condition of roadsides themselves, but also suggest that roads act as sources of exotic propagules (Amor and Stevens 1976, Schmidt 1989, Lonsdale and Lane 1994) and as conduits for human disturbances that promote invasion (Frenkel 1970, Greenberg et al. 1997). Conversely, the idea that roadless habitats act as refuges for native plant diversity is part of the conventional wisdom of invasion ecology and conservation biology (Noss and Cooperrider 1994, Soulé and Terborgh 1999).

Nonetheless, few studies have explored the effect of distance from roads on entire plant communities at a large spatial scale. Thus, we know little about whether roads affect the distribution and abundance of native

---

Manuscript received 20 February 2001; revised 18 March 2002; accepted 29 May 2002; final version received 22 July 2002. Corresponding Editor: C. C. Horvitz.

[1] E-mail: jgelbard@ucdavis.edu

species or just those of selected exotics. Nor do we know over what spatial scales the effect of roads may threaten natural communities, or how important the road effect may be relative to other factors that influence exotic invasion and native persistence. Addressing such questions requires a landscape-level analysis with careful attention to multiple causal factors. Such a study could also provide clues about the future of invasions; if native species are more prevalent at sites distant from roads, and if environmental variation does not appear to explain this pattern, it would suggest that the displacement of natives by exotics across a landscape is not yet complete. That is, a carefully chosen spatial sequence of sampling sites at different distances from roads might be interpretable as a chronosequence.

Valley and foothill grasslands of California are an important setting for examining landscape-level patterns of invasion, because their native component is critically endangered. In the 200 yr since the arrival of Europeans, native perennial-dominated grasslands have been almost entirely overtaken by Mediterranean annual grasses (e.g., *Avena*, *Bromus* spp.) and forbs (e.g., *Centaurea*, *Erodium* spp.) (Mooney et al. 1986, Wagner 1989, Heady 1995). Remnant native-dominated grasslands still exist at scattered sites (Murphy and Ehrlich 1989, Stromberg and Griffin 1996, Harrison 1999, Safford and Harrison 2001), yet we lack a general model of where remnant native grasslands occur and why (Heady 1995). Examining the effect of distance from roads in this ecosystem, together with other major interacting factors that influence landscape patterns of invasion, could help form the basis for improved large-scale strategies for the management and restoration of native Californian grasslands.

In this as in other ecosystems, the replacement of natives by exotics is influenced by multiple factors that are likely to interact, including substrate, moisture, fire regime, and current and past land uses as well as distance from the original point of introduction (McNaughton 1968, Murphy and Ehrlich 1989, Wagner 1989, Heady 1995, Stromberg and Griffin 1996, Harrison 1999; Gelbard and Belnap, *in press*). Adding to this complexity, a full quantification of the replacement process requires measuring multiple response variables, including the numbers of and cover by natives, exotics, specific species, and life-forms (e.g., grasses and forbs), each of which may respond differently to the various causal factors (Menke 1989, Maron and Jeffries 2001). Here we attempted to develop a general approach to dealing with this complexity that may be useful in other regions and ecosystems. The main features of our approach were: (1) using geographic information systems to determine where to sample over a large landscape, (2) choosing spatially distinct samples that may be somewhat representative of a chronosequence, (3) stratifying the sampling by several categorical factors, as well as measuring numerous covariates, and (4) analyzing the effects of these factors and their interactions on multiple response variables to search for combinations of environmental and management conditions that influence the relative prevalence of natives vs. exotics.

In addition to distance from roads, the categorical factors that we examined included soil, aspect, and livestock grazing. Infertile soils are known to be an important refuge for native Californian grassland species; the best-known example is serpentine soil, characterized by a low Ca^{++}:Mg^{++} ratio and low macronutrient (N and P) levels (Kruckeberg 1984, Murphy and Ehrlich 1989, Harrison 1999, Safford and Harrison 2001). In experimental studies, richer soils generally favor exotics such as medusahead (*Taeniatherum caput-medusae*) and yellow starthistle (*Centaurea solstitialis*) over their native competitors (Hobbs 1989, Huenneke et al. 1990, Roche et al. 1994). Native species are also known to be more prevalent in mesic microhabitats (such as cool north-facing aspects) rather than xeric microhabitats (such as warm south-facing aspects) (McNaughton 1968, Evans et al. 1975, Menke 1989, Wagner 1989, Harrison 1999, Safford and Harrison 2001). In contrast, exotic annuals appear more tolerant of xeric conditions (Jackson and Roy 1989, Armstrong and Huenneke 1992, Heady 1995).

Livestock grazing has variable effects on grassland species composition (Mack 1989, Heady 1995, Holland and Keil 1995). In some cases, grazing may reduce native diversity and accelerate invasions (Mack 1989, Holland and Keil 1995, Belsky and Gelbard 2000, Masters and Sheley 2001, Stohlgren et al. 2001), but in others, moderate grazing may benefit native diversity by suppressing competitively dominant species and reducing exotic plant litter (Menke 1992, Noy-Meir 1995, Collins et al. 1998). The effects of grazing may vary depending on environmental context and plant life-form; it typically favors annual forbs over grasses (Menke 1989), and appears to promote exotic forbs on nonserpentine, but native forbs on serpentine soil (Safford and Harrison 2001.)

We selected 92 sites stratified by distance from roads (10–1000 m), soil (nonserpentine and serpentine) and aspect (cool, warm, and neutral slopes), and sampled them for two successive years. We measured a large suite of environmental covariates related to topography, soil quality, and livestock grazing and other disturbances. We used these data to test our principal hypothesis that native species would be more prevalent, and exotics less so, with increasing distance from roads; we also used them to test for the main effects of soil, slope, and grazing and their interactions with each other and with distance from roads. We used environmental covariates to test whether any apparent effects of our categorical variables could be explained by disturbance, soil quality, or other forms of environmental variation.

METHODS

Site description

The 130 000-ha study region consists of portions of the Putah and Cache Creek watersheds (Napa, Lake, and Colusa Counties, California, USA), centered on a major topographic feature known as Blue Ridge (38°45′/122°15′). The climate is Mediterranean, with warm, dry summers and cool, moist winters. Mean annual temperature ranges from 3.9°–7.6°C in January to 17.8°–21.3°C in July; mean annual precipitation is 800–1500 mm, depending on elevation, which ranges from 140–1300 m (Major 1995). This region's geology, soils, and vegetation are diverse (Lambert and Kashiwagi 1978, Smith and Broderson 1989, Hickman 1993). On soil types derived from sedimentary rock, soils tend to be fertile, well-drained silt loams and loams derived from sandstone and shale. These sites support vegetation that consists primarily of open grassland and savannah under 20–50% cover by blue oaks (*Quercus douglassi*). There are also extensive areas of nonserpentine chaparral dominated by chamise (*Adenostoma fasciculatum*) and other evergreen shrubs. Dominant species are the exotic annual grasses *Avena fatua*, *Bromus hordeaceus*, *B. diandrus*, *Lolium multiflorum* and *Taeniatherum caput-medusae*, and such exotic annual forbs as *Centaurea solstitialis*, *Erodium botrys*, *Medicago polymorpha*, and *Trifolium hirtum*.

On soil types derived from serpentine, soils are well-drained gravelly loams and clays of low fertility (Lambert and Kashiwagi 1978, Smith and Broderson 1989). These soils contain high levels of iron and magnesium and low levels of calcium and primary nutrients (N, P, K), characteristics that lead to markedly lower productivity and a flora that includes many fewer exotic species than natives (e.g., Kruckeberg 1984, Huenneke et al. 1990). The proportion of native species in our study area increases with the ratio of magnesium to calcium, and biomass increases in proportion to N and P levels (Harrison 1999, Safford and Harrison 2001). Serpentine grasslands tend to support native grass species such as *Nassella pulchra*, *Poa secunda*, *Melica californica*, and *Vulpia microstachys*, and a rich complement of native forbs including *Clarkia* and *Castelleja* spp., *Gilia tricolor*, *Lasthenia californica*, and *Calochortus* spp. Exotics include barbed goatgrass (*Aegilops triuncialis*) and, in sites with deeper soils, yellow starthistle (*Centaurea solstitialis*) and medusa-head (*Taeniatherum caput-medusae*).

GIS analyses

To identify suitable study sites, we acquired GIS (geographic information system) data detailing roads, topography, soils, and land ownership within the study region. We used ARC INFO and ARCVIEW software (ESRI, Redlands, California, USA) to create a grid illustrating the location of sites 0–10 m, >10–100 m, >100–1000 m and >1000 m from roads. In addition, we created a grid illustrating grassland habitats by (1) joining digital raster graphs (digitized 1:24 000 USGS topographic maps) of the study region, (2) converting the joined DRG to a grid with a 30-m cell size, and (3) reclassifying areas with no overstory cover (colored white on maps) as grasslands. We used this grid in conjunction with the distance-from-roads grid to create a regional-scale map of grasslands located 0–10 m, >10–100 m, >100–1000 m, and >1000 m from roads. We used GIS to estimate the relative abundance of roadless grasslands in the study area by comparing the total area of grasslands, oak woodlands, and chaparral with the areas of these habitats that are ≤100 m, >100–1000 m and >1000 m from roads.

Site-selection protocol

Before the 2000 field season, we acquired permission from private landowners to access sites and ground-truthed (verified in the field) the GIS-created map of roadless and roaded grasslands to identify suitable sampling sites, excluding any sites that landowners indicated had been tilled or logged in the past. Once we identified candidate sites, we created a landscape-scale sampling design in which we stratified study sites by distance from roads, soil type (serpentine vs. nonserpentine), and aspect (cool slopes: aspect of 330–90 degrees and >10 degrees inclination; warm slopes: 180–270 degrees and >10 degrees inclination; and neutral slopes: all others, but <10 degrees inclination). For each candidate site >1000 m from roads we located environmentally comparable sites (e.g., same degree of rockiness and disturbance) on different aspects. We then visited grasslands ~10 m (beyond the influence of roadside disturbance) and 100 m from paved roads to locate sites that were comparable to the roadless sites to form matching blocks of near, intermediate, and distant sites on different aspects and soil types. All actual distances for near and intermediate sites were within the ranges 5–15 and 75–125 m; all sites were >500 m apart to ensure independence of observations. We repeated this process until we had at least four replicates of each distance × soil type × aspect stratum. Total sample size was 47 non-serpentine and 45 serpentine sites. Within non-serpentine, there were 14 near, 14 intermediate, and 19 distant sites, and within serpentine, 14 near, 14 intermediate, and 17 distant sites.

Field data collection

Between late March and June in 2000 and 2001 we sampled five 1-m^2 quadrats along a transect at each of the 92 sites. Within each site, we randomly selected a point to begin vegetation sampling (without any prior knowledge of plant species at that point), marked the Universal Transverse Mercator coordinates of the site with a global positioning system (GPS) and recorded slope steepness, aspect, and topographic position. From the central sampling point, we established a 40-m transect in a random direction and placed 1-m^2 quadrats at

10-m intervals along this transect. Within each 1-m^2 quadrat we recorded microtopographic characteristics including percentage cover by rock, gravel, and soil, and on top of the soil the percentage cover of litter and bare ground. We also recorded disturbances within the quadrat, including presence and cover of livestock disturbances (dung, hoof prints) and wildlife disturbances (gopher mounds and tailings, other animal tracks and dung). We then recorded the presence of all native and exotic grass and forb species within the quadrat and estimated the total percentage cover by native vs. exotic species. Species definitions followed Hickman (1993). We revisited sites between late May and late June 2000 and 2001 to capture late-season plant species. At our last visit to each site, we collected a compound soil sample from the top 10 cm of soil near each quadrat and clipped end-of-season biomass at the ground level from a 0.1-m^2 area of the first quadrat. We dried biomass samples, removed litter from previous growing seasons, and weighed each sample.

Soil samples were analyzed at A & L Western Agricultural Laboratories (Modesto, California, USA) for organic content, phosphorus, exchangeable Ca^{++}, Mg^{++}, and K^{+} (millimoles of charge per 100 grams), cation exchange capacity (CEC), and particle size. Remaining soils in each sample were passed through a 60 mesh sieve and analyzed at the Soil Analytic Laboratory of the Division of Agriculture and Natural Resources, University of California (Davis, California, USA) for total N and C.

Precipitation varied considerably between the two study seasons. Total January–April rainfall was 610 mm in 2000 (20% above average) and 430 mm in 2001 (16% below average). Mean January–April temperature was 12.3°C in 2000 (17% above average) and 11.5°C (10% above average) in 2001.

Statistical analyses

We averaged measurements from the five quadrats in each transect into single replicate measures and conducted statistical analyses at this transect scale. We conducted statistical analyses using JMP 4.0 (SAS institute 2000). We transformed all percentage values by arcsine square root.

To test whether there was a significant effect of distance from roads, soil type, aspect, year, and livestock grazing on the number and cover of native and exotic species, we performed multivariate analyses of variance (MANOVA). Dependent variables included mean native and exotic plant cover per square meter, the percentage of species that were native (derived by dividing the number of native species per square meter by the number of total species per square meter), and the mean number of native and exotic grass and forb species per square meter. Independent variables included distance class, aspect, soil type, presence of livestock disturbance, year, and all second-order interactions.

We found a highly significant whole-model interaction effect between distance class and soil type, and therefore performed subsequent analyses separately by soil type. After repeating the MANOVA with the soils separated (which allowed us to ask whether relationships among dependent variables could alter our results), we used soil-specific ANOVAs to ask whether (1) sites farther from roads had a greater number of and cover by native species and lower number of and cover by exotic species, (2) whether such effects differed between grasses and forbs, and (3) whether distance from roads interacts with other environmental variables. We used the same dependent variables as for the initial MANOVA; independent variables included distance class, aspect, year, presence of livestock disturbance, and all second and third-order interactions. Where we found a significant effect of distance from roads or a distance × grazing interaction, we used Tukey's hsd multiple-range test to determine which pairs of means were significantly different. Where we found a significant grazing × aspect interaction, we used ANOVA to identify significant differences between grazed and ungrazed sites within each exposure. To ask at what spatial scale distance from roads affects native vs. exotic diversity, we determined the distance from roads that significantly affected the numbers of and cover by native and exotic species (10 m, 100 m, or $>$1000 m).

To ask whether any significant effects of distance from roads seen in the ANOVAs were due to distance vs. to environmental differences not accounted for by ANOVAs (e.g., slope steepness, soil fertility, rockiness), we performed analyses of covariance (ANCOVA). Before conducting each test, we removed any covariate that violated the assumption of homogeneity of slopes among distance classes. We first performed forward stepwise model selection to reduce the independent variables (distance class, slope steepness, biomass, organic matter, total N, total C, P, K^{+}, Ca^{++}, Mg^{++}, CEC, percentage silt, percentage rock cover) to those with significant main effects. We repeated the process for each response variable, including native and exotic cover, the percentage of species that were native, and the numbers of native grass and exotic forb species per square meter, all on non-serpentine only. We then conducted ANCOVAs with remaining independent variables.

We used MANOVA to ask whether the abundances (frequency per total quadrats) of individual species were affected by distance from roads, aspect, soil type, year, presence of livestock disturbance, and all second-order interactions. We only investigated species that we recorded in $>$10 sites. We focused on exotic species believed to be spreading, such as *Centaurea solstitialis*, *Aegilops triuncialis*, and *Taeniatherum caput-medusae*, as well as well-established invaders such as the forbs *Sonchus asper* and *Erodium botrys* and the grasses *Bromus hordeaceus* and *Avena fatua*. Native species included the grasses *Elymus elymoides*, *Hordeum brach-*

TABLE 1. Whole-model effect of distance from roads, aspect, year, livestock grazing, and interactions on the cover by native and exotic species, the percentage of species that were native, and the number of native and exotic grass and forb species per square meter, as determined by multivariate analysis of variance (MANOVA).

Parameter	Wilks' λ	df	*F*	*P*
Main effects				
Distance from roads	0.87	14, 132	1.54	0.09
Soil type	0.37	7, 151	36.72	<0.0001
Aspect	0.77	14, 302	3.01	0.002
Year	0.83	7, 151	4.34	0.0002
Livestock	0.84	7, 151	2.47	0.02
Interaction effects				
Soil type × Distance	0.73	14, 302	3.62	<0.0001
Soil type × Aspect	0.76	14, 302	3.19	0.0001
Soil type × Year	0.88	7, 151	2.90	0.007
Soil type × Livestock	0.84	7, 151	4.18	0.0003
Distance × Aspect	0.80	28, 539	1.26	0.17
Distance × Year	0.98	14, 302	0.24	0.99
Distance × Livestock	0.89	14, 302	1.35	0.18
Aspect × Year	0.92	14, 302	0.94	0.51
Livestock × Year	0.96	7, 151	0.99	0.44
Livestock × Aspect	0.83	14, 302	2.15	0.01

yantherum, *Melica californica*, *Nassella pulchra*, *Poa secunda,* and *Vulpia microstachys*. Where we found a significant effect of distance from roads or a distance × soil interaction, we used Tukey's hsd multiple-range test to determine all pairs of means (within each soil type, where appropriate) that were significantly different.

RESULTS

Effects of distance from roads

Distance from roads had a marginally significant effect on cover by native and exotic plants and on the numbers of native and exotic species, but its effect interacted strongly with soil type (Table 1). In serpentine grasslands there was no effect of distance from roads on the numbers of or cover by native or exotic species (Table 2, Figs. 1–2). In nonserpentine grasslands, the percentage cover per square meter of native species and the percentage of species that were native were greatest in sites >1000 m from roads and lowest in sites 10 m from roads, while exotic cover showed the reverse pattern (Table 2, Fig. 1). Native grasses were more diverse and exotic forbs marginally less diverse in sites most distant (>1000 m) from roads (Table 2, Fig. 2). There was also a marginal distance × grazing interaction effect on the number of native grass species (Table 2), which was significantly greater in distant (1.0 ± 0.1 species/m^2 [mean ± 1 SE]) than in near (0.2 ± 0.2 species/m^2) or intermediate (0.5 ± 0.2 species/m^2) ungrazed sites, but not significantly different between near (0.3 ± 0.1 species/m^2), intermediate (0.4 ± 0.1 species/m^2) and distant (0.6 ± 0.1 species/m^2) grazed sites. These effects remained significant (all $P < 0.05$) in ANCOVAs that compensated for any differences in productivity, slope steepness, rockiness, and soil chemistry and texture among near, intermediate, and distant sites.

There was a significant effect of distance from roads on the frequencies of selected native and exotic species (Wilks' λ = 0.55, df = 44, 1774, $F = 2.12$, $P = 0.0001$), as well as a significant ($P = 0.004$) interaction between distance from roads and soil type for some species (Table 3). Two exotics, *Centaurea solstitialis* and *Aegilops triuncialis*, occurred more frequently in plots close to roads than in plots distant (100 m and >1000 m) from roads on both soils, while two other exotics, *Convolvulus arvensis* and *Polypogon monspeliensis*, occurred more frequently in plots close to roads only on nonserpentine soils (Table 3). A native bunchgrass, *Nassella pulchra*, occurred slightly more frequently in plots far from roads than in plots near roads on both soils, while another native, *Poa secunda*, occurred more frequently in distant sites only on nonserpentine soils (Table 3). The exotics *Hypochaeris glabra*, *Avena fatua*, and *Polypogon monspeliensis* occurred most frequently in distant sites on serpentine, and *Brachypodium distachyon* occurred most frequently in distant sites on nonserpentine (Table 3).

Soil type, aspect, livestock grazing, and other environmental correlates of native and exotic cover and richness

Soil type, aspect, year, and livestock grazing had significant main effects on the set of dependent variables (Table 1). The numbers of and cover by native species per square meter were significantly greater, and the numbers of and cover by exotic species per square meter were significantly lower, in serpentine vs. nonserpentine grasslands (Table 1, Figs. 1 and 2). We also observed significant interactions of soil type with distance, aspect, year, and livestock grazing on the set of

TABLE 2. Effects of distance from roads, aspect, year, livestock grazing, and interactions on the cover by and numbers of native and exotic plant species per square meter for two years in nonserpentine (Nserp) and serpentine (Serp) grasslands.

Independent variable	Native cover		Exotic cover		Percentage of species native		Number of native grass species		Number of native forb species		Number of exotic grass species		Number of exotic forb species	
	Nserp	Serp	Nserp	Serp	Nserp	Serp	Nserp	Serp	Nserp	Serp	Nserp	Serp	Nserp	Serp
Distance from roads	**0.007**	0.20	**0.04**	0.26	**0.04**	0.86	**0.002**	0.88	0.66	0.44	0.55	0.39	**0.06**	0.16
Aspect	**0.02**	**0.03**	**0.09**	**0.09**	**0.0007**	**0.02**	0.35	0.45	**0.0006**	0.19	0.43	0.25	0.46	0.01
Year	0.87	0.86	0.76	0.26	0.91	0.97	0.71	0.55	0.27	**0.08**	**0.09**	**0.06**	0.45	0.98
Grazing	0.94	**0.02**	0.97	**0.01**	0.81	**0.03**	0.75	0.57	0.95	**0.002**	0.21	0.27	0.12	**0.04**
Distance × aspect	0.88	0.36	0.96	0.62	0.57	0.45	0.71	0.99	0.57	0.93	0.67	0.17	0.13	0.26
Distance × year	0.69	0.58	0.68	0.60	0.75	0.64	0.28	0.25	0.89	0.78	0.89	0.17	0.71	0.76
Distance × grazing	0.59	0.34	0.88	0.48	0.98	0.76	**0.10**	0.45	0.89	0.97	0.67	0.91	0.80	0.13
Aspect × year	0.75	0.42	0.77	0.59	0.85	0.70	0.62	0.56	0.71	0.82	0.92	**0.08**	0.82	0.27
Grazing × aspect	**0.05**	0.21	**0.09**	0.74	**0.02**	**0.04**	0.27	0.68	0.19	0.16	0.17	0.30	0.13	**0.02**
Grazing × year	0.94	0.46	0.93	0.31	0.84	0.68	0.65	0.68	0.65	0.42	**0.02**	0.38	0.85	0.53
Distance × grazing × year	0.82	0.55	0.43	0.50	0.42	0.85	0.89	0.69	0.67	0.99	0.52	0.91	0.73	0.97
Distance × aspect × year	0.79	0.79	0.72	0.60	0.93	0.95	0.99	0.40	0.88	0.94	0.63	0.11	0.73	0.84
Distance × grazing × aspect	0.23	0.47	0.43	0.61	0.57	0.88	0.77	0.64	0.79	0.92	0.82	0.99	0.95	0.99
Grazing × aspect × year	0.79	0.94	0.88	0.81	0.67	0.95	0.98	0.70	0.67	0.42	0.26	0.38	0.86	0.94
R^2	0.45	0.37	0.32	0.31	0.48	0.34	0.37	0.17	0.40	0.45	0.44	0.33	0.41	0.42

Notes: P values are from soil-specific ANOVAs that included all the listed independent variables. All independent variables that were significant at $P < 0.05$ in these ANOVAs were also significant in MANOVAs of all the dependent variables, with the two soils either separate or combined. Significant effects are indicated in boldface.

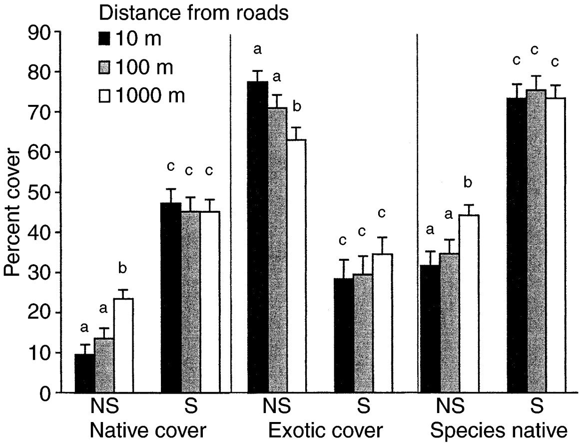

FIG. 1. Percent cover by native and exotic species and percentage of species that were native in sites 10 m, 100 m, and >1000 m from roads in nonserpentine (NS) and serpentine (S) grasslands (n = 92 sites). Data are means + 1 SE. Bars with different lowercase letters (ab for nonserpentine, cd for serpentine) indicate significant differences ($P < 0.05$) among distance classes within each soil type as indicated by Tukey's hsd multiple-range test (overall significance of effect indicated by ANOVA; Table 2).

dependent variables (Table 1). Below we describe the effects of environmental variables on native and exotic cover and richness separately for nonserpentine and serpentine grasslands.

Nonserpentine grasslands.—In nonserpentine grasslands, native cover was significantly greater on cool and neutral (relatively flat) slopes than on warm slopes (Table 2, Fig. 3). There was also a significant interaction between livestock grazing and aspect (Table 2). Native cover was greater on ungrazed compared to grazed cool slopes (23.0 ± 5.7% vs. 14.0 ± 3.9% [mean ± 1 SE]), but was not significantly affected by livestock grazing on warm or neutral slopes. Native cover was significantly negatively correlated with litter cover (df = 1, F = 5.19, P = 0.03) and K^+ (df = 1, F = 13.00, P = 0.0005), and positively correlated with P (df = 1, F = 6.96, P = 0.01) and the cover of rock (df = 1, F = 3.88, P = 0.05) (ANCOVA). The percentage cover by exotic species showed the opposite patterns with aspect and livestock grazing (Table 2, Fig. 3). There were also significant positive effects of biomass (df = 1, F = 5.99, P = 0.02) and total N (df = 1, F = 8.44, P = 0.004), and significant negative effects of P (df = 1, F = 11.07, P = 0.001) and the cover of rock (df = 1, F = 5.02, P = 0.03) (ANCOVA).

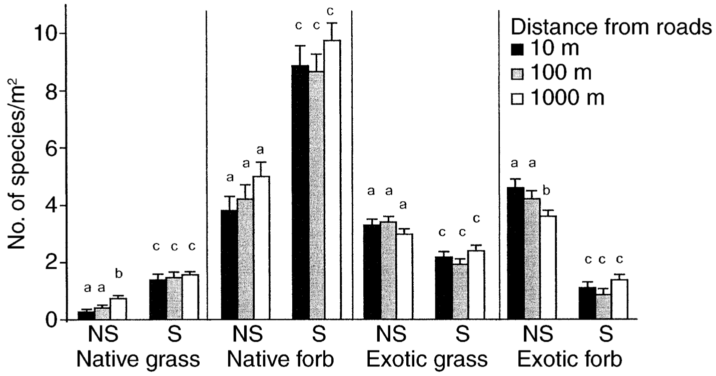

FIG. 2. The mean number of native grass, native forb, exotic grass, and exotic forb species in sites 10 m, 100 m, and >1000 m from roads in nonserpentine (NS) and serpentine (S) grasslands ($n = 92$ sites). Data are means + 1 SE. Bars with different lowercase letters (ab for nonserpentine, cd for serpentine) indicate significant differences ($P < 0.05$) among distance classes within each soil type as indicated by Tukey's hsd multiple-range test (overall significance of effect indicated by ANOVA; Table 2).

The percentage of species that were native was greater on cool and neutral slopes than on warm slopes (Table 2, Fig. 3). There was also a significant interaction between livestock grazing and aspect (Table 2). On cool slopes, the percentage of species that were native was greater in ungrazed than in grazed sites, but there was no effect of livestock grazing on the percentage of species that were native on neutral or warm slopes (Fig. 4). The percentage of species that were native was also strongly positively correlated with the cover of rock (df = 1, $F = 8.96$, $P = 0.004$) and slightly positively correlated with P (df = 1, $F = 3.65$, $P = 0.06$), was negatively correlated with slope steepness (df = 1, $F = 5.52$, $P = 0.02$), and was slightly negatively correlated with biomass (df = 1, $F = 3.37$, $P = 0.07$) and K^+ (df = 1, $F = 3.34$, $P = 0.07$) (ANCOVA).

The number of native grass species per square meter was marginally greater in ungrazed than grazed distant sites only, and was significantly positively correlated with slope steepness (ANCOVA, df = 1, $F = 8.10$, $P = 0.006$). The number of native forb species per square meter was marginally greater on cool and neutral slopes than on warm slopes (Table 2, Fig. 5). The number of exotic grass species was slightly greater in 2001 than in 2000 (3.5 species vs. 2.8 species; Table 2). There was also a marginally significant interaction between livestock grazing and year (Table 2). The number of

TABLE 3. Frequency of occurrence (percentage of total quadrats during 2000 and 2001) of selected native and exotic species, by distance from roads; significance of differences among distance classes is determined by MANOVA.

	Nonserpentine			Serpentine		
Species	10 m	100 m	>1000 m	10 m	100 m	>1000 m
Exotic forbs						
*Centaurea solstitialis****	72.8	55.0	20.9	31.6	22.5	2.3
Convolvulus arvensis§	4.0	3.8	0.6	0.00	3.3	1.1
Erodium botrys	32.0	37.4	55.0	11.0	10.7	9.7
Hypochaeris glabra§	26.4	25.2	45.6	5.2	6.0	10.2
Lactuca serriola	4.8	11.5	3.3	18.7	12.6	12.5
Medicago polymorpha	32.8	19.9	20.9	9.7	15.9	21.6
Sonchus asper	6.4	2.3	1.7	0.7	3.3	4.0
Exotic grasses						
Aegilops triuncialis†	8.8	4.6	1.7	18.1	11.9	1.1
Avena fatua§	42.4	52.7	31.3	28.4	28.5	40.3
Brachypodium distachyon§	6.4	15.3	14.3	1.9	0.7	1.1
Bromus hordeaceus	84.0	79.4	91.8	76.6	68.2	87.5
Lolium multiflorum	41.6	40.5	45.1	51.0	33.1	48.9
Poa bulbosa	9.6	9.2	0.00	0.00	0.00	0.00
Polypogon monspeliensis§	6.4	4.6	0.6	6.5	4.0	14.8
Taeniatherum caput-medusae	66.4	47.0	48.9	35.5	35.8	52.3
Native grasses						
Elymus elymoides	0.00	0.00	5.5	10.3	5.3	8.0
Hordeum brachyantherum	0.00	0.8	0.6	12.9	8.6	13.1
Melica californica	0.8	5.3	10.4	5.2	6.0	10.2
Nassella pulchra†	10.4	17.6	38.1	30.3	21.9	44.3
Poa secunda§	5.6	11.5	23.1	36.8	42.4	41.5
Vulpia microstachys	0.8	4.6	11.0	46.5	48.3	50.6

† $P < 0.1$; *** $P < 0.001$.
§ Distance × Soil interaction, rather than distance effect.

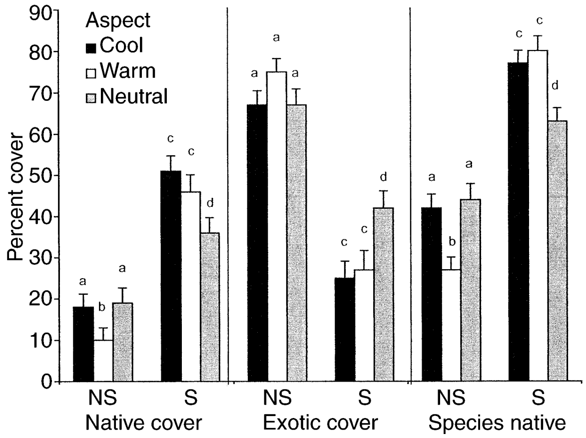

FIG. 3. Percent cover by native and exotic species and percentage of species that were native on cool, warm, and neutral aspects in nonserpentine (NS) and serpentine (S) grasslands (n = 92 sites). Data are means + 1 SE. Bars with different lowercase letters (ab for nonserpentine, cd for serpentine) indicate significant differences ($P < 0.05$) among aspects within each soil type as indicated by Tukey's hsd multiple-range test (overall significance of effect indicated by ANOVA; Table 2).

exotic grass species was greater in grazed compared to ungrazed sites in 2001 (3.9 ± 0.2 species/m^2 vs. 3.0 ± 0.2 species/m^2 [mean ± 1 SE]), but there was no difference between grazed and ungrazed sites in 2000 (2.8 ± 0.2 species/m^2 vs. 2.9 ± 0.2 species/m^2). The number of exotic forb species was significantly positively correlated with percentage silt (df = 1, F = 7.10, P = 0.009) and negatively correlated with P (df = 1, F = 5.03, P = 0.03), Mg^{++} (df = 1, F = 15.23, P = 0.0002) and litter cover (df = 1, F = 9.23, P = 0.003) (ANCOVA).

Serpentine grasslands.—In serpentine grasslands, native cover was greater on cool and warm slopes than on neutral slopes (Table 2, Fig. 3). Native cover was also significantly greater in sites grazed (49.2 ± 2.1%) compared to ungrazed (35.4 ± 3.7% [mean ± 1 SE]) by domestic livestock (Table 2). Exotic cover was slightly lower on cool and warm slopes than on neutral slopes (Table 2, Fig. 3). In addition, exotic cover was greater in ungrazed compared to grazed sites (46.0 ± 4.9% vs. 27.0 ± 2.8%; Table 2).

The percentage of species that were native was greater on cool and warm slopes than on neutral slopes (Table 2, Fig. 3). There was also a significant interaction effect between livestock grazing and aspect, with grazed neutral slopes averaging a greater percentage of species that were native than ungrazed neutral slopes, but no significant grazing effect on cool or warm slopes (Table 2, Fig. 4).

The number of native grass species per square meter was not significantly affected by any environmental variables (Table 2). The number of native forb species per square meter was marginally greater in 2001 than in 2000 (10.2 ± 0.5 species vs. 8.1 ± 0.5 species; Table 2), and was greater in grazed compared to ungrazed sites (10.0 ± 0.4 species vs. 6.4 ± 0.6 species; Table 2).

The number of exotic grass species was slightly greater in 2001 than in 2000 (2.4 ± 0.1 species/m^2 vs. 1.9 ± 0.1 species/m^2), and was slightly greater on warm and neutral than cool slopes in 2001 (2.8 ± 0.2 species and 2.5 ± 0.2 species vs. 2.0 ± 0.2 species), but not 2000 (1.8 ± 0.3 species and 2.1 ± 0.2 species vs. 1.9 ± 0.2 species) (Table 2). The number of exotic forb species per square meter was greater on neutral slopes than on cool and warm slopes (Table 2, Fig. 5). There was also a significant interaction between livestock grazing and aspect, with ungrazed neutral slopes averaging a greater number of exotic forb species than grazed neutral slopes (2.7 ± 0.3 species/m^2 vs. 0.9 ± 0.2 species/m^2), but no significant grazing effect on cool or warm slopes (Table 2).

Abundance of grasslands distant from roads

Within the 130 000-ha study area, 20% was 0–100 m from paved and improved roads, 50% was >100–1000 m from roads, and 30% was located >1000 m from paved and improved surface roads. Approximately 20% of the landscape was grasslands and 30% of oak woodlands, with the remainder largely chaparral. Of lands >1000 m from roads, 5% were grasslands, 20% were oak woodlands, and 75% were chaparral. Thus, only 15% of all grasslands were >1000 m from roads, and these grasslands composed only 1.5% of the landscape.

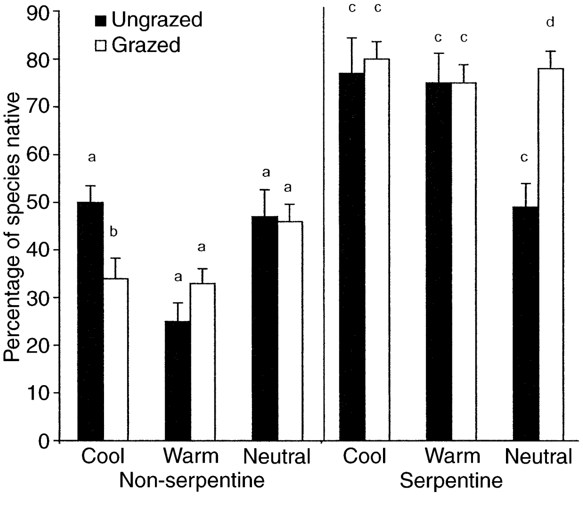

FIG. 4. Interactive effects of livestock grazing, soil type, and aspect on the percentage of species that were native (n = 92 sites). Data are means + 1 SE. Bars with different lowercase letters (ab for nonserpentine, cd for serpentine) indicate significant differences ($P < 0.05$) between grazed and ungrazed sites within each aspect and soil type as indicated by soil-specific ANOVAs blocked by aspect (overall significance of interactions indicated by ANOVAs; Table 2).

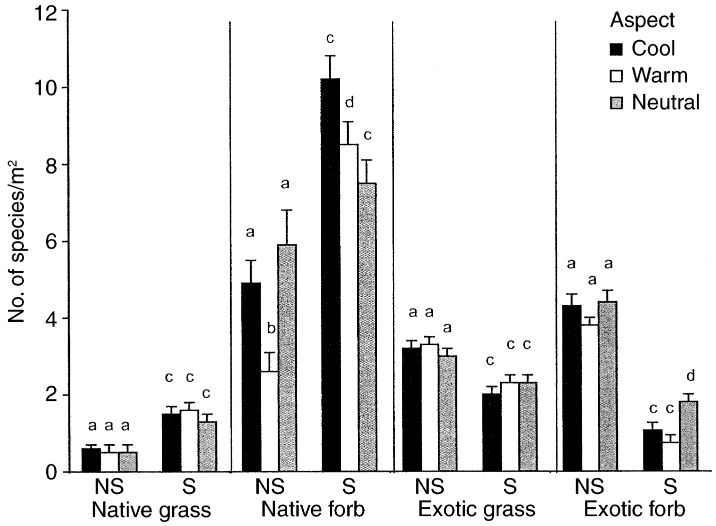

FIG. 5. The mean number per square meter of native grass, native forb, exotic grass, and exotic forb species on cool, warm, and neutral aspects in nonserpentine (NS) and serpentine (S) grasslands ($n = 92$ sites). Data are means + 1 SE. Bars with different lowercase letters (ab for nonserpentine, cd for serpentine) indicate significant differences ($P < 0.05$) among aspects within each soil type as indicated by Tukey's hsd multiple-range test (overall significance of effect indicated by ANOVA; Table 2).

DISCUSSION

We found a significant effect of distance from roads, which interacted strongly with soil type. In nonserpentine grasslands the percentage cover by native species, the percentage of species that were native, and the number of native grass species increased with distance from roads, while the cover by exotic species and number of exotic forb species decreased; in contrast, serpentine grasslands did not show any effects of road proximity. The above effects remained significant after we included in our models a large number of environmental variables, representing such potentially confounding factors as soil type, aspect, climate, livestock grazing, productivity, soil fertility, and rockiness. Our results therefore indicate that habitats distant from roads may provide a significant refuge for California's native grassland species on nonserpentine soils. In addition, our findings are consistent with the idea that this effect is due to distance as an indication of dispersal limitation, rather than to differences in topography, soil fertility, rockiness, or disturbances between sites near to roads and distant from roads. Unfortunately, these results suggest that, on nonserpentine soils, exotic species are still continuing to spread, and natives are continuing to lose ground.

Of the individual species that we examined, the exotics *Aegilops triuncialis*, *Centaurea solstitialis*, *Convolvulus arvensis*, and *Polypogon monspeliensis* were significantly less prevalent, and the natives *Nassella pulchra* and *Poa secunda* were significantly more prevalent in sites more distant from roads on at least one soil type. A number of factors may explain the presence or absence of a distance effect. First, distance from roads may be a more important influence on the distribution of recent compared to older invaders. Many of the most common exotics such as *Erodium*, *Avena*, and *Bromus* species may have already essentially completed their invasions at the landscape scale. Second, lack of a distance effect may indicate that the spread of some exotics is controlled by factors whose intensity is not strongly related to distance from roads; possible examples include wildlife, wind, streams, and perhaps livestock grazing (Stohlgren et al. 1998, Belsky and Gelbard 2000, Mack and Lonsdale 2001). Third, a species may not be sufficiently common to show statistically significant patterns.

Large spatial scale and explicit consideration of environmental variability were two crucial aspects of our study. While we found significant differences in the numbers of and cover by native and exotic plant species between sites located 10 m and >1000 m from roads, we observed no significant differences between sites 10 m and 100 m from roads. Also, we would have been unlikely to find significant effects if we had not stratified by soil type and aspect, which, as in other studies, exerted strong effects on the distribution of native and exotic species (McNaughton 1968, Harrison 1999, Safford and Harrison 2001). On resource-poor soils, which appear to be more resistant to invasion in semi-arid systems (Harrison 1999, Stohlgren et al. 1999, 2001, Belnap and Phillips 2001), distance from roads may be a less important influence on the numbers of and cover by native and exotic species than on resource-rich soils. We conclude that the effect of distance from roads depends on variation in environmental conditions that can render grasslands differentially vulnerable to invasions originating from roadsides (Evans and Young 1989, Murphy and Ehrlich 1989, Knops et al. 1995; Gelbard and Belnap, *in press*).

Within each soil type, numerous environmental variables showed significant correlations with the numbers of and cover by native and exotic species. For the most part, these patterns are consistent with previous studies (e.g., Rice 1989, Wagner 1989, Huenneke et al. 1990, Stromberg and Griffin 1996, Harrison 1999). For example, the numbers of and cover by native species tended to be greater and the numbers of and cover by exotic species tended to be lower in serpentine than in nonserpentine grasslands. There was also a general tendency for native species to be more prevalent and exotics less prevalent on sites of lower fertility, whether infertility was manifested as serpentine soil, low biomass, N, P, K^+, or high rock cover. On nonserpentine, exotic species were most prevalent on warm aspects, which receive high solar radiation. However on serpentine, exotic species were most prevalent in relatively flat sites, which are typically characterized by deep alluvial soils and more favorable moisture availability than on slopes. These results suggest the important influence of moisture availability on the prevalence of native and exotic species (McNaughton 1968, Evans et al. 1975).

We found intriguing interactive effects of aspect and grazing, which differed qualitatively by soil type. Previous work in this region showed that grazing by cattle was associated with a higher richness of exotic species on nonserpentine soils, while on serpentine soils, grazing was associated with more native species (Safford and Harrison 2001). But our results show that aspect further affects the grazing × soil interaction. On nonserpentine soils, grazing was associated with lower success of native species on cool slopes, but there was no grazing effect on warm or neutral slopes. On serpentine, grazing was associated with a greater prevalence of native species on neutral slopes, but there was no grazing effect on cool or warm slopes. These patterns may reflect interacting factors influencing the relative competitive ability of native and exotic species. On nonserpentine soils, moist conditions such as on north-facing slopes may favor the persistence of native species under competitive pressure from exotics (McNaughton 1968, Daubenmire 1970, Billings 1990), but soil compaction by livestock hooves could undermine this effect by reducing infiltration and soil water capacity (Menke 1989, Dahlgren et al. 1997). This effect may be less prevalent on south-facing slopes, where there are typically few native species to begin with. In serpentine grasslands, grazing may benefit native species, especially forbs, by releasing them from competition with exotics (e.g., Collins et al. 1998, Safford and Harrison 2001), but this effect may be less prevalent on steep slopes, where there are few exotic species to begin with.

Life-form adds another dimension to this complex picture. On nonserpentine, grazing appeared to have different effects on grass and forb species, as grazed sites contained fewer native grass species in distant sites, but there was no effect of grazing on native forb species. On serpentine, grazed sites contained greater numbers of native forbs, but not native grasses, as Safford and Harrison (2001) also found. A similar tendency for disturbance to favor forbs over grasses was observed experimentally by Maron and Jeffries (2001), who found that mowing coastal California grasslands increased native and exotic forb richness, but decreased exotic grass richness. While experiments are clearly needed to understand the causes and implications of these patterns, they provide evidence that conservation managers may need to consider different regimes of grazing for different soils, aspects, and target species.

Conclusions and implications for conservation

Roadless grasslands are a scarce habitat that appears to provide a significant refuge for native Californian species on nonserpentine soils. It was surprising to find such clear evidence for the importance of distance from roads given the 200-yr history and severity of invasion in the grasslands of the California floristic province (Mooney et al. 1986, Murphy and Ehrlich 1989, Heady 1995, Gerlach et al. 1998). Although it is premature to say whether our results are likely to be general, we speculate that the effects of distance from roads may be even more pronounced in less thoroughly invaded landscapes, such as remote grasslands and shrublands of the Colorado Plateau and Great Basin (Driscol 1964, Kindschy 1994; J. L. Gelbard, *personal observation*).

We believe the pattern of native and exotic plant diversity that we observed is dynamic, not static, and both natural and human influences can substantially speed or slow the rate of continued invasion. Thus, careful management is warranted to protect the remaining roadless habitats in California's grassland landscapes. Appropriate measures may include preventing construction of new roads, especially in more fertile grasslands; carefully regulating road maintenance to favor native species (e.g., Benefield et al. 1999); limiting off-highway vehicle access into grasslands with low road densities; and monitoring of recreational trails and grazing allotments within roadless habitats to detect and eradicate new infestations (Moody and Mack 1988). Our results support the general idea of focusing control and management efforts on eradicating ''nascent foci'' where problematic exotic species are just beginning to invade (Moody and Mack 1988, Hobbs and Humphries 1995).

Appropriate management also involves identifying a regime of livestock grazing that favors the persistence of natives over the continued spread of exotics (DiTomaso 2000, Belnap and Lange 2001, Masters and Sheley 2001). We found evidence that grazing had different impacts on native and exotic grasses vs. forbs, and that these effects further varied among soils and aspects. These results agree with previous studies showing that the effects of livestock grazing vary among habitats and life-forms (e.g., Mack 1989, Safford and Harrison 2001). Given this complexity, heterogeneity of grassland management at the landscape scale may be an appropriate way to maximize native biodiversity (Fuhlendorf and Engle 2001). In inland California grasslands, light or no grazing may be appropriate for maintaining patches dominated by native perennial bunchgrasses, but moderate grazing may be more appropriate for maintaining native annual forb diversity, especially on serpentine soils.

We believe that our approach provides a model that can be used by other researchers attempting to disentangle the effects of various factors on the replacement of native communities by exotic associations across a region. It appears important to use a multifactorial approach in cases where interactions among causal factors may otherwise confound the understanding of invasion patterns. Of course, the strata used in the experimental design and the measured environmental variables should differ depending on the type of ecosystem, its potential causal factors, and its relevant science and management questions.

ACKNOWLEDGMENTS

We are grateful to Hugh Safford for plant identification and review of an earlier draft; Carol Horvitz and two anonymous reviewers; Brian Inouye for invaluable statistical and sampling advice; Joe Callizo for plant identification; and the Land Trust of Napa County's Wantrup Wildlife Sanctuary for hospitality. For access to sites, we thank the individuals who represent the Blue Ridge–Berryessa Conservation Partnership, the UC Natural Reserve System, U.S. Bureau of Land Management Knoxville and Cache Resource Districts, U.S. Bureau of Reclamation Berryesa Recreation Area, Homestake Mining Company, Bar X Ranch, Paradise Valley Ranch, Bear Valley Ranch, Mead Ranch, Gamble Ranch, Todd Ranch, Hardin Ranches, and the City of Napa.

LITERATURE CITED

Amor, R. L., and P. L. Stevens. 1976. Spread of weeds from a roadside into sclerophyll forests at Dartmouth, Australia. Weed Research **16**:111–118.

Armstrong, J. K., and L. F. Huenneke. 1992. Spatial and temporal variation in species composition in California grasslands: the interaction of drought and substratum. Pages 213–233 *in* A. J. M. Baker, J. Procter, and R. D. Reeves, editors. The vegetation of ultramafic (serpentine) soils. Intercept, Andover, UK.

Belnap, J., and O. L. Lange. 2001. Biological soil crusts: structure, function and management. Springer-Verlag, Berlin, Germany.

Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications **11**:1261–1275.

Belsky, A. J., and J. L. Gelbard. 2000. Livestock grazing and weed invasions in the arid west. Oregon Natural Desert Association, Bend, Oregon, USA.

Benefield, C. B., J. M. DiTomaso, G. B. Kyser, S. B. Orloff, K. R. Churches, D. B. Marcum, and G. A. Nader. 1999. Success of mowing to control yellow starthistle depends on timing and plant's branching form. California Agriculture **53**:17–21.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301–322 *in* G. M. Woodwell, editor. The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, New York, New York, USA.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280**:745–747.

Dahlgren, R. A., M. J. Singer, and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. Biogeochemistry **39**:45–64.

Daubenmire, R. F. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin **62**.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts and management. Weed Science **48**:255–265.

Driscol, R. S. 1964. A relict area in the central Oregon juniper zone. Ecology **45**:345–353.

Evans, R. A., B. L. Kay, and J. A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia **43**:79–102.

Evans, R. A., and J. A. Young. 1989. Characterization and analysis of abiotic factors and their influences on vegetation. Pages 13–28 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function. California annual grassland. Kluwer Academic Press, Dordrecht, Germany.

Forcella, W., and S. J. Harvey. 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madrono **30**:102–109.

Frenkel, R. E. 1970. Ruderal vegetation along some California roadsides. University of California Press, Berkeley, California, USA.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience **51**:625–632.

Gelbard, J. L., and J. Belnap. *In press.* Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology.

Gerlach, J., A. Dyer, and K. Rice. 1998. Grassland and foothill woodland ecosystems of the central valley. Fremontia **26**:39–43.

Greenberg, C. H., S. H. Crownover, and D. R. Gordon. 1997. Roadside soil: a corridor for invasion of xeric scrub by nonindigenous plants. Natural Areas Journal **17**:99–109.

Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. Oecologia **121**:99–106.

Heady, H. F. 1995. Valley grassland. Pages 491–514 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Fourth edition. Publication number 9. California Native Plant Society, Sacramento, California, USA.

Hickman, J. C. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389–405 *in* J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley and Sons, Chichester, UK.

Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology **9**:761–770.

Holland, V. L., and D. J. Keil. 1995. California vegetation. Kendall/Hunt Publishing Company, Dubuque, Iowa, USA.

Huenneke, L. F., S. Hamburg, R. Koide, H. A. Mooney, and P. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology **71**:478–491.

Jackson, L. E., and J. Roy. 1989. Comparative ecology of annual grasses: native versus Californian habitats. Pages 81–92 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Press, Dordrecht, Germany.

Johnson, H. B., F. C. Vasek, and T. Yonkers. 1975. Productivity, diversity, and stability relationships in Mojave Desert roadside vegetation. Bulletin of the Torrey Botanical Club **102**:106–115.

Kindschy, R. R. 1994. Pristine vegetation of the Jordan Crater kipukas: 1978–91. Pages 85–88 *in* S. B. Monsen and S. G. Kitchen, editors. Proceedings—Ecology and Management of Annual Rangelands. General technical report INT-GTR-

313. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Knops, J. M. H., J. R. Griffin, and A. C. Royalty. 1995. Introduced and native plants of the Hastings reservation, central coastal California: a comparison. Biological Conservation **7**:115–123.

Kruckeberg, A. R. 1984. California serpentines: flora, vegetation, geology, soils and management problems. University of California Press, Berkeley, California, USA.

Lambert, G., and J. Kashiwagi. 1978. Soil survey of Napa County, California. United States Natural Resource Conservation Service [formerly Soil Conservation Service], Washington, D.C., USA.

Londsdale, W. M., and L. A. Lane. 1994. Tourist vehicles as vectors of weed seeds in Kakadu National Park, northern Australia. Biological Conservation **69**:277–283.

Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pages 155–179 *in* J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley and Sons, Chinchester, UK.

Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. BioScience **51**:95–102.

Major, J. 1995. California climate in relation to vegetation. Pages 11–74 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Fourth edition. Publication number 9. California Native Plant Society, Sacramento, California, USA.

Maron, J. L., and R. L. Jeffries. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecological Applications **11**:1088–1100.

Masters, R. A., and R. L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. Journal of Range Management **54**:502–517.

McNaughton, S. J. 1968. Structure and function in California grasslands. Ecology **49**:962–972.

Menke, J. 1989. Management controls on productivity. Pages 173–200 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Press, Dordrecht, Germany.

Menke, J. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia **20**:22–25.

Moody, M. E., and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology **25**:1009–1021.

Mooney, H. A., S. P. Hamburg, and J. A. Drake. 1986. The invasion of plants and animals into California. Pages 250–272 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer Verlag, New York, New York, USA.

Murphy, D. D., and P. R. Ehrlich. 1989. Conservation biology of California's remnant native grasslands. Pages 201–212 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Press, Dordrecht, Germany.

Noss, R. F., and A. Cooperrider. 1994. Saving nature's legacy. Island Press, Washington, D.C., USA.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. Journal of Vegetation Science **6**:701–710.

Rice, K. J. 1989. Competitive interactions in California annual grasslands. Pages 59–72 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Press, Dordrecht, Germany.

Roche, B. F., C. T. Roche, and R. C. Chapman. 1994. Impacts of grassland habitat on yellow starthistle (*Centaurea solstitialis* L.) invasion. Northwest Science **68**:86–96.

Safford, H. D., and S. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. Ecological Applications **11**:1112–1122.

SAS Institute. 2000. JMPin, Version 4.0.3. SAS Institute Cary, North Carolina, USA.

Sawyer, J. O., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, California, USA.

Schmidt, W. 1989. Plant dispersal by motor cars. Vegetatio **80**:147–152.

Smith, D. W., and W. D. Broderson. 1989. Soil survey of Lake County, California. United States Natural Resource Conservation Service [formerly Soil Conservation Service], Washington, D.C., USA.

Soulé, M. E., and J. Terborgh, editors. 1999. Continental conservation. Island Press, Washington, D.C., U.S.A.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schnell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25–46.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology **138**:113–125.

Stohlgren, T. J., Y. Otsuki, C. A. Villa, M. Lee, and J. Belnap. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. Biological Invasions **3**: 37–50.

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications **6**:1189–1211.

Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology **6**:253–262.

Wagner, F. H. 1989. Grazers, past and present. Pages 151–162 *in* L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Press, Dordrecht, Germany.