FIRE AND GRAZING IMPACTS ON PLANT DIVERSITY AND ALIEN PLANT INVASIONS IN THE SOUTHERN SIERRA NEVADA

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Abstract. Patterns of native and alien plant diversity in response to disturbance were examined along an elevational gradient in blue oak savanna, chaparral, and coniferous forests. Total species richness, alien species richness, and alien cover declined with elevation, at scales from 1 to 1000 m^2. We found no support for the hypothesis that community diversity inhibits alien invasion. At the 1-m^2 point scale, where we would expect competitive interactions between the largely herbaceous flora to be most intense, alien species richness as well as alien cover increased with increasing native species richness in all communities. This suggests that aliens are limited not by the number of native competitors, but by resources that affect establishment of both natives and aliens.

Blue oak savannas were heavily dominated by alien species and consistently had more alien than native species at the 1-m^2 scale. All of these aliens are annuals, and it is widely thought that they have displaced native bunchgrasses. If true, this means that aliens have greatly increased species richness. Alternatively, there is a rich regional flora of native annual forbs that could have dominated these grasslands prior to displacement by alien grasses. On our sites, livestock grazing increased the number of alien species and alien cover only slightly over that of sites free of livestock grazing for more than a century, indicating some level of permanency to this invasion.

In chaparral, both diversity and aliens increased markedly several years after fire. Invasive species are rare in undisturbed shrublands, and alien propagules fail to survive the natural crown fires in these ecosystems. Thus, aliens necessarily must colonize after fire and, as a consequence, time since fire is an important determinant of invasive presence. Blue oak savannas are an important propagule source for alien species because they maintain permanent populations of all alien species encountered in postfire chaparral, and because the vegetation mosaic in this region places them in proximity to chaparral. The speed at which alien propagules reach a burned site and the speed at which the shrublands return to their former closed-canopy condition determine alien invasion. Frequent burning of this vegetation alters the balance in favor of alien invasion.

In the higher-elevation coniferous forests, species diversity was a function of fire severity and time since fire. High-intensity fires create gaps that decrease canopy coverage and increase light levels and nutrients for an ephemeral successional flora. Few species have persistent seed banks, so the time since fire is an important determinant of colonization success. There was a highly significant interaction between fire severity and time since fire for understory cover, species richness, and alien richness and cover. Understory was sparse in the first year after fire, particularly in low-severity burns, and increased substantially several years after fire, particularly on high-severity burns. Both fire severity and time since fire affected alien species richness and dominance. Coniferous forests had about one-third as many alien species as the foothill oak savannas, and fewer than half of the species were shared between these communities. Unburned coniferous forests were largely free of alien species, whereas some burned sites had a significant alien presence, which presents a challenge for fire restoration of these forests.

Key words: aliens; biological invasions; blue oak savanna; chaparral; colonization; coniferous forest; elevational patterns; fire severity; forest understory; plant diversity; Sierra Nevada (USA); species–area curves; species richness.

INTRODUCTION

Non-native plants have historically been viewed as nuisance species that readily invade anthropogenic dis-

turbances such as roadsides, croplands, and overgrazed pastures. In recent decades there has been greater focus on invasions of natural communities, where aliens are increasingly recognized as threats to ecosystem structure and function (e.g., Vitousek 1990, Mooney and Hobbs 2000). Land management practices have a potential role that is of profound interest to both environmental and economical sectors of society. It is be-

coming increasingly important for resource managers to be able to predict which species are likely invaders, which communities are most at risk, and how land management practices influence the invasion process.

Considerable discussion has focused on identifying determinants of invasives' success and predicting future threats. It is important to understand species characteristics that determine the success of invasives (e.g., Roy 1990, Rejmánek 1996). Rejmánek and Richardson (1996) have distinguished life history attributes of pine that correlate with invasive ability. Ultimately, this approach must be coupled with one considering community characteristics that lead to susceptibility to invasion (Rejmánek 1989, 1999). For example, why have South African fynbos shrublands experienced heavy pine invasion (Richardson and Higgins 1998), whereas the climatically and physiognomically similar Californian chaparral has remained resistant to pine invasion despite attempted introductions (Burns and Sauer 1992)?

Natural diversity patterns have long been considered to play a role in providing ecological communities some level of resistance to invasion (Elton 1958), but the relationship between diversity and invasiveness remains to be clearly elucidated (Levine and D'Antonio 1999, Dukes 2001). Presumably, species in a community utilize a common resource base and it is likely that the extent to which resources are "fully utilized" is a function of species packing. For reasons not thoroughly understood, some communities are capable of closer species packing, and thus higher species richness (i.e., species density) than other communities. Presumably, areas of high species richness should also be areas in which limiting resources are utilized more completely, and thus are less susceptible to invasion by new species (e.g., Tilman 1997). Data both support (Fox and Fox 1986, cf. Levine and D'Antonio 1999) and refute this prediction (Robinson et al. 1995, Stohlgren et al. 1999a). Potential explanations include differential impacts of different growth forms and different scales over which species richness is examined (Huston 1994). In considering plant invasions, focus is often placed on native plant diversity, but diversity of other components of the biota and diversity of interactions may also be involved (e.g., Richardson et al. 2000).

Also affecting a community's biotic resistance to invasion is the equilibrium between coexisting species, which is often a function of time since disturbance. Disturbances that create a disequilibrium in distribution of resources potentially alter species composition through shifts in resource availability (but cf. Mackey and Currie 2001). This may, in turn, create conditions favoring invasion of alien species (Hobbs 1991, Davis et al. 2000). Two important disturbance factors in the western United States are grazing and fire, both linked to plant invasions (Mack 1989, Parsons and Stohlgren 1989, D'Antonio and Vitousek 1992, Haidinger and

Keeley 1993, Knick and Rotenberry 1997, Stapanian et al. 1998, D'Antonio et al. 1999, D'Antonio 2000). Although both grazing and fire cause a disequilibrium, they are not expected to show great overlap in the shifts in resource availability (Turner and Bratton 1987) or an identical impact on species invasion.

These two disturbance factors are distributed differently in terms of duration and severity. Grazing impacts may vary seasonally and as a function of livestock type, stocking density, timing, and duration. The impact of grazing on native species richness and community invasibility is variable and likely to be complicated by grazing severity and timing, individual species responses, and abiotic factors such as soil characteristics and light availability (e.g., Huenneke et al. 1990, Zhang 1998, Stohlgren et al. 1999b, Safford and Harrison 2001).

Fire, on the other hand, is a pulse that exerts its most obvious impact during a brief period of time followed by a period of "recovery." The severity of this impact is such that in woody vegetation, species lacking a mechanism for persistence or postfire recruitment may be extirpated from the site. In western North American shrublands and forests, many species have life history characters that allow either persistence of adults (resprouting or surviving due to thick bark and self-pruning) or recruitment of new genets following fire. Although some alien species (e.g., *Cytisus* spp., *Brassica* spp., etc.) also have dormant fire-stimulated seed banks (Keeley and Fotheringham 2000), this is not common in the alien flora of the western United States. Invasives are more commonly generalist colonizers that invade disturbances caused by a variety of factors. Thus, an important parameter determining susceptibility to invasion is the length of time for postfire colonization, namely the time between fire and canopy closure. As this duration increases, we may expect increased opportunities for colonization and increased risk of invasion. Coupled with this are likely to be important factors related to the structure of fire effects, e.g., the spatial pattern of low-severity surface fires and high-severity surface and crown fires that generate larger gaps in the forest canopy.

In addition to the invasive potential of alien species and the invasibility of native communities, a third critical factor is "propagule pressure" (Lonsdale 1999, D'Antonio et al. 2001). Differential patterns of alien invasion may be explained more by patterns of propagule availability than by innate characteristics of species or communities. Although invasion potential and invasibility are readily investigated by comparing characteristics of species and landscapes, propagule potential often is more a function of site history and thus is more difficult to control or evaluate.

In this study, our objective was to evaluate the role of grazing and fire disturbance on community patterns of native species richness and alien vascular plants in low- and mid-elevation communities of the southern

Sierra Nevada Range. We evaluated disturbance patterns due to grazing in the foothill blue oak savanna community and fire in higher elevation closed-canopy communities. We restricted our attention to sites below 2500 m because in this region invasive plants have limited occurrence at higher elevations (Neuman 1990, Sylvia Haultain, *personal communication*). In order to separate effects that are evident at different grain (Palmer and White 1994, Stohlgren et al. 1997), we examined different scales, from point diversity (1 m^2) to community diversity (1000 m^2).

This region has had a long, complicated history of grazing (Menke et al. 1996), but we took advantage of the broad patterns generated by different land management on Department of Interior lands in the southern Sierra Nevada. The bulk of the grasslands and savannas in Sequoia National Park have been untouched by livestock grazing for well over a century, whereas those on adjacent Bureau of Land Management (BLM) lands have had high density of cattle grazing for a century or more. A local pasture within the Park utilized for packhorse grazing was included for comparison.

Fire effects were examined on woody communities, particularly chaparral, yellow pine, and mixed coniferous forests. In the chaparral shrublands, fires are normally high-severity crown fires, and the primary variable driving postfire patterns is expected to be time since fire. However, the forests considered here have a fire regime that comprises a mixture of low-severity surface fire and high-severity scorching or crown fire. Thus, both fire severity and time since fire are expected to be significant determinants of biodiversity and alien invasion.

STUDY SITES AND METHODS

This study focused on the western foothills and mid-elevation range of the southern Sierra Nevada. Except for the cattle-grazed oak savanna, sites were in either Sequoia or Kings Canyon national parks (Fig. 1). Foothill blue oak savanna sites were in the Ash Mountain area of Sequoia National Park or adjacent Bureau of Land Management lands (Fig. 2). Dominant trees were *Quercus douglasii* and *Aesculus californica*, but the sites were mostly open grassland. Sites were between 440 and 680 m in elevation and were sampled during late spring and early summer of 1999. Sites differed with respect to their livestock grazing history: five had been grazed seasonally by horses, five grazed seasonally by cattle, and five had no livestock grazing for the past century. Fire history for the oak savanna sites was uncertain and there was no evidence of recent fires.

In the slightly higher chaparral, 10 sites in south-facing drainages between 860 and 1280 m a.s.l. were selected. Five sites from near Lookout Point in the East Fork of the Kaweah Watershed had burned in 1998, and five sites south of Shepherd's Saddle in the Middle Fork of the Kaweah had burned in 1996 (1 and 3 years,

respectively, before sampling). Based on shrub skeletons and resprouts, it appeared that prior to the fires, both areas had similar shrub dominants: (*Adenostoma fasciculatum*, *Arctostaphylos viscida*, and *Ceanothus cuneatus*. Sites differed substantially in their prior fire history, as determined by ring counts on stem sections (see Keeley 1993). Based upon ring counts from *Arctostaphylos viscida* skeletons, it appeared that the East Fork sites had remained unburned for 125 years prior to the 1998 controlled burn, whereas the Shepherd's Saddle sites were 10–25 years of age prior to burning in a wildfire in 1996 (Sequoia National Park Resources Division GIS database).

Between 1400 and 2400 m, 103 coniferous forest sites were selected in the Cedar Grove, Lewis Creek, and Sugarloaf areas of Kings Canyon National Park and Mineral King and Giant Forest areas of Sequoia National Park (Fig. 1). These included yellow pine forest (*Pinus ponderosa*) and mixed coniferous forests (*Abies concolor*, *Calocedrus decurrens*, *Pinus jeffreyi*, *P. lambertiana*, *P. ponderosa*, and *Sequoiadendron giganteum*, the last species occurring only in a few Giant Forest sites). Most sites treated as unburned controls had no recorded fire history for at least 75 years, and as is typical of many forests in the Sierra Nevada, had heavy surface fuel accumulations (Fig. 3). Two sites treated as controls had been lightly underburned in 1980. All burned sites had been burned with prescribed fires or natural lightning-ignited fires between 1994 and 1998, with the majority having burned in 1996 or 1998. Sampling was done in 1999 or 2000; for analysis purposes, burned sites were classified as either first year postfire (but included a few second-year burns) or third year postfire (including some four- and five-year-old burns). A few sites had burned more than once between 1994 and 1998.

Sites were selected by first constructing a GIS layer of plant association types and a layer of each of the required treatment conditions. Areas within 50 m of a road or >200 m from a road (or otherwise not easily accessible) were removed from consideration and then study sites were selected by picking random numbers for UTM (Universal Transverse Mercator) coordinates within the potential area. If ground truthing revealed unanticipated disturbances, those sites were eliminated and new coordinates were selected. No GIS layer existed for fire severity in the coniferous forests. Thus, sites of high-severity fires were selected based on a visual estimation of heavy tree mortality, and a low-severity burned site (burned but with little canopy tree mortality) was selected more or less adjacent to the high-severity burned site. Control sites were selected as close to the burned areas as possible on a range of slope aspects and inclinations similar to those represented by the burned sites.

Sampling was a 0.1-ha nested plot design (Keeley et al. 1995, Schwilk et al. 1997). A 20 × 50 m site was laid out with the long axis parallel to the slope
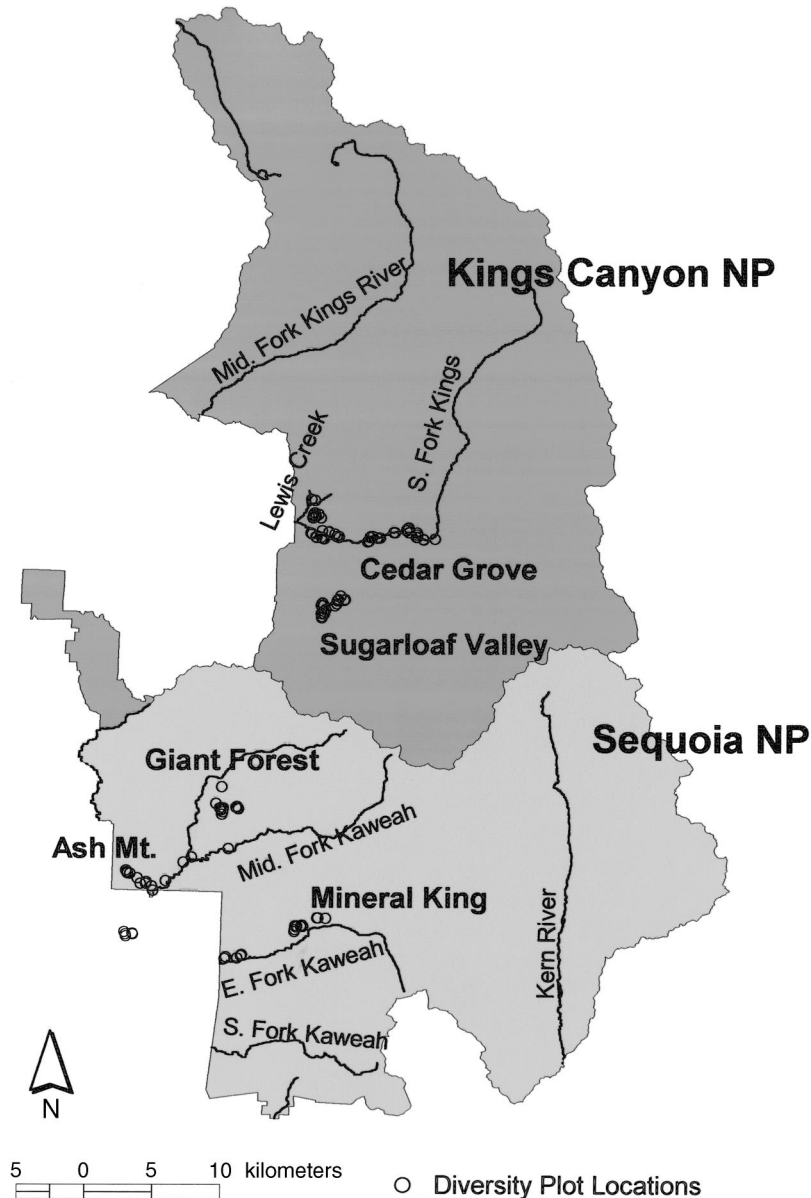
FIG. 1. Study area in Sequoia and Kings Canyon national parks, California, USA. Blue oak savanna sites were located in the Ash Mountain area, chaparral sites were located in this area and along the road to Mineral King, and coniferous sites were located (from north to south) near Lewis Creek, Cedar Grove, Sugarloaf Valley, Giant Forest, and Mineral King.

contour. These 0.1-ha sites were subdivided into 10 non-overlapping 100-m^2 (10 × 10 m) plots. Within each plot were two 1-m^2 (1 × 1 m) subplots in opposite corners of the plot (subplots along the inner edge were offset 1 m from center). Because of the much higher herbaceous density in blue oak savanna sites, only the outer edge subplot was sampled in each of the 10 plots. Within each subplot, density and cover were estimated for each species; in the 100-m^2 plot, additional species not in the subplots were recorded. Density was recorded if there were <5 individuals, and otherwise was categorized as 10, 25, 50, 75, 100, 150, 200, or the nearest

hundred up to 1000, and then estimated to the nearest 1000 individuals. Cover was taken as the percentage of ground surface covered by the shadow of the foliage, estimated as <1, 5, 10, 25, 50, 75, 90, >95%.

Site factors recorded were: canopy coverage (as determined by a densiometer reading from the center of each 10 × 10 m plot), slope aspect, and slope inclination. The northwest corner of each site was located with GPS and elevation was later determined with GIS. Annual solar insolation was calculated from slope aspect, inclination, and latitude (Frank and Lee 1966). From three alternate plots at each site, surface litter

Fig. 2. Foothill blue oak savanna (and mosaic with chaparral at higher elevations) at Ash Mountain, Sequoia National Park (photo by J. Keeley).
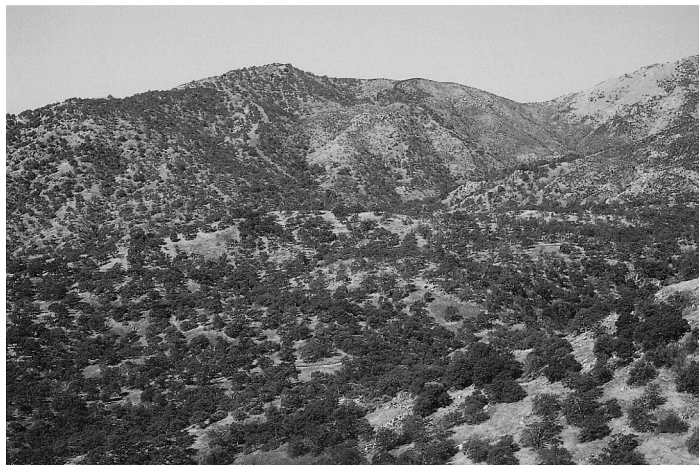
was collected within a 20 cm diameter hoop, dried, and weighed. Three soil samples from the top 6 cm were collected from alternate plots and combined and dried in paper bags. Texture analysis was done according to Cox (1995). From a subsample, pH was determined in an equal mixture of soil and dH_2O incubated overnight at room temperature. Soil nutrients (NO_3, NH_4, P, and K) were determined from a subsample at the Soils Laboratory, University of California–Davis. Plant nomenclature follows Hickman (1993).

Data were analyzed and graphically displayed with SYSTAT 10.0 (SYSTAT 2000). Relationships between variables were tested for significance by correlation analysis and significant correlations were fitted with least squares regression lines. Plots of residuals were used to evaluate patterns of variation for some variables. Where bivariate data did not seem to fit an arithmetic relationship, semilog and log–log transformations were compared and the one giving the highest adjusted r^2 value was presented. Between-treatment comparisons used one-way and multi-way ANOVA for additive and multiplicative models. Post hoc comparisons between treatments were made with the Bonferroni test. Ratios were arcsine-transformed prior to analysis. To assess community composition similarities, we calculated the Jaccard Index, which is calculated as the number of species shared between two sites divided by the total species list for both sites: $J = A/(A + B + C)$, where A is the number of species shared by two sites, B is the number of species in one site, and C is the number of species in the other site.

RESULTS

Elevational patterns

In total, 373 plant species were recorded from the 128 0.1-ha plots. With increasing elevation, species richness declined significantly at all scales ($P < 0.001$, $n = 128$ plots), but the variation explained by elevation declined from scales of 1 m² to 100 m² to 1000 m²

Fig. 3. Mixed coniferous forest in the Mineral King area of Sequoia National Park unburned for more than 125 years, typically with fuel loads of 50–100 Mg/ha; 1 Mg = 1 metric ton (E. Knapp and J. E. Keeley, *unpublished data*; photo by J. Keeley).
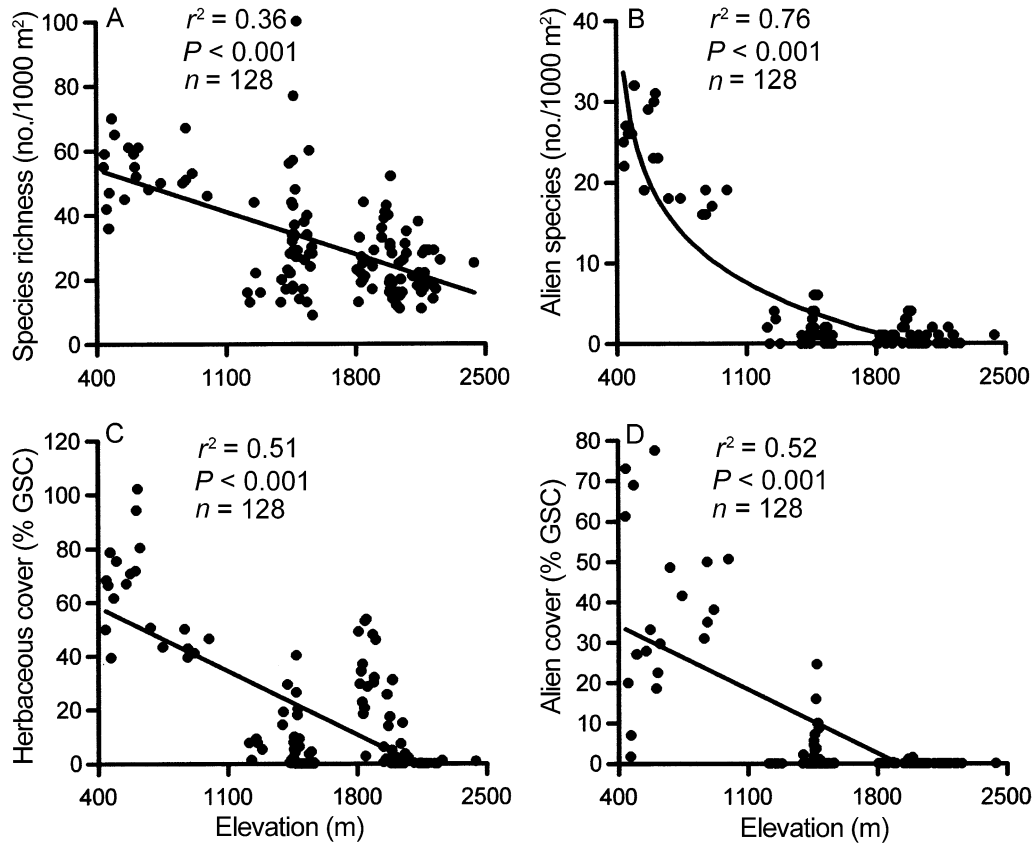
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FIG. 4. Elevational distribution of (A) species richness, (B) alien species richness, (C) herbaceous cover, and (D) alien cover in Sequoia and Kings Canyon national parks for all sites in blue oak savanna, chaparral, and coniferous forests (% GSC is percentage of the ground surface covered by plant canopies). Alien species richness (panel B) was fitted with a power curve because the log–log equation yielded a higher adjusted r^2.

(adjusted $r^2 = 0.68$, and 0.36, respectively; e.g., Fig. 4A). Herbaceous cover decreased with elevation (Fig. 4C), as did the percentage of herb cover contributed by annuals and by grasses ($P < 0.001$, adjusted $r^2 = 0.36$ and 0.69, respectively, $n = 128$ plots).

Alien plants declined rapidly with increasing elevation, both in number of species (Fig. 4B) and cover (Fig. 4D). The high concentration of aliens in the foothill savannas was a driving factor in the elevational decline in species richness (Fig. 4A), as evidenced by the fact that native species richness declined only weakly with elevation ($P < 0.05$, $r^2 = 0.04$, $n = 103$ plots). There were 61 alien species, and all but four (93%) were annuals. Across the elevational gradient there were differences in patterns of alien composition. Blue oak savannas had 56 alien species and chaparral had 27 alien species, all of which were represented in the blue oak savannas. Coniferous forest sites had only 17 alien species, and fewer than half of those were shared with lower elevation oak communities. The four perennial aliens encountered in this study were restricted to coniferous forests. The highest elevation sites had very few aliens; Giant Forest had two (*Lactuca serriola* and *Sonchus oleraceas*), and Sugarloaf

had three (*Bromus tectorum*, *Polygonum arenastrum*, and *Taraxacum officinale*).

Across this gradient from 440 to 2440 m, soil phosphorus, pH, surface litter, and sand content all decreased with elevation (Table 1). Inspection of the residual plots revealed that the bulk of variation in pH, P, and litter was in the higher elevation coniferous forests, associated with different burning treatments, whereas variation in soil texture was more or less evenly distributed across the elevational gradient. Tree canopy cover increased significantly with elevation, but was extremely variable ($P < 0.01$, adjusted $r^2 = 0.06$, $n = 128$ plots). Based on a plot of the residuals (not shown), variability was largely due to different fire histories at the higher elevation sites.

Blue oak savanna

Tree canopy coverage averaged 20% across all 15 sites and 96% of the understory coverage was from annual species. Species richness averaged 11.9 species at the 1 m² scale, 24.6 species at 100 m², and 53.4 species at 1000 m², and at the lower two scales alien species comprised >50% of the flora. Grazing history affected species richness (Fig. 5A), but this was scale

TABLE 1. Correlations of elevation with environmental parameters across the elevational gradient in the southern Sierra Nevada ($n = 128$ 0.1-ha plots).

Parameter	Correlation with elevation		
	P	$+/-$	Adjusted r^2
Slope inclination	NS		
Slope aspect	NS		
Annual insolation	NS		
Surface litter	<0.01	−	0.07
Soil			
Rock	NS		
Sand	<0.001	−	0.18
Clay	<0.001	+	0.17
pH	<0.05	−	0.04
K	NS		
P	<0.001	−	0.20
NH_4	NS		
NO_3	NS		

Note: Nonsignificant correlations ($P > 0.05$) are designated NS.

dependent, being significant at the 1-m² level, but not significant at larger scales. Alien species dominated all sites, although both alien species richness (Fig. 6A) and cover (Fig. 6B) were 20–30% higher on grazed sites.

In the vast majority of 1-m² subplots, there were more alien than native species, but at the 1000-m² level, both grazed and ungrazed sites commonly had more native species. The relationship between native and alien species richness varied considerably with scale (Fig. 7A and B). At the smaller point scale (1 m²), alien richness increased markedly with increasing native richness, but at the community scale (1000 m²), there was no relationship. Grazing, however, was an important factor. Whereas grazed sites showed no significant relationship, ungrazed sites had a significant positive relationship between native and alien species richness ($P < 0.05$, adjusted $r^2 = 0.73$, $n = 5$ plots).

Dominant natives on most sites were annual forbs, predominantly *Amsinckia menziesii*, *Claytonia perfol-*
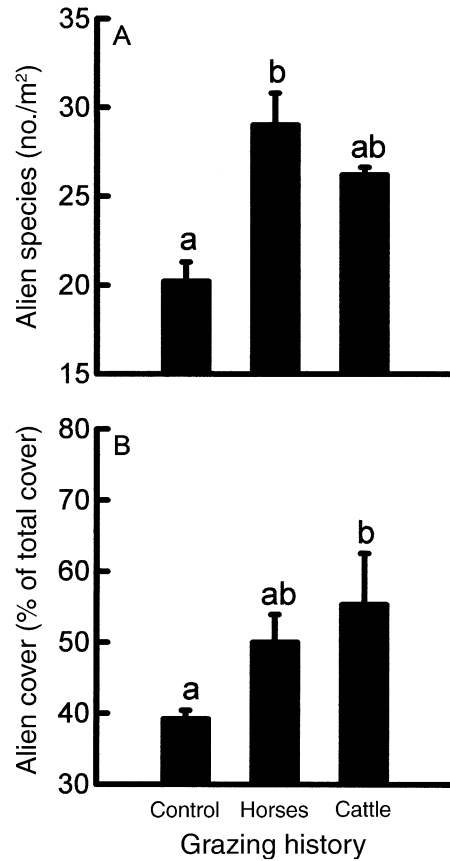
FIG. 6. Blue oak savanna grazing impacts on (A) alien species richness and (B) alien species cover in blue oak savannas (with standard errors). Bars with the same letter are not significantly different at $P > 0.05$.

iata, *Holocarpha heermannii*, *Plagiobothrys nothofulvus*, and *Trifolium microcephalum*. In contrast, the dominant aliens were mostly annual grasses: two species of *Avena*, seven species of *Bromus* (mostly *B. diandrus* and *B. hordeaceous*), two species of *Hordeum*,
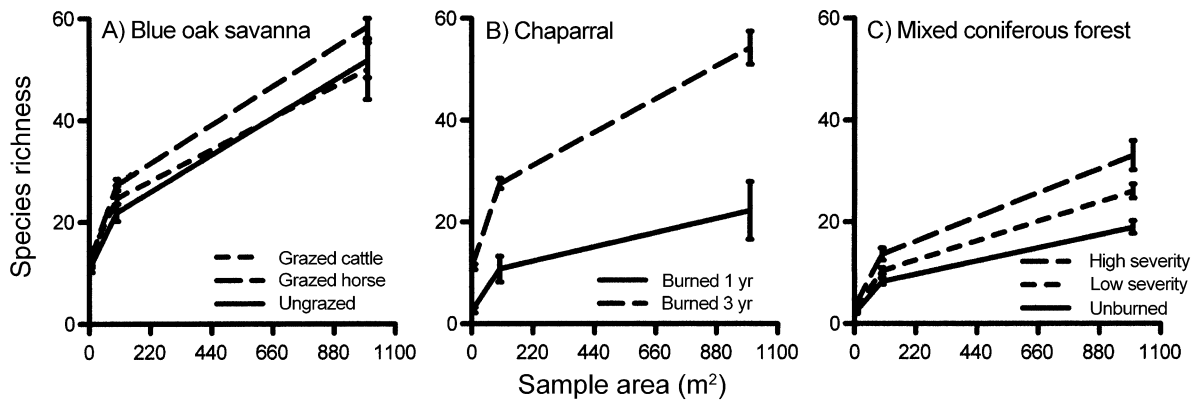
FIG. 5. Species richness at 1-m², 100-m², and 1000-m² scales for different disturbance regimes in (A) blue oak savanna, (B) chaparral, and (C) coniferous forest in the southern Sierra Nevada under high and low fire severity, based on nested plots (error bars indicate ±1 SE).
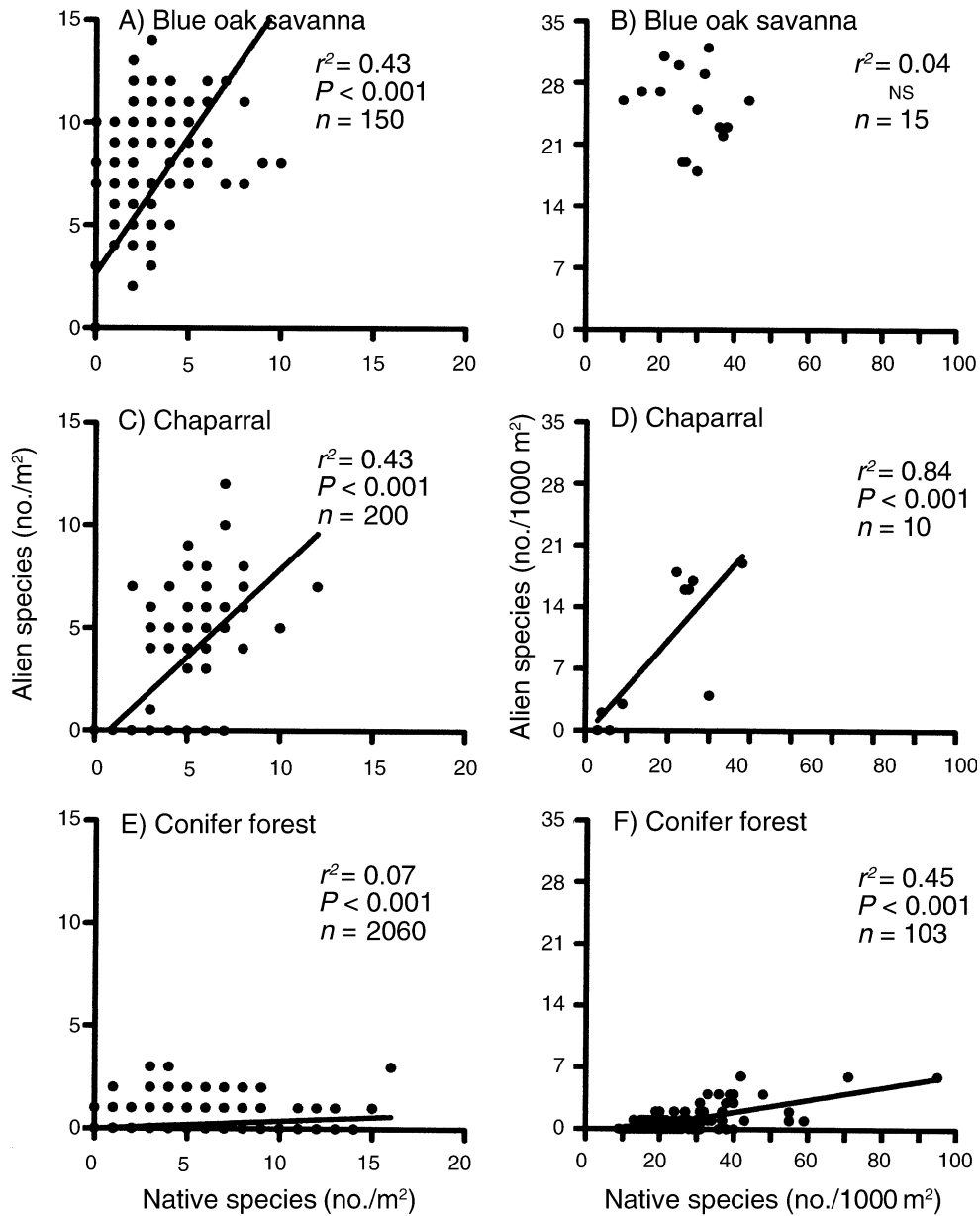
FIG. 7. Relationship between alien species richness and native species richness in (A,B) blue oak savanna, (C,D) chaparral, and (E,F) coniferous forests at two spatial scales in the southern Sierra Nevada.

Lolium multiflorum, and *Vulpia myuros*. Some alien forbs were important as well: *Centaurea melitensis*, *Geranium molle*, *Cerastium glomeratum*, four species of *Erodium*, *Silene gallica*, and two species of *Torilis*. Of the total alien flora, 10 species had significantly different cover values in response to grazing.

Total understory cover did not differ significantly between grazing treatments, but the proportions of growth forms differed. Grass cover was significantly greater on horse-grazed plots ($P < 0.05$, $n = 5$ plots) and the density of herbaceous perennials was higher on the cattle-grazed plots ($P < 0.05$, $n = 5$ plots).

Chaparral

Contrasting first-year postfire with third-year postfire illustrates significant differences in many characteristics (Table 2), e.g., NH_4 and NO_3, levels in first-year burn over one order of magnitude greater than in the older burns. Shrub cover increased fivefold between the first- and third-year burns. Species richness was >2.5 times greater at all scales in the third-year burns, and much of this increase was due to alien species, primarily annual grasses (*Aira caryophyllea*, *Bromus madritensis*, *B. hordeaceous*, and *Vulpia myuros*),

TABLE 2. Chaparral site parameter comparisons of first-year and third-year burns ($n = 5$).

Parameter	First-year burn		Third-year burn		
	$\bar{X}$	1 SD	$\bar{X}$	1 SD	P
Surface litter (g/m^2)	0.3	0.2	0.4	0.2	NS
Soil					
Rock (%)	0.06	0.06	2.04	4.45	NS
Sand (%)	62.7	3.76	56.3	1.46	<0.01
Clay (%)	13.1	5.35	19.6	5.84	<0.01
pH	6.2	0.1	5.8	0.2	<0.01
K (ppm)	205.8	38.1	155.8	48.6	NS
P (ppm)	33.1	11.2	18.6	5.8	<0.05
NH$_4$ (ppm)	51.6	13.4	5.9	0.8	<0.001
NO$_3$ (ppm)	51.4	10.7	1.3	0.5	<0.001
Total cover (% GSC†)	14.2	4.7	84.7	14.0	<0.001
Grass cover (% GSC)	0.0	0.0	38.1	1.4	<0.001
Shrub cover (% GSC)	7.8	1.4	39.4	14.4	<0.001
Species richness					
No./m^2	2.7	1.1	11.2	1.2	<0.001
No./100 m^2	10.7	5.7	27.6	2.3	<0.001
No./1000 m^2	22.2	12.6	54.2	7.3	<0.001
Alien species (no./1000 m^2)	1.8	1.8	17.2	1.3	<0.001
Alien cover (% GSC*)	0.0	0.0	39.1	7.1	<0.001

Note: NS indicates nonsignificant ($P > 0.05$).
† Percentage of the ground surface covered.

which formed a substantive portion of the cover (Table 2). In the first-year burns, grasses were absent and aliens comprised only 8% of the flora, whereas in the third-year burns, aliens comprised 32%. The first-year burns were resampled in the second year after fire and showed that aliens increased to 23%, consistent with the patterns observed in the ''space-for-time'' comparison used here.

Mixed coniferous forests

The five forested areas in the parks differed markedly in forest structure (Table 3). Also, the broad elevational patterns evident across the entire gradient were mirrored within the coniferous sites that ranged between 1400 and 2400 m. In general, there were more species and a greater alien presence in the lower elevation yellow pine forests than in the higher elevation mixed coniferous forests. Specifically, within this conifer belt,

mean species richness at all scales decreased significantly with elevation ($P < 0.001$, adjusted $r^2 = 0.11$, 0.14, and 0.10, for 1 m^2, 100 m^2, and 1000 m^2, respectively; $n = 103$ plots). Also, alien species richness and cover (both absolute and cover as a percentage of the understory) decreased significantly with increasing elevation at all scales ($P < 0.001$, adjusted $r^2 = 0.13$, 0.11, and 0.15, respectively; $n = 103$ plots). These elevational trends all had relatively low r^2 values, reflecting the fact that, within the coniferous zone, elevation accounted for only a small portion of the variation in species richness and alien presence.

Alien species richness increased with native species richness at both 1-m^2 and 1000-m^2 scales (Fig. 7E and F). Also this relationship was statistically significant when control, low-severity, and high-severity treatments were analyzed separately as well as combined. Aliens comprised a greater percentage of the flora in

TABLE 3. Site comparisons averaged across burned and unburned plots for species richness and cover of native and aliens, with P values from one-way ANOVA.

| Park parameter	Kings Canyon National Park			Sequoia National Park		
	Cedar Grove	Lewis Creek	Sugarloaf	Mineral King	Giant Forest	P
Mean elevation (m)	1480	1884	2170	1975	2050	<0.001
No. sites	38	16	18	13	18	
Live trees >20 cm dbh (no./ha)	201	131	154	242	138	<0.001
Live trees ≤20 cm dbh (no./ha)	275	156	61	97	31	<0.001
Understory cover (% GSC)†	14	37	11	27	7	<0.001
Species richness (no./m^2)†	3.4	3.3	2.5	3.6	1.8	<0.001
Species richness (no./100 m^2)	32.9	24.6	21.5	32.8	20.6	<0.001
Alien species richness (no./1000 m^2)	1.6	0.7	0.3	1.2	0.22	<0.001
Alien cover (% of understory cover)	10	0.1	0.0	0.6	0.0	<0.001

† Percentage of the ground surface covered.
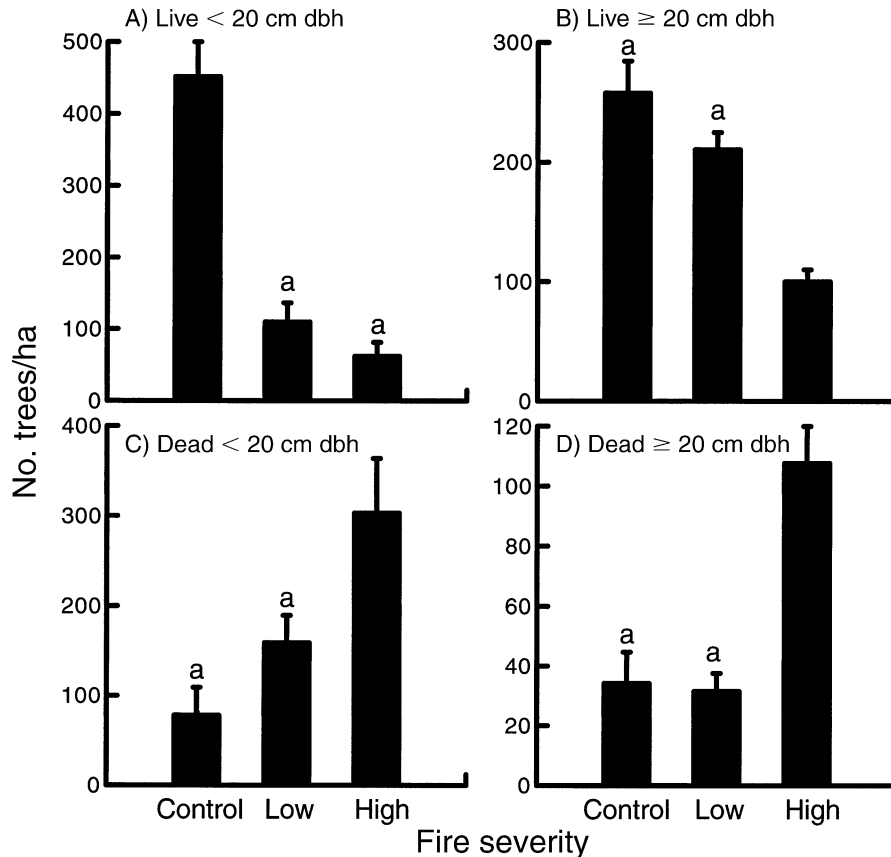
FIG. 8. Density of (A,B) live and (C,D) dead trees larger or smaller than 20 cm dbh in coniferous forest sites designated as unburned controls, low-severity burns, and high-severity burns (with standard errors); bars with the same letter are not significantly different ($P > 0.05$).

burned sites (high and low severity combined) than in unburned controls (3.4% vs. 0.3%, $P < 0.001$ with one-tailed t test).

Between the southern sites at Mineral King and northern sites at Cedar Grove (including nearby Lewis Creek), understory floras differed markedly. One exception was the native annual *Gayophytum eriospermum*, which was one of the few species that was widespread in both parks but largely restricted to postfire sites. Jaccard's Index showed that unburned controls differed much more in floristic composition between sites and that third-year burned sites were consistently more similar in composition. To illustrate this, all sites within the Cedar Grove area of Kings Canyon National Park were used (because of the large sample size; Table 3) and Jaccard's Index was calculated for all possible combinations of sites within a treatment. Unburned controls had the lowest index (0.26), first-year postfire low- and high-severity burns were intermediate (0.36 and 0.37, respectively), and third-year postfire low- and high-severity sites showed the greatest similarity in composition (0.41 and 0.40, respectively). There was no significant difference between low- and high-severity classes, but time-since-fire had a highly signif-

icant ($P < 0.001$ with two-tailed t test) effect on Jaccard's Index.

With respect to aliens, the dominant species in the Cedar Grove, Lewis Creek, and Mineral King areas was the annual grass *Bromus tectorum*, but it was not recorded from Giant Forest and was only occasionally present at Sugarloaf.

In the field, fire severity classes were based on a visual estimation of fire-caused tree mortality, quantified here in terms of live and dead trees (Fig. 8). High-severity burned sites had significantly more dead trees ≥20 cm dbh than did either the low-severity burned sites or controls. Low-severity burned sites had significantly fewer live trees <20 cm dbh than did controls.

Another indicator of fire severity was canopy cover (Fig. 9A), which was significantly less on high-severity burn plots than on either controls or low-severity burn plots. Understory cover was comparable between controls and low-severity burns, but increased substantially in the high-severity burn sites (Fig. 9B). Annuals comprised the bulk of the cover in high-severity burns and there was a significant inverse relationship between annual species cover and tree canopy (Fig. 10).
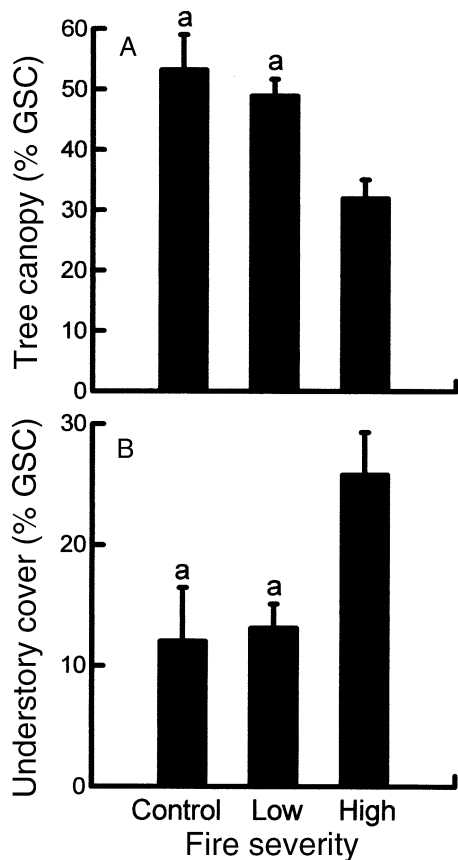
FIG. 9. Effect of fire severity on (A) tree canopy and (B) understory cover for all coniferous forest sites (% GSC is the percentage of the ground surface covered by plant canopies; error barrs indicate +1 SE. Bars with the same letter are not significantly different ($P > 0.05$).
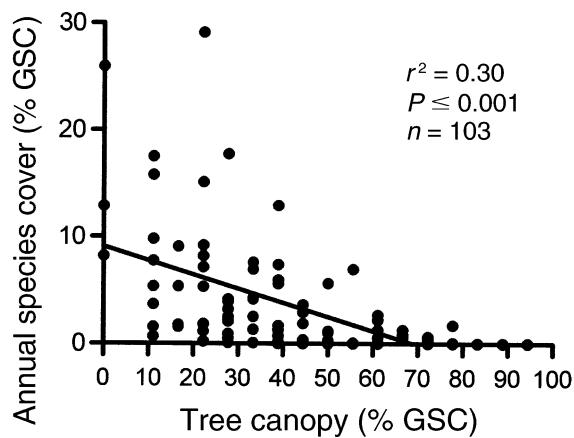

FIG. 10. Relationship between annual species coverage and tree canopy cover in coniferous forests (% GSC is as defined in Fig. 9).
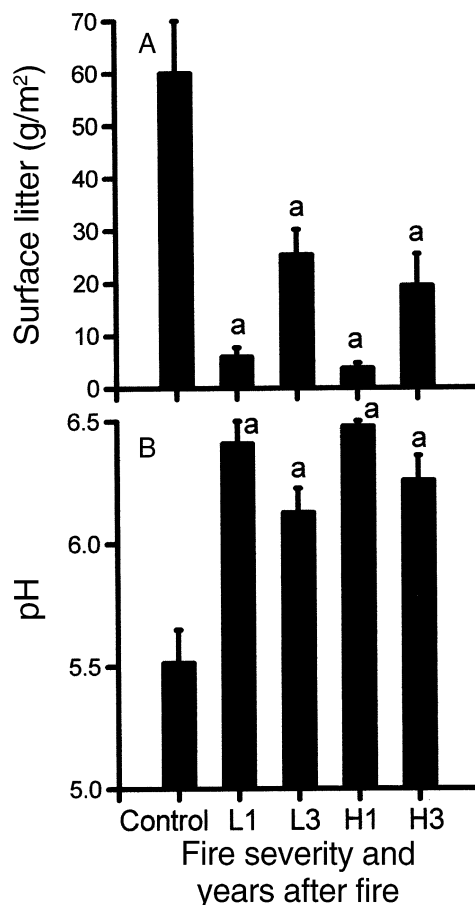
FIG. 11. Impact of fire severity and time since fire in coniferous forests on site parameters: (A) surface litter and (B) soil pH. Fire severity and years after fire are designated as L1, low first year; L3, low third year; H1, high first year; H3, high third year (error bars indicate +1 SE). Bars with the same letter are not significantly different at $P > 0.05$.

Species richness was positively correlated with understory cover ($P < 0.001$; adjusted $r^2 = 0.28$, 0.12, and 0.05 at 1 m², 100 m², and 1000 m², respectively; $n = 103$ plots), and negatively correlated with canopy cover ($P < 0.001$; adjusted $r^2 = 0.15$; $n = 103$ plots). At all spatial scales from point to community level, species richness was highest in high-severity burn sites (Fig. 5C).

In addition to fire severity, time since fire was an important determinant of both biotic and abiotic parameters (Fig. 11). For example, inorganic nitrogen and potassium peaked in the first postfire year but dropped to control levels by the third year (Fig. 12). In contrast, potassium peaked in the third postfire year, but there was extraordinary site to site variation across the range of forest types.

Complicating the picture of postfire response is the highly significant interaction between fire severity and time since fire for understory cover, species richness, and alien richness and cover (Table 4). Time was consistently a significant factor for these parameters, whereas fire severity was a significant factor only for species richness parameters. In general, understory was
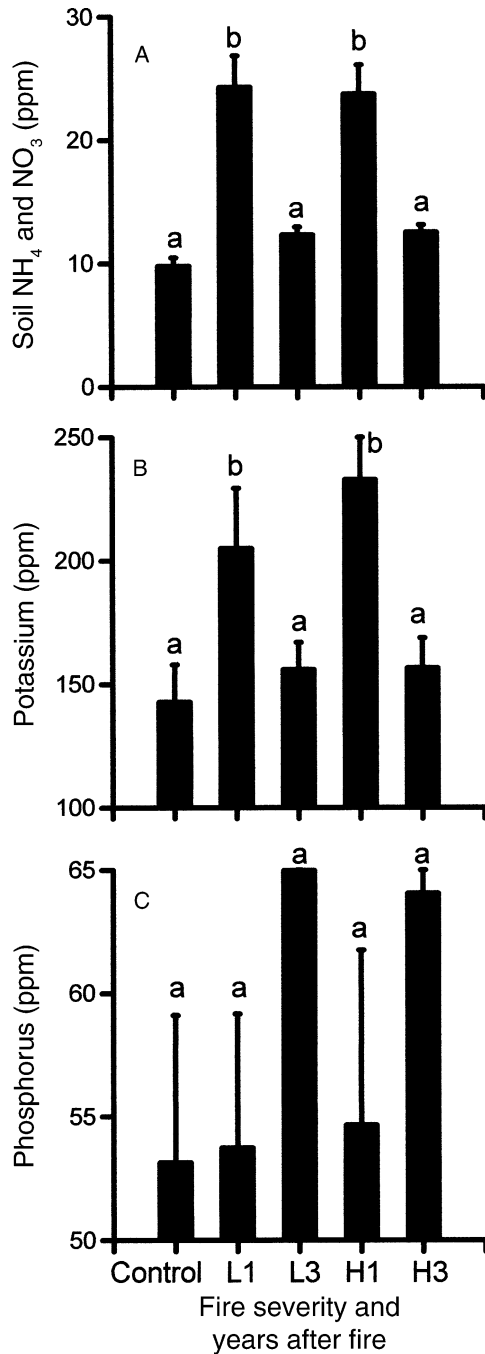
FIG. 12. Impact of fire severity and time since fire in coniferous forests on soil parameters: (A) nitrogen, (B) potassium, and (C) phosphorus (see Fig. 11 legend for details).

sparse in the first year after fire, particularly in low-severity burns (Fig. 13), and increased substantially several years after fire, particularly on high-severity burns (Figs. 14 and 15). Both fire severity and time since fire (Fig. 16A–C) affected alien species richness and dominance. For sites that had burned three or more years prior to sampling, there was no significant dif-

ference between those burned once vs. those burned twice in the past decade for any parameter.

DISCUSSION

Elevational patterns

In the southern Sierra Nevada of California, plant diversity and aliens covary along gradients of elevation and disturbance, both being more diverse and dominant at lower elevations (Fig. 4). This elevational pattern has been noted before (e.g., Mooney et al. 1986, Schwartz et al. 1996, Randall et al. 1998), but limited attention has been given to the factors influencing the relationship. Along this elevation gradient, covariates with increasing elevation include greater tree canopy cover (and thus decreased light levels at the soil surface), reduced growing season, decreased soil aridity, different disturbance regimes, decrease in the potential propagule source, and decrease in the frequency and severity of past and present human disturbance.

In the foothill blue oak savannas, the open-canopy environment and large annual floras in the California Floristic Province are important factors accounting for the greater diversity relative to chaparral and forests (Fig. 5). Closed-canopy woody communities approach the high species richness of savanna environments only when the canopy is temporarily removed by fire. In addition, the extreme seasonality of the Sierran foot-hills is considered to be an important factor in the incidence of the annual growth form (Richerson and Lum 1980). Summer drought rather than "environmental extremes" per se is likely a driving factor, because montane forests are highly seasonal in terms of temperature fluctuations.

Elevational trends in species richness are influenced by scale: relative to coniferous forests, blue oak savannas had four times more species at the 1 m² scale, but only two times more at the 0.1-ha scale. This may reflect structural differences in these habitats, possibly tied to the negative relationship between species richness and canopy coverage. In oak savannas, most 1-m² subplot samples were on open sites and thus richness was consistently high at this scale. However, in both burned and unburned conifer forests, mean species richness at the 1-m² scale was affected by the fact that only some were in gaps, and richness at the 0.1-ha scale was the sum of species found in all microhabitats within the site.

The elevational decline in the importance of alien species probably is tied, to some extent, to past and present human activities. Most invasive species in California have their origins in the Mediterranean Basin, including southern Europe, North Africa, and Eurasia (Shmida 1981, Baker 1989, Fox 1990, Reichard 1997). There they potentially have been in association with anthropogenically altered landscapes through a significant portion of the Holocene (Baker 1974, Pignattii 1983, Naveh and Kutiel 1986, Le Floc'h et al. 1990,

TABLE 4. Two-way ANOVA for the effects of fire severity and time since fire on understory cover, species richness, and aliens in coniferous forest sites ($n = 2060$ 1-m^2 subplots).

Source	SS	df	F	P
Understory cover				
Severity	274.720	1	1.222	0.290
Time	9341.830	2	7.438	0.001
Severity × time	63 277.846	2	50.382	0.000
Understory species richness				
Severity	20.455	1	4.684	0.031
Time	500.131	2	57.262	0.000
Severity × time	29.576	1	6.773	0.009
Alien species richness				
Severity	7.220	2	31.419	0.000
Time	7.113	1	61.905	0.000
Severity × time	1.438	1	12.516	0.000
Alien cover (% understory cover)				
Severity	274.675	1	1.222	0.290
Time	8827.222	2	18.023	0.000
Severity × time	920.720	1	3.780	0.050

Rundel 1999, Prinzing et al. 2002). Valleys and foothills in the Old World have had the longest history of intensive land use and have presented the greatest opportunity for coevolution with human-perturbed landscapes. In California, these valley and foothill habitats were also the ones most immediately and thoroughly exploited by Europeans (Kinney 1996), creating favorable sites for the establishment of aliens preadapted to such disturbed landscapes. Montane sites in both the Old and New Worlds have had the shortest history of anthropogenic disturbance (Moe and van der Knaap 1990, Duane 1996, Menke et al. 1996). This would imply that there are many fewer species with colonizing attributes in Old World montane environments than in foothill habitats, a hypotheses yet to be tested.

Perhaps reflective of a different suite of invasives between foothills and montane sites is the fact that the vast majority of aliens in the foothill blue oak savannas were not encountered in the higher elevation coniferous forest sites. Alternatively, the higher elevation sites may not have had sufficient time for adequate propagule dispersal (Rejmánek 1989, Lonsdale 1999, D'Antonio et al. 2001). However, the potential for propagule transfer has been present for well over a century. The bulk of invasive species in the foothill flora have been present in the Central Valley and surrounding foothills since at least the mid-1800s (Bossard et al. 2000). There have been many opportunities for propagule transfer from the 19th century annual sheep drives that ran large herds from the valley to most montane meadows (Vankat 1970, Dilsaver and Tweed 1990, Kinney 1996). Subsequently, there has been potential propagule transfer via humans as the coniferous study sites have been popular tourist attractions since the early 20th century. Thus, it would seem that propagule limitation is not a compelling explanation for these elevational patterns. An alternative hypothesis for the depauperate alien flora in coniferous forests is that the full complement of savanna alien species is poorly adapted to the forest habitat and the number of Eurasian

FIG. 13. First postfire year following low-severity fire in mixed coniferous forest of Sequoia National Park (photo by J. Keeley).

FIG. 14. Third postfire year following a high-severity fire in mixed coniferous forest of Sequoia National Park (photo by J. Keeley).

colonizing species available for colonization of these higher-elevation sites is limited.

Role of disturbance

Blue oak savannas.—Grazing is commonly thought to degrade grass-dominated ecosystems, leading to reduced species diversity (e.g., Waser and Price 1981) and increased alien invasion (Belsky and Gelbard 2000; but cf. Stohlgren et al. 1999*b*). In the southern Sierra Nevada, it appears that grazing does increase the presence of aliens, but it is also associated with increased species richness. Most surprising from our study was the rather modest drop in alien species richness and cover (Fig. 6) on sites in the national park that have been free of livestock grazing for a century or more. Although these sites were all localized in the southern end of Sequoia National Park (Fig. 1), observations suggest that protection from grazing is not a highly effective means of reducing alien dominance anywhere in the blue oak savanna range. Generalizations are difficult to make because of marked variation in community composition observed in blue oak savannas and woodlands (Borchert et al. 1991). Also, this study did not consider either annual variation, which can be considerable (Bartolome and McClaran 1992, Hobbs and

Mooney 1995), or the potential impact of different fire regimes on the understory flora of these foothill savannas (Parsons and Stohlgren 1989).

It is particularly striking that, at the 1-m² scale, these blue oak savannas consistently had more alien than native species (Fig. 7A). An intriguing question is what have these aliens displaced? It is widely regarded that the alien annuals have taken the place of perennial bunchgrasses, such as *Nassella pulchra* and *Poa secunda* due to excessive grazing and drought (Heady et al. 1992, Hamilton 1997). Such a scenario is consistent with studies showing that loss of functional group richness is tied to success of alien plant invasion (Symstad 2000). However, the diversity of these native grasses does not approach the number of alien species now present. Either these aliens have greatly increased the species richness of blue oak savannas or they have displaced native annuals, which comprise a rich flora in this region (Richarson and Lum 1980). Recent experiments suggest that loss of native diversity may exacerbate the invasion by alien species (Lyons and Schwartz 2001). This may help explain the present-day resistance of this alien-dominated system to change, despite a century of livestock exclusion.

Chaparral.—Relative to other chaparral sites in California, the first-year burned sites studied here were remarkably depauperate in native diversity. For example, average species richness at 1 m² and 1000 m² was 2.7 and 22.2, respectively (Table 2), in contrast with values that are several times higher in southern California postfire chaparral (Keeley 1998). Whether or not these values fall within the natural range of variation in the southern Sierra Nevada is unknown because of a lack of comparable studies. However, based upon general floristic patterns throughout the state (Richarson and Lum 1980), there is little reason
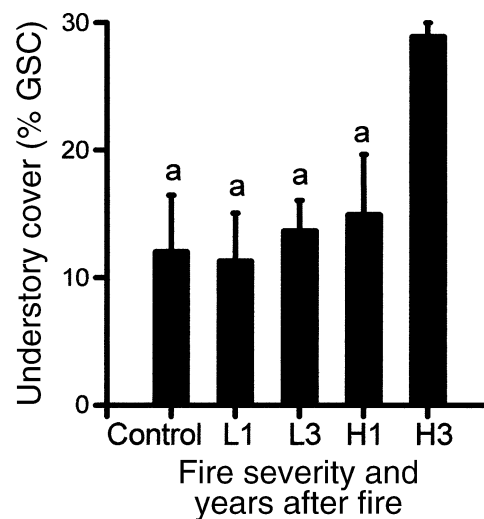

FIG. 15. Impact of fire severity and time since fire in coniferous forests on understory coverage (%GSC is as in Fig. 9). See Fig. 11 legend for details.
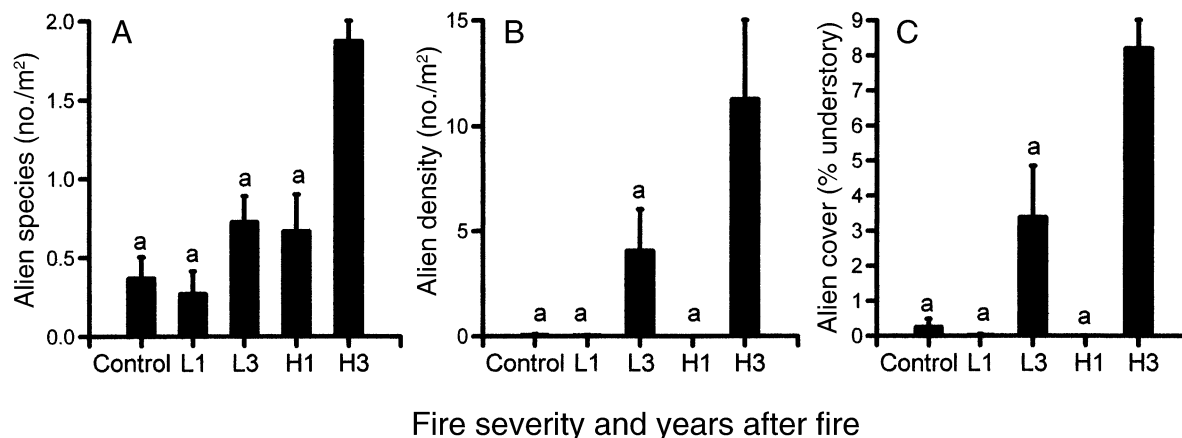
Fig. 16. Impact of fire severity and time since fire in coniferous forests on (A) alien species richness, (B) alien density, and (C) alien cover (see Fig. 11 legend for details).

to expect dramatic differences in species richness between the Sierra Nevada chaparral and southern California chaparral. An alternative explanation for the limited diversity in the first postfire year is the very long hiatus of fire prior to the 1998 prescribed fires in the East Fork of the Kaweah River (Lookout Point sites). The last time these sites burned was described by John Muir in 1875 (Muir 1901). The actual longevity of soil seed banks is not known for chaparral sites in general (Parker and Kelly 1989); therefore, it is possible that the 125-year hiatus between fires in the East Fork may have been long enough for significant seed bank deterioration. If this is the case, it would provide sound justification for fire restoration, something not generally recognized as needed on most chaparral landscapes (Keeley 2002b). Further studies of this potential regional difference in chaparral fire history are badly needed in order to effectively manage prescription burning in these shrubland ecosystems.

The general pattern of alien invasion observed in these southern Sierra Nevada chaparral stands is similar to that reported for other parts of California (Keeley 2000). Immediate postfire sites are remarkably free of invasive species, in part because the closed canopy of prefire shrublands reduces the alien populations and thus limits the alien seed bank present at the time of fire. Equally important is the fact that high-severity fires destroy any alien seed bank that may be in the soil (Keeley 2002a). Time since fire is generally the most critical factor in alien invasion. In this study, aliens were largely restricted to later successional years, undoubtedly due to the time needed for colonization of the site rather than any intrinsic environmental change in subsequent postfire years. In a sense, alien invasion is a drama between the speed at which alien propagules reach a site and the speed at which the shrublands return to their former closed-canopy condition. In this study, the high alien composition of some older sites was undoubtedly exacerbated by the

fact that they had been repeatedly burned in recent decades, thus altering the competition between alien annuals and native shrubs.

Invasive species necessarily must colonize from source populations, and thus landscape patterns determine the success of invasions. Blue oak savannas are an important propagule source because they maintain permanent populations of all alien species encountered in chaparral and because the vegetation mosaic in this region places them in proximity to chaparral. Roadsides, of course, are another important source of alien propagules (Frenkel 1970, Amor and Stevens 1975). Because our studies were biased by selecting sites with reasonable access to roads, we have presented data that may not be representative of alien invasion patterns in more remote areas.

Coniferous forests.—In these montane forests, humans have disturbed the natural ecosystem processes through a century of fire suppression activities that have resulted in fire exclusion over a large portion of the landscape. This has had profound impacts on landscape patterns as the frequency and size of forest canopy gaps has declined (Skinner [1995]; but these changes may have led to other gap-forming processes, e.g., Rizzo and Slaughter [2001]). Although gap formation is perhaps reduced on contemporary landscapes, the potential has increased for substantially larger gaps from wildfires in the future, due to increased fuels (Keeley and Stephenson 2000). Today this impact is being mitigated through managed restoration of fire. The return of this natural ecosystem process has had the positive effect of increasing species richness, evident in this study and others (Naumburg and DeWald 1999). However, increased gap formation also carries with it the potential for increasing invasion by alien plant species (Fig. 16), evident here and in other studies (Hobbs and Huenneke 1992, Crawford et al. 2001, Griffis et al. 2001).

Fires generate conditions conducive to the establishment of many species otherwise absent from unburned forests, through increased resources of light and nutrients (Tilman 1982). On our sites, tree canopy cover was significantly reduced on high-severity burned sites (Fig. 9). Combined nitrate and ammonium nitrogen exhibited significant increases in burned sites in the first year after fire (Fig. 12), with increases similar to those reported for other coniferous forests (Wan et al. 2001). Interestingly, none of the coniferous forest sites came close to the nitrogen pulse seen in first-year postfire chaparral (Table 2). We hypothesize that this may reflect the potential for much greater soil heating in surface-fire regimes (and potential soil sterilization) than in crown-fire regimes.

Propagule sources are also an important determinant of diversity and invasive patterns. Unlike chaparral shrublands, where there is a rich diversity of species with dormant seedbanks cued by fire (Keeley 2000), conifer forests have relatively few species with persistent seedbanks. In our studies, we found two annuals (*Gayophytum eriospermum* and *Mentzelia distans*) and several species of shrubs (*Ceanothus* and *Arctostaphylos*) with dormant soil seed banks triggered to germinate by fire. These native genera are widely distributed in disturbed understories of forests throughout the Sierra Nevada (Mellmann-Brown and Barbour 1995). The vast majority of species in our burned forests either resprouted from vegetative structures or, as in the case of all alien species, colonized from source populations. Consequently, time since fire is consistently an important factor determining postfire diversity and alien patterns (Figs. 15 and 16).

Proximity of seed sources, both native and alien, appears to be fundamentally important to colonization following disturbance in these and other forests (Amor and Stevens 1975, Wiser et al. 1998). Thus, landscape patterns of burning may have profound impacts on postfire colonization, as observed in other landscape studies of burned coniferous forests (Turner et al. 1997). One of the critical elements is the perimeter-to-area ratio that affects the distance propagules must travel to colonize sites. In particular, Turner et al. (1997) noted that small burns had a greater probability of attracting alien species because of the increased potential that perimeters with surviving alien populations were better positioned to invade a greater proportion of the burned site. Proximity of roads is important because they are often sites with permanently established alien populations (Frenkel 1970), although the dense roadside thickets of native saplings characteristic of many forests may be substantial obstacles to alien invasion (Brothers and Springern 1992). Another factor in need of study is the impact of pre-fire fuel manipulations that are designed to open the canopy by ≥40% (Agee et al. 2000), and thus are likely to harbor source populations of alien species poised to colonize burned areas as the opportunity arises.

Alien invasion of high-severity burned patches is consistent with the observation that closed-canopy forests are not generally favorable sites for invasive plants (Rejmánek 1989). This is a widespread pattern interpreted as direct resource limitations on understory species (McKenzie et al. 2000). Thus, one explanation for the limited number of alien species in coniferous forests may be tied to the extraordinarily long and successful campaign to exclude fire from these environments.

Despite the observed increase in aliens on burned forest sites, aliens generally do not represent a major problem at present. In this study, they comprised only 0.3% of the understory flora in unburned forests and 3.4% in burned forests. In other Sierran forests, however, other disturbances created by timber harvesting may result in many times greater alien composition (Battles et al. 2001). The invasive problem in southern Sierra Nevada forests centers around *Bromus tectorum*, although this could change as future introductions pose new threats. Managing fires in these forests to avoid high-severity burns may act to diminish the alien threat, but two points are worth considering. One is that high-severity fire is an important gap formation process and is necessary for successful recruitment of the dominant overstory trees (Keeley and Stephenson 2000). In addition, the bulk of the native flora of these forests is largely restricted to high-severity fire gaps; thus, alterations in the fire regime that reduce the formation of such gaps will undoubtedly diminish natural biodiversity.

Lastly, the very different diversity relationships between oak savanna and coniferous forests (Figs. 5 and 7), and the very different disturbance regimes, may explain why Stapanian et al. (1998), in a broad regional comparison of eight woodland and forest types, failed to detect any relationship between alien invasion and disturbance in California.

Theoretical implications

Elton (1958) proposed that community diversity acts to inhibit invasion. This effect should be most evident at the 1-m^2 point scale, where competitive interactions would be most intense. However, at this scale in blue oak savanna, chaparral, and coniferous forests, alien species richness and cover increase with increasing native species richness (Fig. 7).

In contrast, modeling studies generally support Elton's principle (Levine and D'Antonio 1999), and reconciling these with field studies that reach opposite conclusions requires close inspection of model assumptions. For example, Case (1990) produced a model of the invasion process that could be interpreted to mean that high diversity will inhibit invasion. However, his model is based on the assumption that invaders are ecologically similar and are drawn from the same distribution of competitive abilities. This model would not apply to our savannas, where the dominant aliens are

aggressive annual grasses, which are in short supply in the indigenous flora. At our study sites, it is possible that aliens are filling a niche created by Holocene drying (Keeley 2002a), a somewhat novel condition for most of the past 1.6×10^6 years.

Naeem et al. (2000) produced experimental evidence in favor of Elton's principal and proposed that refutations of the principle that often are observed in field studies result from "covarying extrinsic factors" such as disturbance. However, experimental studies are not without confounding factors (e.g., Huston 1997, Wardle 2001). In the present study, it was noted that the positive relationship between alien richness and native richness was evident at the 1-m^2 scale under control, grazed, or burned conditions, combined or separately. The only instance in which the relationship broke down was the grazed-oak treatments and then only at the community scale (1000 m^2). Otherwise, at the 1-m^2 level there was consistently a positive relationship between alien and native species richness. This suggests that alien invasions are limited not by competitors, but by site factors that increase resources for establishment of a wide range of species, native and alien. Alternatively, it may be that diversity per se promotes diversity of aliens in some as yet unknown mechanism (Palmer and Maurer 1997).

The primary role of disturbance has been to alter community equilibrium in resource availability. Grazing and drought may have caused more or less permanent changes in resource availability in grasslands and savannas, resulting in a new quasi-equilibrium in which aliens dominate. Near-complete removal of many of the native species has diminished the propagule pressure sufficiently to make these communities seemingly immune to recolonization by natives. Fluctuating resources following periodic burning in both chaparral and coniferous forests provide stages suitable for colonization by both natives and aliens. The proportion of natives vs. aliens is heavily dependent upon proximity of seed sources and other disturbances, both natural (e.g., drought) and anthropogenic (e.g., trampling by humans and livestock), that may alter the competitive balance. Persistence of alien and native colonizers will be a function of the rate and extent of canopy closure, which changes the quality of resources by reducing light and soil nutrients and increasing surface litter.

Management implications

Alien invasion in the foothill blue oak community of the national park lands of the southern Sierra Nevada does not seem to pose a tractable management problem because a century of livestock exclusion has not substantially altered dominance by these alien species. Thus, some have resigned themselves to welcoming these aliens as "new natives" (Heady 1977). Whether this alien invasion derives from the displacement of native bunchgrasses (Heady et al. 1992) or shrublands (Cooper 1922) may be relevant to management. Restoring native bunchgrasses in the face of massive alien grasses has so far proven rather difficult, if not impossible. However, if the original understory was a shrub or subshrub layer, as proposed by Cooper (1922; see examples in Borchert et al. 1991), attempts to "restore" these foothill savannas with native bunchgrasses may prove futile. In this case, returning these foothill communities to a more closed-canopy woodland/shrubland may be the only means of reducing the extent of alien invasion.

A century of fire suppression in the coniferous forests has nearly excluded fire, except where intentionally reintroduced. These forests have historically burned with a mixture of low-intensity surface fires and high-intensity surface and localized crown fires (Show and Kotok 1923). Species richness is generally increased in gaps produced by high-severity fires. Thus, fires that generate a mosaic pattern of fire intensities are likely to approach the natural historical range of variation in biodiversity patterns. However, these conditions are also conducive to alien invasion, although currently this seems to be of more localized importance in the lower elevation onderosa pine forests. Proximity of alien propagules may be an important determinant of colonization success; hence, fire management must include a landscape perspective of source populations of alien species when planning prescription burns. These patterns support the conclusion of Stohlgren et al. (1999a) that biodiversity "hotspots" may often be the sites of greatest alien plant invasion. Both native diversity and invasion by aliens are promoted by the same environmental factors, posing significant challenges for resource scientists.

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