
Ecological Heterogeneity in the Effects of Grazing and Fire on Grassland Diversity

S. HARRISON,* B. D. INOUE, AND H. D. SAFFORD

Department of Environmental Science and Policy, University of California–Davis, One Shields Avenue, Davis, CA 95616, U.S.A.

Abstract: *Grazing and fire are major forces shaping patterns of native and exotic species diversity in many grasslands, yet both of these disturbances have notoriously variable effects. Few studies have examined how landscape-level heterogeneity in grassland characteristics, such as soil-based variation in biomass and species composition, may contribute to variation in the effects of fire or grazing. We studied the effects of livestock grazing and fire in a mosaic of serpentine and nonserpentine soils in California, where most grasslands are dominated by exotic annuals and serpentine soil is the major refuge for native grassland species. We predicted that the effects of disturbance would be proportional to productivity and therefore would be greater on nonserpentine than serpentine soils. We measured species composition at 80–100 grazed or ungrazed sites for 2 years before (1998–1999) and 2 years after (2000–2001) an autumn wildfire. Both disturbances increased total species richness on both soils. However, fire enhanced total and exotic species richness more on nonserpentine soils and enhanced native species richness more on serpentine soils. Grazing increased native species richness on serpentine soils but not on nonserpentine soils. These soil-disturbance interactions suggest that the use of fire and grazing to manage native species diversity in wildlands must be done with careful attention to background ecological heterogeneity.*

Key Words: diversity, exotic species, fire, grasslands, grazing, invasion, serpentine, species richness

Heterogeneidad Ecológica en los Efectos del Pastoreo y los Incendios sobre la Diversidad del Pastizal

Resumen: *El pastoreo y los incendios son las principales fuerzas que moldean los patrones de diversidad de especies nativas y exóticas en muchos pastizales, sin embargo, ambas perturbaciones tienen efectos notablemente variables. Pocos estudios han examinado la manera en que la heterogeneidad de las características a nivel de paisaje, como la variación de biomasa y composición de especies basada en el suelo, puede contribuir con la variación de los impactos de incendios o pastoreo. Estudiamos los efectos del pastoreo de ganado e incendios en un mosaico de suelos serpentinos y no serpentinos en California, donde la mayoría de los pastizales están dominados por especies anuales exóticas y el suelo serpentino es el refugio principal para especies nativas del pastizal. Predicimos que los efectos de la perturbación serían proporcionales a la productividad y, por lo tanto, será mayor en suelos no serpentinos que en los serpentinos. Medimos la composición de especies en 80–100 sitios pastoreados o no pastoreados por dos años antes (1998–99) y dos años después (2000–2001) de un incendio descontrolado de otoño. Ambas perturbaciones incrementaron la riqueza total de especies en ambos suelos. Sin embargo, el incendio incrementó más la riqueza de especies exóticas en suelos no serpentinos e incrementó más la riqueza de especies nativas en suelos serpentinos. El pastoreo incrementó la riqueza de especies nativas en suelos serpentinos, pero no en suelos no serpentinos. Estas interacciones suelo-perturbación sugieren que el uso de incendios y pastoreo para manejar la diversidad de especies nativas en tierras silvestres debe ser realizado poniendo cuidadosa atención a la heterogeneidad ecológica del entorno.*

*email spbarrison@ucdavis.edu

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Introduction

The role of natural disturbance in maintaining species diversity is a central tenet of ecology (e.g., Paine & Levin 1981; Pickett & White 1985; Petraitis et al. 1989), and in recent years, the maintenance of appropriate disturbance regimes has also become recognized as a general principle in conservation biology (e.g., Meffe & Carroll 1997). Yet in a world of ever-increasing movement of propagules across former biotic boundaries, wildlands managers face a fundamental dilemma. Whether disturbances are natural, accidental, or managed, they tend to promote exotic species invasions (Hobbs & Huenneke 1992). It is critical, therefore, to better understand the variation in environmental conditions that determines how much a given disturbance will promote native versus exotic species (Stohlgren et al. 1999). Because disturbances by definition involve the removal of above-ground biomass, responses to disturbance may be generally stronger on more-fertile soils, where both above-ground biomass and the proportion of "weedy," disturbance-adapted species may be higher (Grime 1979; Huston 1979; Pickett & White 1985).

We examined livestock grazing and fire in Californian grasslands, and asked how native and exotic species richness depends on soil, disturbance, and the interaction between the two. Grazing by livestock may enhance grassland species diversity through the classical mechanism of reducing biomass and slowing competitive displacement (MacNaughton 1968; Noy-Meir 1995; Collins et al. 1998). It is used by conservation-oriented grassland managers to suppress exotic species and enhance native species (e.g., Menke 1989; Thomsen et al. 1993; Barry 1998). Yet livestock grazing may also eliminate sensitive species and promote the spread of exotic species in grasslands (e.g., Waser & Price 1981; Hobbs & Huenneke 1992; Fleischner 1994), and its positive effects on species richness may only be seen at small spatial scales (Olf & Ritchie 1998; Stohlgren et al. 1999). Important sources of variation may include both grazing characteristics, such as its intensity and timing, and grassland characteristics, such as productivity and species composition. In general, grazing is expected to have stronger positive effects on diversity in systems with higher productivity (e.g., Grime 1979; Milchunas et al. 1988; Proulx & Mazumder 1998). Few researchers have asked, however, how the effects of grazing may vary within a landscape as a function of ecological heterogeneity (Stohlgren et al. 1999).

Fire likewise has highly variable effects on grasslands. Typical responses include a flush of forb germination and flowering and a transient increase in overall productivity as the removal of litter enhances the availability of nutrients, space, and light (Vogl 1974; Parsons & Stohlgren 1989; Whelan 1995). Carefully timed fires are often successful at suppressing particular weeds (e.g.,

Menke 1989; diTomaso et al. 1999) and may sometimes increase the cover or diversity of native species (Menke 1989; Parsons & Stohlgren 1989; Meyer & Schiffman 1999). In degraded or low-productivity grasslands, however, fire may create monocultures of fire-resistant species (Vogl 1974), and in some cases fire may be a significant promoter of exotic species (Heady 1977; d'Antonio 2000). Livestock grazing may modify the effects of fire in various ways, often by reducing the fuel load (Collins 1987; Noy-Meir 1995). As with grazing, almost no generalizations are available about how the effects of grassland fires are modified by ecological variation at the landscape scale.

Soil is a major source of environmental variation that determines grassland species composition and productivity within our study region. On most soils in California, native bunchgrasses and forbs have been replaced by annual grasses and forbs from the Mediterranean region (Heady 1977; Mooney et al. 1986). This transformation may have been aided by changes in the grazing and fire regimes when Europeans arrived 200 years ago, but there is presently no simple relationship between livestock grazing, fire, and the persistence of native species in California grasslands (Heady 1977; Stromberg & Griffin 1996). One of the most important refuges for many grassland species native to California is soil derived from serpentine rock, which is relatively resistant to invasion because it is poor in calcium and nutrients and contains high levels of magnesium and various metals (Kruckeberg 1984; Huenneke et al. 1990).

Our study area was a large suite of grasslands on serpentine and nonserpentine soils, supporting about 50–80% and 30–40% native species per square meter, respectively; the former generally support considerably lower biomass (Harrison 1999a; Safford & Harrison 2001). Roughly half our sites on each soil type were grazed by cattle, whereas on the other half cattle were removed in 1985. We measured species composition at 80 permanently marked sites in 1998–1999. Following a wildfire in the autumn of 1999 that burned 35 sites, we chose and marked 20 more sites and continued the measurements in 2000–2001. We used univariate and multivariate analyses of this 4-year data set to test several predictions.

First, we expected that grazing and fire would affect species richness more on nonserpentine than on serpentine soils because of the difference in productivity (Grime 1979; Pickett & White 1985). Second, we expected that grazing and fire would affect species composition differently on the two soils because the relative prevalence of native versus exotic species, annuals versus perennials, and/or grasses versus forbs is likely to differ between soils and to be affected by the interaction between disturbance and soil (Evans & Young 1972; Hobbs et al. 1988; Huenneke et al. 1990; Menges & Hawkes 1998). Finally, we asked whether our results were dependent

on spatial scale (Stohlgren et al. 1999), whether responses to disturbance were proportional to biomass within each soil, and how the responses of individual species varied between soils.

Study System and Methods

Our study system was the 3100-ha Donald and Sylvia McLaughlin University of California Natural Reserve, in Napa, Lake, and Yolo Counties (lat. 38°51'N, long. 123°30'W), 120 km north of San Francisco, California (U.S.A.). Elevations range from 370 to 945 m. Climate is Mediterranean, with warm, dry summers and cool, moist winters. Annual precipitation averages 725 mm (160 mm in January, 0.3 mm in July), and mean annual temperature is approximately 18.1° C (11.4° C in January, 27.8° C in July). Geologic substrates include ultramafic and mafic rocks of the Coast Range Ophiolite (serpentine, peridotite, gabbro, and greenstone), Mesozoic sandstones and shales of the Great Valley Sequence, and Quaternary Clear Lake volcanics (Fox et al. 1973; Lambert & Kashiwagi 1978; Wagner & Bortugno 1982). The soils, geology, flora, and vegetation of this area are further described by Harrison (1997, 1999a, 1999b) and the University of California–Davis Natural Reserve System (2000). Species nomenclature in this paper follows that of Hickman (1993).

Serpentine soils in this region generally support chaparral dominated by leather oak (*Quercus durata*, Fagaceae) or Macnab's cypress (*Cupressus macnabiana*, Cupressaceae), but there are scattered grasslands on alluvial or colluvial soils formed from serpentine and related mafic to ultramafic parent materials in the Henneke, Montara, and Okiota soil series. The grasslands supported by these soils include many native forbs, such as *Lasthenia californica* (Asteraceae), and native perennial bunchgrasses, such as *Poa secunda*, *Melica californica*, and *Nassella pulchra* (Poaceae). Mediterranean annual grasses and forbs are present but much less dominant than in nonserpentine grasslands. There are no species restricted (endemic) to serpentine in the grassland flora.

Dominant vegetation on nonserpentine soils includes blue oak (*Quercus douglasii*) woodland, chamise (*Adenostoma fasciculatum*, Rosaceae) chaparral, and California mixed chaparral. The nonserpentine grasslands in this region occur on loams formed from sandstones, mudstones, and shales in the Maymen, Millsholm, Lodo, Bressa, and Dibble soil series. Open grasslands on these substrates intergrade with blue oak savanna and woodland. The grasslands are dominated by Mediterranean annuals such as *Avena fatua*, *A. barbata*, *Bromus hordeaceus*, *Lolium multiflorum*, and *Taeniatherum caput-medusae* (Poaceae), which germinate in fall and flower in late spring, and exotic forbs such as yellow starthistle (*Centaurea solstitialis*, Asteraceae).

Native and exotic species richness were sampled at 38 serpentine and 42 nonserpentine grassland sites in 1998 and 1999 (Harrison 1999a). Approximately half the sites on each soil had been grazed year-round for many decades, with roughly one cow and calf per 10 ha. The other half had been similarly grazed until cattle were removed from various areas during the construction of a mine in 1985. These sites were well interspersed around the 3100-ha study area, such that soil type and grazing status were independent of latitude and longitude (Harrison 1999a). Serpentine grasslands were dominated by native species (mean = 81% native species in 1 m² plots), whereas the flora of nonserpentine grasslands was largely exotic (mean = 43% native species). Serpentine grasslands were significantly higher in soil magnesium and lower in biomass, cover, soil depth, nitrogen, phosphorus, and calcium than nonserpentine grasslands. Within serpentine grasslands, the proportion of native species increased with a decreasing ratio of calcium to magnesium, whereas within nonserpentine grasslands the proportion of native species was higher on cooler (north- to northeast-facing) slopes than on warmer slopes. Grazed and ungrazed sites did not differ significantly in native or exotic species richness on either soil (Harrison 1999a).

On 16 October 1999, a 16,000-ha arson wildfire burned 35 study sites (8 serpentine, 27 nonserpentine). To increase the sample sizes, we added 10 burned serpentine, 3 unburned serpentine, and 7 unburned nonserpentine sites, for a total of 45 burned sites (18 serpentine, 27 nonserpentine) and 55 unburned sites (33 serpentine, 22 nonserpentine). The 20 new sites were selected in the same way as the earlier ones: we chose a transect origin by using random distances along and distances from roads, and we chose a transect direction randomly using a digital watch. Sites were ≥50 m apart, and no more than three sites were located within the same contiguous area of grassland. Cattle were present on 43 sites (21 serpentine, 22 nonserpentine), and cattle were removed in 1985 from the other 57 sites (31 serpentine, 26 nonserpentine).

We sampled these 100 sites in mid-April and late May 2000 and 2001, using the same procedure as in 1998 and 1999. At each site, five 1-m² quadrats were sampled at 10-m intervals along a 40-m linear transect. Within each quadrat at each site and sampling date, we recorded the identity of each species present. These data were used to calculate total, native, and exotic species richness at the 5-m² scale (all quadrats per site) and 1-m² scale (average of the five quadrats per site), and the average frequency of each species (number of quadrats occupied out of five). We also clipped, dried, and weighed aboveground biomass in random 30 × 30 cm subquadrats at each site in 1998 and 2001.

To aid in soil classification, we collected 300–500 g of soil from a depth of 1–10 cm at each study site. Soil sam-

ples were oven-dried, sifted, and then analyzed by A & L Western Agricultural Laboratories, Modesto, California, for exchangeable calcium and magnesium. Soils from our serpentine sites had a mean $\text{Ca}^{2+}:\text{Mg}^{2+}$ ratio of 0.40 (± 0.21 SD), whereas soils from our nonserpentine sites had a mean $\text{Ca}^{2+}:\text{Mg}^{2+}$ ratio of 3.25 (± 2.09 SD). Nonserpentine soils had a mean of 2085 (± 701) ppm Ca^{2+} and 913 (± 640 SD) ppm Mg^{2+} , whereas the serpentine soils had a mean of 846 (± 382) ppm Ca^{2+} and 2275 (± 673 SD) ppm Mg^{2+} . Four sites had soil chemistry that was neither clearly serpentine nor clearly nonserpentine. Because the results were robust to either excluding these four sites or reversing their soil designations, we included them and used their original, visually-based soil designations.

We used repeated-measures analysis of variance (ANOVA; Proc Mixed, SAS 8.0) to determine whether total species richness at the 5-m² scale was affected by year, soil, grazing, fire, and the interactions of these variables. We repeated this using mean richness at the 1-m² scale (average of the five quadrats) to determine whether the results were dependent on scale. To determine whether the effects of grazing or fire were dependent on biomass, we regressed the postfire change in richness for the burned sites (i.e., their richness in 2000 or 2001 minus their richness in 1999) on their prefire (1998) biomass.

We used repeated-measures ANOVA to determine how the numbers of native and exotic species at the 5-m² scale were affected by year, soil, grazing, fire, and their interactions. To help interpret the results of this analysis, we tabulated the average richness at the 5-m² scale of native and exotic species by life form (annual vs. perennial, grass vs. forb) in burned and unburned and grazed and ungrazed sites on the two soils. Three of the eight possible life-form categories are not shown because there were only two exotic perennial grasses (*Poa bulbosa* and *Dactylis glomerata*), one uncommon exotic perennial forb (*Rumex crispus*), and one common native annual grass (*Vulpia microstachys*).

To examine changes in species composition as opposed to richness, we used a principal components analysis of the frequencies of all 218 species across all sites and years. We analyzed the first three principal components as responses in a multivariate analysis of variance (MANOVA), with year, soil, grazing, fire, and the interactions of these variables. Canonical correspondence analysis yielded qualitatively similar results (not shown), but we used the principal component axes because they explained a larger proportion of the variance in species composition.

To examine variation in the responses of individual species, we selected the most common ones (i.e., those that occurred in at least one-third of the sites). We used repeated-measures ANOVA to analyze the frequencies of these species (number of quadrats in which they oc-

curred out of five per site) with respect to year, soil, grazing, fire, and the interactions of these variables.

Results

Species Richness

We found 217 species in this study, of which 151 (70%) were shared between soils, 34 were found only on serpentine soils, and 32 were found only on nonserpentine soils. Total species richness at the 5-m² scale was significantly affected by year, soil, year*soil, year*fire, year*soil*fire, and year*fire*grazing (Table 1). Species richness was initially higher in unburned serpentine than unburned nonserpentine grasslands, but richness increased considerably more in response to fire on nonserpentine than serpentine soils. One year after the fire, species richness on burned sites on the two soils was roughly equal. Two years after the fire, total richness returned to approximately the same levels as before the fire (Fig. 1). Thus, all effects of fire on richness were reflected in interaction terms that included year.

Species richness at 1 m² showed the same effects as richness at 5 m² (repeated-measures ANOVA, $p < 0.05$) except for the year*fire*grazing interaction, which was no longer significant. The ratio of richness at the 1-m² scale to richness at the 5-m² scale was affected by grazing (repeated-measures ANOVA, $p < 0.05$) and soil*grazing ($p < 0.01$), but not by any other factors. On nonserpentine soils, grazing had a homogenizing effect: the ratio between richness at 1 m² and that at 5 m² increased from 0.46 to 0.52. On serpentine soil the ratio changed in the opposite direction, from 0.52 to 0.49.

Biomass was not a significant main or interactive effect in any of our models for species richness at the 1-m² or 5-m² scale. Considering only the burned sites, the increase in richness after the fire (i.e., their richness in 2000 or 2001 minus their richness in 1999) was not significantly correlated with their prefire biomass or by the interaction between biomass and soil (ANOVA, $p > 0.10$).

Native and exotic species richness were affected by most of the same factors as was total species richness, including year, soil, year*fire, and year*soil*fire (Table 1). Both native and exotic species richness increased in response to fire on both soils. On nonserpentine soils, however, the postfire increase was strongest for exotic species, especially annual forbs, whereas on serpentine soils fire caused a greater increase in native species richness (Table 2). In addition, native species richness was affected by a soil*grazing interaction (Table 1). On serpentine soils, grazed sites had a greater richness of native forbs than ungrazed sites, but on nonserpentine soils, grazed sites had a lower richness of native forbs than ungrazed sites (Table 2). The trend for exotic spe-

Table 1. Results of repeated-measures analysis of variance for total, native, and exotic species richness as a function of year, soil, fire, grazing, and their interactions.

Model effect	df	Total		Native		Exotic	
		F	p	F	p	F	p
Year	3	36.36	<0.001 ^a	34.88	<0.001 ^a	8.00	<0.001 ^a
Soil	1	12.90	<0.001 ^a	104.21	<0.001 ^a	214.42	<0.001 ^a
Fire	1	0.85	0.360	0.35	0.554	0.29	0.593
Grazing	1	0.23	0.629	0.20	0.659	0.24	0.626
Year:soil	3	4.78	0.004 ^a	2.85	0.041 ^b	2.90	0.039 ^b
Year:fire	1	5.82	0.018 ^b	5.08	0.026 ^b	1.68	0.198
Soil:fire	1	1.51	0.223	0.10	0.751	2.93	0.090
Year:grazing	3	0.10	0.958	0.55	0.649	0.74	0.528
Soil:grazing	1	2.22	0.140	4.50	0.037 ^b	0.40	0.531
Fire:grazing	1	0.13	0.724	0.01	0.914	0.02	0.889
Year:soil:fire	1	12.34	<0.001 ^a	7.43	0.008 ^a	4.52	0.036 ^b
Year:soil:grazing	3	1.20	0.314	1.09	0.357	0.95	0.418
Year:fire:grazing	1	9.08	0.003 ^a	8.91	0.004 ^a	1.93	0.168
Soil:fire:grazing	1	1.23	0.270	0.16	0.688	0.26	0.609
Residuals	96						

^ap < 0.01.^bp < 0.05.

cies was in the opposite direction: grazing was associated with higher exotic species richness on nonserpentine soils but not on serpentine soils (Table 2).

Species Composition

The first principal component (PC1) was negatively associated with several common exotic species (*Avena fatua* and *Taeniatherum caput-medusae*, Poaceae; *Centaurea solstitialis*, Asteraceae). The second principal component (PC2) was negatively associated with a grazing-intolerant exotic grass (*Avena fatua*) but

positively associated with a grazing-tolerant native forb (*Hemizonia congesta*, Asteraceae). The third principal component (PC3) had a strong negative association with two exotic grasses (*T. caput-medusae* and *Lolium multiflorum*). The species with the largest loadings for the first three principal components tended to be more-common species; however, the exotic grass *Bromus hordeaceus*, which was the most frequently seen species in the data set, had relatively small loadings because it was found in nearly every site (Table 3). The first three principal components together explained 30% of the variance in the original data.

The first three principal components were significantly affected by year, soil, grazing, fire, soil*fire, and soil*grazing*fire (Table 4). Nonserpentine grasslands were lower than serpentine grasslands on PC1 ("nativeness") and higher on PC2 ("grazing tolerance"). Nonserpentine grasslands responded consistently to fire (decrease on PC1) and grazing (increase on PC2), whereas serpentine grasslands responded more weakly to grazing (increase on PC2) and inconsistently to burning (burned sites were not consistently higher or lower on either axis than unburned sites).

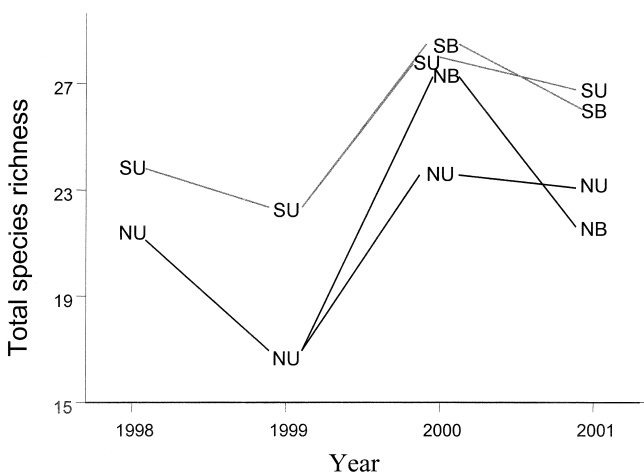


Figure 1. Interactive effects of year, soil, and fire on total species richness (native plus exotic) per site. Fire increases species richness on nonserpentine soils for 1 year after the fire. Abbreviations: SB, serpentine, burned; SU, serpentine, unburned; NB, nonserpentine, burned; NU, nonserpentine, unburned.

Responses of Individual Species

Three exotic and four native species were present at one-third or more of the sites and thus common enough to analyze. Of these, only one species, the exotic *Bromus hordeaceus*, showed no main or interactive effects of fire or grazing on its frequency (number of quadrats occupied per site). Frequencies of the other six species showed interactive effects of soil and grazing, soil and fire, or both (ANOVA, $p < 0.05$). Species that showed

Table 2. Plant species richness (average numbers of species/5 m²) by life form, soil, and grazing or burn treatment.

	<i>Nonserpentine</i>				<i>Serpentine</i>			
	<i>burned</i>	<i>unburned</i>	<i>grazed</i>	<i>ungrazed</i>	<i>burned</i>	<i>unburned</i>	<i>grazed</i>	<i>ungrazed</i>
Exotic species*								
AF	7.1	5.5	6.1	3.0	1.2	1.2	1.1	1.3
AG	4.9	4.1	4.2	4.1	3.5	3.2	3.4	3.1
subtotal	12.0	9.6	10.3	7.1	4.7	4.4	4.5	4.4
Native species								
AF	8.7	8.5	8.6	8.5	16.6	16.2	17.6	15.4
PF	3.0	2.6	1.6	3.0	3.5	2.6	3.2	2.5
PG	0.6	0.3	0.4	0.5	1.7	1.1	1.4	1.1
subtotal	12.3	11.4	10.6	12.0	21.8	19.9	22.2	19.0

*Abbreviations: AF, annual forb; PF, perennial forb; AG, annual grass; PG, perennial grass.

soil*grazing interactions included the exotic grass *Avena fatua* and the native forbs *Dichelostemma capitata* (Liliaceae) and *Hemizonia congesta* (Asteraceae). Species that showed a soil*fire interaction included the exotic grasses *Avena fatua* and *Taeniatherum caput-medusae*, the native grass *Vulpia microstachys*, and the native forb *Plantago erecta*. The direction of these interactive effects was highly variable among species (Table 5).

Discussion

Our results showed limited agreement with the prediction that disturbance would affect diversity more on

sites with higher productivity. Species richness showed a sharper increase in response to fire in nonserpentine than serpentine grasslands (Fig. 1). We could not tie this difference clearly to productivity because within each soil type there was not a significant relationship between biomass and the increase in species richness following fire. Instead, it seems most reasonable to conclude that disturbance can increase diversity in both types of grassland and that differences in the details of this effect are probably related more to variation in species composition than to variation in biomass.

More significant from a conservation and management standpoint were the differences we found in the effects of grazing and fire on native versus exotic species. Livestock grazing was associated with an increased richness of native species (especially native annual forbs) on serpentine soils but with decreased native richness on nonserpentine soils. Trends in the effects of grazing on exotic-species richness were in the opposite direction. Fire increased native-species richness more than exotic-species richness in serpentine grasslands, but it increased

Table 3. Principal component loading of plant species composition.^a

<i>Species</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
% variance explained	19.1	6.4	4.4
<i>Plantago erecta</i>	0.26	0.37	
<i>Avena fatua</i> ^b	-0.26	-0.152	
<i>Vulpia microstachys</i>	0.33		
<i>Taeniatherum caput-medusae</i> ^b	-0.21		-0.568
<i>Hemizonia congesta</i>	0.24	-0.333	-0.263
<i>Dichelostemma capitata</i>	0.29		
<i>Holocarpha virgata</i>		0.457	-0.29
<i>Lupinus biclor</i>	-0.19		
<i>Lotus wrangelianus</i>			-0.211
<i>Agoseris heterophylla</i>	0.22		
<i>Lasthenia californica</i>	0.26		
<i>Erodium cicutarium</i> ^b	-0.17	0.236	
<i>Lolium multiflorum</i> ^b			-0.344
<i>Geranium molle</i> ^b	-0.25		
<i>Centaurea solstitialis</i> ^b	-0.17		
<i>Trifolium bifidum</i>		-0.219	
<i>Nasella pulchra</i>			-0.154
<i>Navarrtia pubescens</i>		0.166	
<i>Ancistrocarphus filagineus</i>	0.17		
<i>Hypochaeris glabra</i> ^b		0.243	
<i>Bromus diandrus</i> ^b			0.22
<i>Castilleja attenuata</i>		0.187	

^aAlthough all 218 species contribute to every principal component (PC), for reasons of clarity only species loadings with a coefficient of > 0.15 are shown.

^bExotic species.

Table 4. Results of multivariate analysis of variance for the first three principal components describing the plant community across all sites.

<i>Model effect</i>	<i>Wilks</i>	<i>F</i>	<i>df 1</i>	<i>df 2</i>	<i>p</i>
Year	0.708	13.78	9	815.45	<0.001 ^a
Soil	0.238	357.02	3	335	<0.001 ^a
Fire	0.970	3.44	3	335	0.0171 ^b
Grazing	0.859	18.37	3	335	<0.001 ^a
Year:soil	0.968	1.21	9	815.45	0.283
Year:fire	0.992	0.89	3	335	0.448
Soil:fire	0.948	6.18	3	335	<0.001 ^a
Year:grazing	0.982	0.66	9	815.45	0.743
Soil:grazing	0.986	1.53	3	335	0.205
Fire:grazing	0.984	1.86	3	335	0.136
Year:soil:fire	0.992	0.96	3	335	0.414
Year:soil:grazing	0.978	0.83	9	815.45	0.588
Year:fire:grazing	0.996	0.50	3	335	0.681
Soil:fire:grazing	0.963	4.23	3	335	0.006 ^b

^ap < 0.01.

^bp < 0.05.

Table 5. Frequency (average number of 1-m² quadrats occupied out of five per site) by the seven species found at less than one-third of all sites.

	Nonserpentine				Serpentine			
	burned	unburned	grazed	ungrazed	burned	unburned	grazed	ungrazed
Exotic species*								
BH	4.7	4.6	4.7	4.5	3.0	3.7	3.6	3.6
AF	4.3	3.0	2.3	3.7	0.8	1.5	1.0	1.6
TC	3.5	2.0	2.6	2.4	0.7	1.3	1.3	1.1
Native species								
PE	0.8	1.5	1.6	1.0	3.0	3.2	3.0	3.2
VM	0.4	0.5	0.3	0.6	3.6	3.1	2.1	3.3
HC	0.3	0.6	0.8	0.2	2.9	3.0	2.5	3.2
DC	0.4	0.5	0.2	0.7	2.7	3.0	3.0	3.0

*Abbreviations: BH, *Bromus hordeaceus* (Poaceae); AF, *Avena fatua* (Poaceae); TC, *Taeniatherum caput-medusae* (Poaceae); P, *Plantago erecta* (Plantaginaceae); VM, *Vulpia microstachys* (Poaceae); HC, *Hemizonia congesta* (Asteraceae); DC, *Dichelostemma capitata* (Liliaceae).

the richness of exotic species (especially exotic annual forbs) more than that of native species in nonserpentine grasslands. Both types of disturbance thus tended to make the “rich get richer and the poor get poorer” in terms of numbers of native and exotic species on the two soils. Perhaps the simplest explanation is that disturbance exacerbates the existing soil-based reversal of competitive abilities. On nonserpentine soils, where exotics generally outcompete natives, exotic annual forbs may effectively preempt the pulse of available space and light created by disturbance and thus reduce the response in the richness of native species. On serpentine soils, where exotic forbs are few and lack a general competitive advantage, native species may be better able to exploit the opportunities created by disturbance.

Grazing tended to have a homogenizing effect on nonserpentine soils, increasing the similarity in species richness at the 1-m² and 5-m² levels. These results support the suggestion by Olff & Ritchie (1998) and Stohlgren et al. (1999) that grazing causes only localized changes in the patterns of species abundance. Fire, in contrast, may be more effective at causing new species to appear at a site, perhaps by stimulating emergence from long-dormant seedbanks (Parsons & Stohlgren 1989).

We can say little about how individual species vary in their response to disturbance because so few species were present at a large number of sites. Of the seven common species we analyzed, the frequencies of all but one (*Bromus hordeaceus*) showed main effects of fire and/or grazing and interactive effects of soil and grazing, soil and fire, or both. This suggests that individual species may respond differently to fire or grazing, depending on the soil. For example, the exotic grasses *Avena fatua* and *Taeniatherum caput-medusae* both increased in frequency in response to fire on nonserpentine soil but decreased after fire on serpentine soil. On both soils, however, grazing was associated with less *Avena fatua* and more *Taeniatherum caput-medusae*. The responses of the common native species *Diche-*

lostemma capitata, *Hemizonia congesta*, *Plantago erecta*, and *Vulpia microstachys* were likewise variable.

Much previous work on the management of California grasslands has emphasized the overriding importance of thatch, or dead matter produced mainly by exotic annual species, and the need to use either grazing or fire to remove thatch (Heady 1956, 1977; Menke 1982, 1989; Facelli & Pickett 1991; Dyer et al. 1996; diTomaso et al. 1999). Our results agree with those of Heady (1977), who pointed out that grazing and fire may both serve to reduce thatch but that exotic as well as native forbs are likely to benefit from this removal.

When grazing or fire are used as tools in conservation management, their timing and intensity are chosen to be as beneficial as possible. In California this often means that they are applied in late spring to early summer to reduce seed production by exotic annual grasses such as medusahead and late-season forbs such as yellow starthistle (Menke 1989; Thomsen et al. 1993; diTomaso et al. 1999; Meyer & Schiffman 1999). The fire we studied occurred in fall, too late to have strong effects of this kind; however, the results of several previous studies show that autumn fires do not differ greatly from summer fires in their effects on species diversity (Parsons & Stohlgren 1989; Meyer & Schiffman 1999). Year-round grazing such as we studied, although not ideal for the control of exotic species, is typical of rangelands throughout our region.

Our findings differ from those of a previous study that found no significant effects of grazing on the same sites (Harrison 1999a); increased statistical power is undoubtedly the reason. In recent work on roadside verges in the same general region, Safford and Harrison (2001) found more native species in adjacent grazed interiors than ungrazed road verges on serpentine soils and more exotic species in grazed interiors than ungrazed verges on nonserpentine soils. Our new results are consistent with these findings but extend and reinforce them in several important ways. First, in the present study we

found that fire and grazing have similar results. Second, we can be confident that the effects represent the broader landscape, away from heavily invaded roadsides. Third, although roadside verges were probably never grazed, our results showed similar patterns in grasslands on which grazing was recently halted.

Our study reinforces the warnings of previous authors that disturbance may tend to increase invasion in precisely those habitats or communities that are already most invaded (Grime 1979; Huston 1979; Burke & Grime 1996). It is unclear yet to what extent our results can be generalized to other cases of grasslands on variable soils and to what extent they are a function of the particular species composition and history of the sites we examined. However, our study does demonstrate the importance of analyzing the interactive effects of disturbance and environmental heterogeneity. On a different note, our study also illustrates how relatively weakly the "management" variables of grazing and fire may affect native diversity compared with the consistent and overwhelming effect of soils. Protecting grassland sites of outstanding native diversity may generally be more important than whether or not they are grazed or burned (Stohlgren et al. 1999).

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