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Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada

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Abstract. Nearly a century of fire suppression has changed fundamental aspects of the structure and functioning of fire-adapted forests throughout the western U.S. Prescribed fire is increasingly used to restore forest structure and reduce surface fuels with limited consideration of its consequences for biological diversity. In this study, we used more than two decades of data from permanent plots in mixed-conifer forests of Sequoia and Kings Canyon National Parks, California, to explore changes in plant diversity and abundance following reintroduction and repeated use of fire. Data on stand structure, fuel loading, fire severity and heterogeneity, and the richness and abundance of major growth forms were collected on 51 plots representing one of three treatments: control, first-entry burn, and second-entry burn. Understories showed distinct compositional changes over time in first- and second-entry burns. Burned plots supported more than twice as many species as controls 10 yr after treatment; first-entry plots showed a nearly threefold increase in richness by year 20. Burned plots supported four to five times as many shrub species as controls 5–10 yr after burning. Total plant cover (dominated by perennial forbs and shrubs) increased in first-entry plots, but did not differ from controls until 20 yr after treatment. Following second-entry, cover did not change through final sampling (year 10). Nonnative species were rare, occurring in only three plots at low abundance. Higher severity fires led to greater numbers of species and to greater plant cover. Species richness was not correlated with burn heterogeneity. Long-term observations suggest that reintroduction of fire in previously unmanaged forests can gradually enhance the diversity and abundance of understory species. Repeated burning—necessary to achieve structural and fuel-reduction objectives—does not appear to have a detrimental effect on plant diversity and may enhance the distributions of species that are adversely affected by fire exclusion. If fire is to play an important role in restoration, however, it will need to be maintained as a frequent and spatially dynamic process on the landscape.

Key words: diversity; fire effects; fire frequency; heterogeneity; mixed-conifer forest; plant dispersal; prescribed fire; Sequoia and Kings Canyon National Parks; severity; understory.

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INTRODUCTION

Fire plays an important role in many forest ecosystems (Payette et al. 1989, Brown and Smith 2000, Bradstock et al. 2002, Otterstrom and Schwartz 2006) including mixed-conifer forests of the Sierra Nevada (Vankat and Major 1978, van Wagtendonk and Fites-Kaufman 2006). Understanding the natural role of fire and its potential for reintroduction in systems from which it has been excluded is of critical importance to resource managers (Stephenson 1999, Bond and Archibald 2003). Historically, frequent fires regulated the successional dynamics, fuel accumulation, and nutrient cycling of Sierran mixed-conifer forests (Kilgore 1973, Stephenson et al. 1991). However, nearly a century of fire suppression has changed fundamental aspects of the structure and functioning of these and other western forests (Covington and Moore 1994, Harrod et al. 1999, van Wagtendonk and Fites-Kaufman 2006). It has led to unprecedented increases in the density of shade-tolerant conifers and surface fuels and increasing potential for large stand-replacing fire (Vankat and Major 1978, Arno and Brown 1991, Agee 1993, Minnich et al. 1995).

In response to these changes and to the increasing risk of catastrophic fire, resource managers on federal lands are using fire in combination with mechanical methods (thinning and mastication) to alter forest structure and reduce fuel accumulations (North et al. 2007, Schwilk et al. 2009, Vaillant et al. 2009). To varying degrees, these approaches have been successful (Harrod et al. 2009, Schwilk et al. 2009, Vaillant et al. 2009). However, the consequences for other ecosystem attributes, e.g., understory structure and diversity, have not been critically evaluated. It is implicitly assumed that by restoring structure and reducing fuels, recovery of other ecosystem components and processes will follow (Sierra Nevada Ecosystem Project 1996, Stephenson 1999). Although formal tests of this assumption are constrained by a lack of historical data on understory structure, studies of the broader implications of reintroducing fire are critical as managers seek to balance ecological values, societal pressures, and the operational constraints of prescribed burning on federal lands.

In this paper, we explore the long-term responses of forest understories to reintroduction (and repeated use) of fire in previously unmanaged, mixed-conifer forests of Sequoia and Kings Canyon National Parks (SEKI), California. The fire management program in SEKI was initiated in the late 1960s—the first in the U.S. system of National Parks. It allows for natural ignitions and employs prescribed fire to achieve diverse ecological, cultural, and societal objectives (Kilgore and Briggs 1972, Rothman 2007). We use data from permanent vegetation plots established in the 1970s as part of an NPS-wide fire-effects monitoring program designed to ensure that resource management goals are met, to detect unanticipated trends, and to identify future research needs.

Previous studies in fire-dependent forests have examined vegetation responses to fuel-reduction treatments that include silvicultural manipulations without fire (Battles et al. 2001), thinning vs. burning (Collins et al. 2007, Wayman and North 2007, Dodson et al. 2008), and different seasons of burning (Kauffman and Martin 1990, Knapp et al. 2007). However, most have been of short duration (2–3 yr) with treatments limited to single entries. Long-term studies in SEKI are unprecedented in their length (multiple decades) and use of repeated burning which may be necessary to achieve structural or fuel-reduction objectives (North et al. 2007).

Fire can have direct or indirect effects on understory plant communities. Direct effects include physical consumption of above-ground structures (Whelan 1995, Agee 2003), mortality of root systems through soil heating (Brown and Smith 2000), and stimulation of soil seed banks (Leck et al. 1989). Indirect effects include changes in microclimate (e.g., light and temperature) and soil resources (moisture and nutrient) via reductions in tree density or consumption of surface fuels (Wan et al. 2001, North et al. 2005, Fites-Kaufman et al. 2006, Ma et al. 2010). The relative importance of these effects can be mediated by the severity, frequency, or spatial heterogeneity of burning. Moreover, plants with differing growth forms and life histories can vary in their responses to fire or to its severity or frequency. Numerous strategies of plant persistence and regeneration have evolved in fire-dependent ecosystems. These range from fire-dependent (e.g., seed-banking shrubs that rely on fire to break dormancy) or fire-enhanced (e.g., annuals that benefit from exposure of mineral soil for germination) to fire-inhibited (e.g., herbs with shallow root systems whose perennating structure are consumed by fire) (McLean 1969, Rowe 1983, Brown and Smith 2000, Fites-Kaufman et al. 2006). In the absence of fire, understories are likely to be dominated by species adapted to shade and deeper accumulations of duff and litter, but more sensitive to fire. Fire-dependent species may be absent or present only in the seed bank. In contrast, forests that have burned more recently are likely to support a greater diversity of species, including those that respond positively to fire. Populations of the latter may expand rapidly due to local seed availability, or negatively depending on their regenerative traits (e.g., ability to resprout), the characteristics of fire, or whether sufficient time has passed for seed banks to be replenished (Keeley and Fotheringham 2000).

Severity of fire can have a large effect on understory response (Halpern 1988, Halpern and Spies 1995, Schimmel and Granstrom 1996, Wang and Kemball 2005). At low severity, plant mortality is low, but fire-dependent species are less likely to establish. As a result, effects on richness, abundance, and composition are likely to be small. At high severity, mortality of fire-inhibited species can be high, but fire-dependent or fire-enhanced taxa are more likely to establish unless limited by seed availability or dispersal. Thus, effects on richness, abundance, and composition should be greater. Spatial variation (or heterogeneity) in burn severity can also affect understory response to fire (Rocca 2009). Greater heterogeneity of post-first environments (microclimates, substrates, and soil properties) should promote greater diversity of species with differing resource and environmental requirements (e.g., Huston 1994). Many factors can contribute to variation in the severity or heterogeneity of fire, including the amount, type, and spatial continuity of fuels (Whelan 1995, Agee 2003). In mixed-conifer forests of the Sierra Nevada, fuel characteristics can differ markedly in stands that have, or have not, burned recently. In the absence of fire, fuel levels are typically high and spatially continuous. As a result, "first-entry" fires are more likely to burn at higher severity and with greater uniformity (Miller and Urban 2000, Knapp and Keeley 2006, Knapp et al. 2007). In contrast, in stands previously treated with fire, fuel loads tend to be lower and less continuous resulting in fires of lower severity and greater heterogeneity (Stephens and Moghaddas 2005, Keifer et al. 2006, Schwilk et al. 2009).

In this study, we use more than two decades of data from permanent experimental plots in mixed-conifer forests of SEKI to explore long-term responses of forest understories to the reintroduction and repeated use of prescribed fire. We address the following questions: (1) Does reintroduction of fire affect the composition, diversity, and abundance of understory plants? (2) How do community composition and the diversity and abundance of plant growth forms change with time since burning? (3) Do responses differ after first- and second-entry burns? (4) How do severity and heterogeneity of fire affect patterns of richness and abundance? Do relationships differ for first- and second-entry fires and do they change over time?

METHODS

Study area

The study area is on the western slope of the southern Sierra Nevada mountain range in Sequoia and Kings Canyon National Parks, California, USA (SEKI). Climate is characterized by cold, wet winters and warm, dry summers. Average minimum air temperatures range from −6.7°C (February) to 11.8°C (August) and average maxima from 3.4°C (December) to 27.4°C (August) ⟨http://cdec.water.ca.gov/⟩. Most precipitation falls in the winter as snow. Mean annual precipitation at Giant Forest (2027 m) is ~105 cm ⟨http://cdec.water.ca.gov/⟩. Sample plots occur between 1750 and 2300 m elevation in mixed-conifer forests of *Abies concolor*, *Pinus lambertiana*, *P. ponderosa*, *Calocedrus decurrens*, *P. jeffreyi*, and *Quercus kellogii*. Additional plots occur in groves of *Sequoiadendron giganteum* at similar elevations within these mixed-conifer forests (Harvey et al. 1980). Soils derive from granitic parent material (Huntington and Akeson 1987). Historically, fires burned frequently (every 2–30 yr) (Swetnam 1993).

Data collection

In total, we used data from 51 fire-effects monitoring plots (0.1 ha, 20 × 50 m) established prior to treatment. In areas scheduled to be burned (or in adjacent areas designated as controls) random points, stratified by vegetation type, were identified with ESRI GIS software (Sequoia and Kings Canyon National Parks 1998). Points were then located in the field. From each point, a random azimuth, distance, and orientation were selected to define the center and long axis of each plot. One to four plots were sampled per burn unit. These represented 24 fire events (15 first entry, 9 second entry) occurring between 1986 and 2005. Most (20) fires were prescribed burns—primarily surface fires of low to moderate severity. Four resulted from natural (lightning) or human-caused ignitions. The time between first- and second-entry burns averaged 13 yr (range of 8–17 yr). Burns occurred between June and November, but most (63%) were during fall (September-November). First-entry burns ranged in area from 2 to 1251 ha (mean of 259 ha) and second-entry burns from 20 to 146 ha (mean of 67 ha). Control plots were established in adjacent unburned areas or areas that were scheduled to burn but did not. Controls have not experienced fire since suppression efforts began in the late 19th or early 20th centuries.

Field sampling followed standard National Park Service fire-effects monitoring protocols (USDI National Park Service 2003). In each plot, cover of bare ground and cover of all understory species was quantified by the point-intercept method (166 points along a 50-m transect); sampling was conducted in mid-summer (July-August). Additional species were recorded if present within a 50 × 10 m belt (500 m^2 plot) centered on each transect. All plants were identified to species, if possible, otherwise to genus or family. Nomenclature follows Hickman (1993).

All live and dead overstory trees in each 0.1 ha plot were tallied and measured for diameter on each sampling date. Ground (litter and duff) and woody (1- to 1000-hr) fuels were assessed before and after burning using Brown's method (Brown 1974) on four randomly placed 15.24 m transects per plot. Burn severity of organic substrates (litter, duff, and woody debris) was assessed within 3 mo of treatment along each transect (ten 2 dm × 2 dm quadrats at ~1.5 m spacing). Each quadrat was rated by severity class (ranging from heavily burned [1] to unburned [5]; USDI National Park Service 2003). For all trees alive before burning, percent crown scorch, maximum scorch height, char height, and post-burn status (live or dead) were recorded.

Plots were sampled 0–2 yr before burning; immediately after burning (for severity and heterogeneity); and 2, 5, 10, and 20 yr after burning. Controls were sampled on the same schedule. For plots burned a second time (second-entry burn) the sampling schedule was reset. For the current study, first- and second-entry burns were represented by different plots.

Data manipulation

Prior to analyses, species were assigned to one of five plant groups based on growth form and longevity (henceforth, growth form): annual/biennial forbs (henceforth, annual forbs), perennial forbs (including subshrubs and ferns), graminoids (grasses and sedges), shrubs, and understory trees (<1.37 m tall). Total and growth form richness were expressed as numbers of species per plot (500 m^2). Total and growth-form cover were computed as the sums of individual species within each group.

For each plot, we calculated various measures of burn severity and heterogeneity that served as potential predictors of vegetation response (see *Methods: Statistical analyses*). For severity these included: substrate burn severity (range of 1–5; mean of 40 quadrats); post-burn duff and litter depth (cm; means of 40 points); consumption of duff and litter (cm; differences between pre- and post-burn depths); percent crown scorch, scorch height, and char height (means of all trees in a plot); and density (number/ha) and basal area (m^2/ha) of both live and dead trees (computed at each sampling date). Measures of burn heterogeneity included the standard deviation (SD) of substrate burn severity, SD of post-burn duff and litter depth, and SD of duff and litter consumption (SD of the change in depth). For litter and duff, we considered both consumption and post-treatment depth to account for pre-treatment variation and the potential for plants to respond differently to burning (consumption) than to post-treatment conditions (depth).

Statistical analyses

For all analyses, plots were treated as independent samples. Although some plots occurred in the same burn unit they were >100 m apart (and typically >0.5 km) and were often ignited on different days. From among the larger set of plots, 34 (8 control, 13 first-entry, and 13 second-entry) were used in analyses of treatment effects on species composition, richness, and cover (questions 1–3). In year 10, sample size declined to 6 for second-entry burns and in year 20 it declined in all treatments (0 second entry, 7 first entry, and 6 control). Rather than limit analyses to fewer plots sampled continuously through time, we retained plots with shorter sampling histories to increase replication of earlier successional times (years 2–10).

Prior to analyzing vegetation responses, we used a series of *t* tests to assess differences in cover of bare ground, burn severity, and burn heterogeneity between first- and second-entry treatments. We then used non-metric multidimensional scaling (NMS; Kruskal 1964) to assess the effects of treatment and time since burning on species composition. Species present in $<5\%$ of plot × time combinations were excluded. A dummy species with a cover value of 0.6% (the smallest value for a species on a plot) was added to all samples (plot × time combinations) to facilitate inclusion of samples for which there was no plant cover (Clarke et al. 2006). Cover data were arcsine square root transformed. NMS was implemented with PC-ORD ver. 5.0 (McCune and Mefford 2006) using the "slow and thorough" autopilot setting, Bray-Curtis as the distance measure, maximum number of iterations of 500 (250 runs with real and randomized data) with a random start, and an instability criterion of 0.0000001 (McCune and Grace 2002).

Following NMS, we used permutation-based multivariate analysis of variance (PERMANOVA; Anderson 2001) to test for differences in species composition among treatments, sampling dates, and their interaction. As with NMS, species present in $<5\%$ of plot × time combinations were excluded, a dummy species was added to all samples, cover data were arcsine square root transformed, and Bray-Curtis was used as the distance measure (McCune and Grace 2002). In addition, cover data were standardized to the maximum value within each species (columns) then relativized within samples (rows) (McCune and Grace 2002). Significance tests were based on 9999 permutations of the data. For significant time × treatment interactions, pair-wise comparisons of means were made to identify the points in time for which there were significant differences in composition among treatments. Analyses were conducted in PRIMER ver. 6 (Clarke and Gorley 2006).

We then used indicator species analysis (ISA; Dufrêne and Legendre 1997) to test whether individual species showed significant associations with particular treatments or points in time. Three analyses were run. The first tested for associations with burning by comparing burned (first- and second-entry) vs. unburned plots. The second tested for associations with first- or second-entry burns (unburned plots were excluded). The final analysis tested for temporal associations by comparing burned plots at four points in time: 2, 5, 10 and 20 yr after fire (unburned plots were excluded). All species were included, but considered indicators only if they had a significant *P* value and $\mathrm{IV}_{max} \geq 25$ (Dufrêne and Legendre 1997). ISA was implemented in PC-ORD ver. 5.0 (McCune and Mefford 2006).

PERMANOVA was also used to test for differences in species richness and cover among treatments and sampling dates, and their interaction (questions 1–3). Cover data were arcsine square root transformed and Euclidean distance was used as the distance measure. Separate tests were run for total plant richness and cover and for richness and cover of each growth form. Because we included pre-treatment data, significant main effects were not of interest. Instead, we focus on significant time × treatment interactions that imply differential responses to treatments. For these, pairwise comparisons of means were used to identify times at which treatments differed.

To explore vegetation responses to burn severity and heterogeneity, and how these changed over time (question 4), we developed stepwise regression models. Response variables included species richness and plant cover (total and by growth form). Predictors included measures of burn severity (for models of richness and cover) or burn heterogeneity (for models of richness). In addition to these predictors, pre-treatment richness or cover were included in each model to test whether, and to what degree, initial conditions explained post-treatment responses. Separate models were run for plots representing first- and second-entry burns, each at two points in time (2 and 10 yr). In total, regression analyses were based on data from 33 plots: 16 of the 34 used to assess treatment effects and 17 for which additional data existed for years 2 and 10. Sample sizes varied among models: 19 for first-entry burns (both years) and 20 and 6 for second-entry burns (years 2 and 10, respectively). Standard diagnostics were used to test the assumptions of normality and constant variance of residuals; cover data were arcsine square root transformed. Predictors were retained in the models at $P < 0.05$ and excluded at $P > 0.1$ (Neter et al. 1996). However, a second predictor was not retained unless it resulted in a relatively large (0.1–0.4) increase in R^2 (variation explained). The vast majority (80%) of final models included a single predictor; for those with two predictors, variance inflation factors (VIF) did not exceed 3.4. Regressions were run in SPSS ver. 12.0 (SPSS 2003).

RESULTS

Overstory structure

Prescribed burning had a significant effect on overstory structure. Density of live trees (primarily *Abies concolor*) declined by >50% after first entry, but much less after second entry (Fig. 1A; Table 1). Subsequent changes were small in both treatments. In control plots, gradual declines in density were due to suppression-related mortality of small *A. concolor*. Significant mortality of *A. concolor* during first entry burns was reflected in a tripling of the density of dead trees (Fig. 1B), but most of stems fell within 10 yr. In contrast, second-entry burns resulted in minimal mortality. In contrast to density, basal area of live or dead trees was not affected by burning (Fig. 1C; Table 1). Plots within each treatment showed considerable variation in basal area (depending on presence/absence of *Sequoiadendron giganteum*) and no detectable temporal trends. In burned treatments, apparent declines after 10–20 yr are artifacts of a reduced sample size, characterized by plots with lower average basal area.

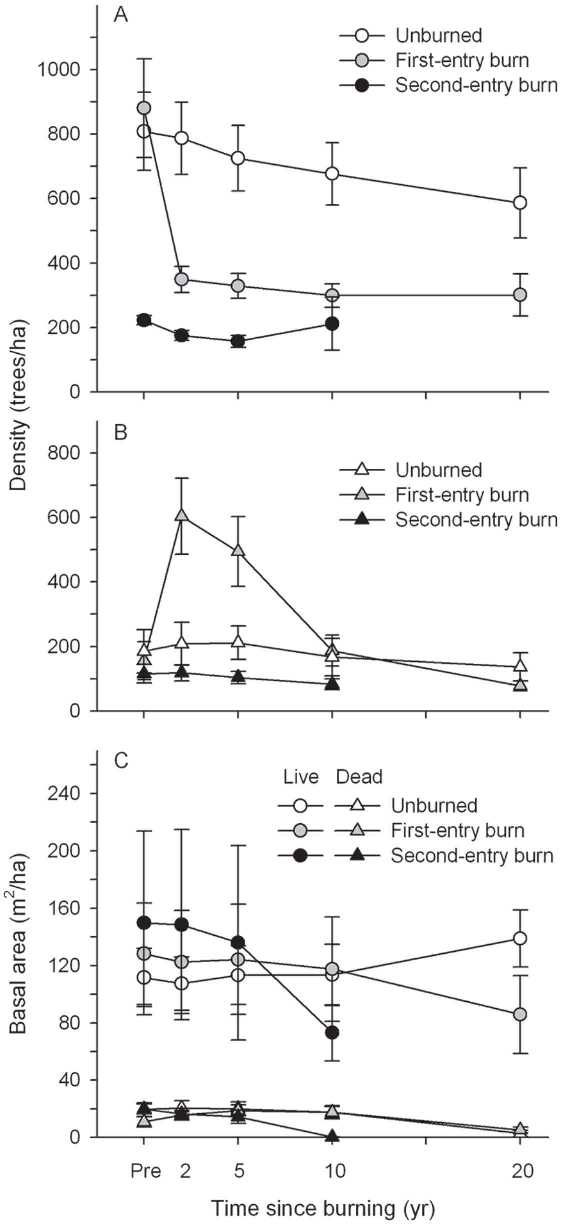

Fig. 1. Trends in (A) density of live trees (≥1.37 m dbh), (B) density of dead trees, and (C) basal area of live and dead trees. Values are means ±1 SE.

Forest-floor conditions, fuel consumption, and measures of burn severity and heterogeneity

Burning resulted in significant exposure of mineral soil which was uncommon prior to treatment (0.1% cover). Exposure was much greater after first- than second-entry burns (63.0 vs. 27.9%, $t = 3.032$, $P = 0.012$). Within 2 yr, however, cover of mineral soil declined dramatically and did not differ between treatments (2.6 vs. 5.6%, $t = -1.669$, $P = 0.108$).

Burning had a significant effect on forest-floor fuel mass and on the contributions of duff, litter, and wood (1–1000 hr fuels) (Fig. 2). First-entry burns reduced total mass by ~75% (Fig. 2A), with greater consumption of ground (Figs. 2C, D) than of woody fuels (Fig. 2B). However, duff and woody fuel mass showed marked increases with time, the latter through accumulation of branches and boles of fire-killed trees. At the time of second entry, fuel mass was lower than in control

Table 1. Results of *t* tests, including means and standard errors (SE), comparing measures of severity and heterogeneity for first- and second-entry burns.

Variable	n_1, n_2†	First entry Mean	First entry SE	Second entry Mean	Second entry SE	*t* statistic	*P*
Measures of severity							
Substrate burn severity (1–5)‡	4, 13	2.6	0.5	3.8	0.2	–2.488	**0.030**
Duff depth (cm)	13, 13	0.5	0.3	1.6	0.2	–3.052	**0.005**
Litter depth (cm)	13, 13	0.5	0.1	1.0	0.1	–2.545	**0.018**
Change in duff depth (cm)	13, 13	6.8	1.2	1.2	0.2	4.625	<**0.001**
Change in litter depth (cm)	13, 13	2.4	0.6	0.3	0.2	4.411	<**0.001**
Percent crown scorch	8, 13	16.8	4.8	23.8	6.8	–0.740	0.468
Scorch height (m)	11, 13	2.8	1.1	3.6	1.0	–0.552	0.586
Char height (m)	12, 13	1.4	0.6	1.6	0.3	–0.309	0.762
Live tree density, year 2 (no./ha)	13, 13	349.2	40.3	175.4	48.6	4.043	**0.001**
Dead tree density, year 2 (no./ha)	13, 13	603.8	117.9	118.5	24.5	4.031	**0.001**
Live basal area, year 2 (m^2/ha)	13, 13	122.4	36.1	148.5	41.2	–0.344	0.734
Dead basal area, year 2 (m^2/ha)	13, 13	15.6	3.3	16.5	3.9	–0.191	0.850
Measures of heterogeneity							
SD substrate burn severity	4, 13	1.07	0.23	1.30	0.07	1.350	0.197
SD duff depth (cm)	13, 13	0.74	0.30	1.51	0.16	–2.270	**0.035**
SD litter depth (cm)	13, 13	0.75	0.14	1.01	0.13	–1.333	0.195
SD change in duff depth (cm)	13, 13	7.71	1.43	2.95	0.42	3.199	**0.006**
SD change in litter depth (cm)	13, 13	2.11	0.31	2.06	0.52	0.088	0.931

Note: Significant differences are in bold.

† Sample sizes for first- (n_1) and second-entry (n_2) burns.

‡ Substrate burn severity ranges from 1 (high) to 5 (low).

plots (Fig. 2A) and composed primarily of woody debris (Fig. 2B). Second-entry burns reduced total mass by ~25%, mainly through consumption of this wood.

Burn severity was significantly greater in first- than in second-entry burns for measures based on forest-floor substrates (Table 1). However, severity did not differ between treatments for measures based on crown scorch or scorch or char height. Burn heterogeneity differed significantly between treatments for measures based on duff depth (Table 1). Post-treatment depth was more variable in second-entry plots, but consumption (change in depth) was more variable in first-entry plots. Measures of heterogeneity based on substrate burn severity or litter depth did not differ between treatments.

Compositional changes

A total of 204 plant species (45 families and 112 genera) was recorded over the period of study (1986-2007) (Appendix). These included 34 annual forbs, 112 perennial forbs, 23 graminoids, 22 shrubs, and 14 trees. The vast majority (88%) of species were present in <5% of samples (plots × sampling dates); only 25 species occurred with greater frequency. Only two non-native species were observed, *Bromus tectorum* and *Poa pratensis*; both were uncommon (present in three plots with very low abundance).

A scree plot of stress vs. dimensionality led to selection of a two-dimensional NMS solution; stress was 31.7 with a final instability value of 0.008 after 500 iterations. Plots representing first- and second-entry burns showed distinct compositional changes over time (Fig. 3A) despite considerable within-treatment variation (Fig. 3B). Sample scores generally increased with time along both axes (Fig. 3A) with second-entry burns displaced further from controls than first-entry burns. In contrast, unburned plots showed relatively small compositional changes in no consistent direction. Fire-dependent and fire-enhanced species such as *Calystegia malacophylla*, *Ceanothus cordulatus*, *Lotus oblongifolius*, *Pteridium aquilinum*, and *Rubus parviflorus*, showed strong positive correlations with NMS1 (Fig. 3C). Species more sensitive to fire and typical of more shaded habitats and deeper accumulations of duff—*Pyrola picta*, *Galium sparsiflorum*, and *Chrysolepis sempervirens*—exhibited strong negative correlations with NMS2.

Species composition showed a significant time × treatment interaction (PERMANOVA, $P = 0.005$), consistent with patterns evident in the NMS. Plots representing first- and second-entry

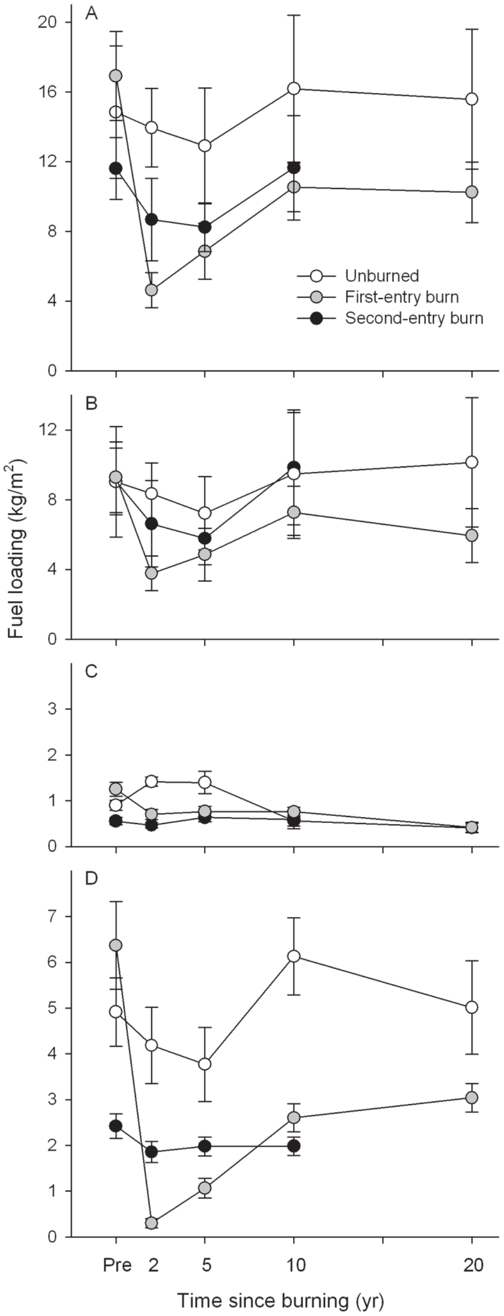

Fig. 2. Trends in (A) total fuel loading and the contributions of (B) woody fuels (1–1000 hr), (C) litter, and (D) duff. Values are means ±1 SE.

burns experienced significant changes in composition, but unburned plots did not. Among treatments, composition did not differ significantly until year 10, when second-entry plots diverged from controls. First- and second-entry plots showed marginally significant differences ($0.05 < P \leq 0.10$) in composition in year 2, but not later.

Indicator species analysis

Many species showed significant associations with treatments (burned vs. unburned, first- vs. second-entry burns) or times since burning. However, indicator values for most of these species were low (<25, Table 2). Among the strongest indicators were *Abies concolor* (burned plots and second-entry burns) and *Carex multicaulis* (second-entry burns). *Pinus lambertiana* and *Sequoiadendron giganteum* were not sufficiently abundant to emerge as indicators, however both were largely restricted to second-entry burns (Appendix). There were no species with high indicator values for first-entry burns or particular times since burning (Table 2).

Changes in species richness

Understories were poor in species. Richness prior to reintroduction of fire averaged <10 species per plot (Fig. 4A). First- and second-entry burns resulted in significant increases in richness (significant treatment × time interaction), but not until year 5 (Fig. 4A). By year 10, burned plots supported more than twice as many species as controls, with first-entry plots showing additional increases in year 20. Over the full period of observation, this represented a nearly threefold increase in richness. Increases were attributable to a diversity of species of varying growth form with low to moderate frequency (Appendix). Any apparent increases in control plots were not significant (results of post-hoc comparisons among temporal samples).

Annual forbs and graminoids were uncommon before treatment (≤1 species per plot; Figs. 4B and C). Lack of significant time × treatment interactions suggests no effect of burning, although trends for both groups suggest positive responses to fire. Perennial forbs, which comprised >50% of the species pool, increased in richness over time (significant time effect), but did not show different responses to treatments (Fig. 4D). Although trends for first-entry burns suggest a positive response to fire (doubling of richness by year 20), small increases among controls (primarily in year 20) limited detection

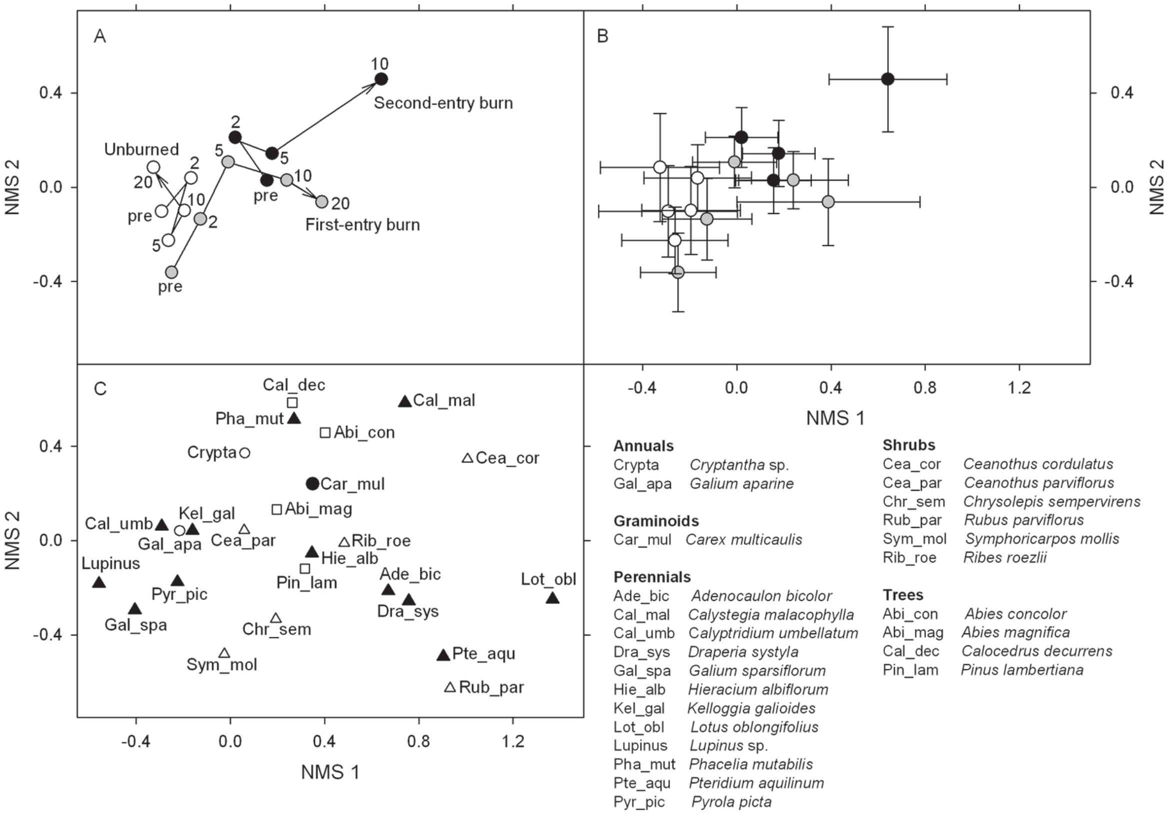

Fig. 3. Results of NMS ordination illustrating (A) trajectories of treatment centroids through time, (B) the same centroids ±1 SE emphasizing compositional variation within treatments × sampling dates, and (C) scores of the 25 species present in >5% of plot × time combinations. Species are coded by growth form (annual/biennial forbs = open circles, graminoids = closed circles, perennial forbs = closed triangles, shrubs = open triangles, and trees = open squares).

of a treatment effect. Shrubs showed significantly greater increases in richness in burned than in unburned plots (significant treatment × time interaction; Fig. 4E). After 5–10 yr, burned plots supported four to five times as many shrub species as controls. Many of these were new to the understory (Appendix). Understory trees showed significant increases in diversity in all treatments (significant effect of time; Fig. 4F), however, differences prior to burning precluded detection of a significant time × treatment interaction.

Changes in cover

Pre-treatment plant cover was low (<10–15%; Fig. 5A), comprised mainly of perennial forbs, shrubs, and understory trees (Figs. 5D-F). Total cover showed a highly significant treatment × time interaction. Cover increased significantly in first-entry plots, although it did not differ from controls until year 20 (means of 41 vs. 8%, respectively). Apparent increases in second-entry burns were not significant. Variation within treatments was high.

Cover of annuals was very low before treatment (<0.6%) and changed little after first-entry burns (Fig. 5B). Although trends in second-entry plots suggest a positive response to fire, variation among plots was high, limiting detection of a significant time × treatment interaction. Graminoids were also sparse before treatment (<0.5% cover; Fig. 5C). Cover increased significantly over time and at different rates among treatments. Cover of perennial forbs was highly variable within and among treatments and over time, resulting in a significant treatment × time

Table 2. Results of indicator species analyses (ISA) testing species' affinities for burned vs. unburned sites, first- vs. second-entry burns, and times since burning.

Comparison	Species	Growth form	IV_{max}	P
Burned vs. unburned				
Unburned	*Chrysolepis sempervirens*	shrub	21.5	<0.001
	Adenocaulon bicolor	perennial forb	10.4	0.016
	Apocynum androsaemifolium	perennial forb	7.8	0.014
	Disporum hookeri	perennial forb	6.8	0.044
	Chimaphila menziesii	perennial forb	5.9	0.041
Burned	*Abies concolor*	tree	33.8	0.002
	Hieracium albiflorum	perennial forb	22.0	0.009
	Ceanothus cordulatus	shrub	17.6	0.006
	Calystegia malacophylla	perennial forb	16.2	0.009
	Carex multicaulis	graminoid	11.5	0.033
	Ceanothus parvifolius	shrub	8.8	0.050
First vs. second entry				
First entry	*Galium sparsiflorum*	perennial forb	19.6	0.046
Second entry	*Abies concolor*	tree	34.4	0.050
	Carex multicaulis	graminoid	28.5	<0.001
	Linanthus ciliatus	annual/biennial forb	15.6	0.003
Time since burning				
Year 2	—			
Year 5	—			
Year 10	*Ceanothus parvifolius*	shrub	14.9	0.050
Year 20	*Ceanothus cordulatus*	shrub	23.5	0.026
	Symphoricarpos mollis	shrub	20.3	0.008
	Ribes roezlii	shrub	20.1	0.050
	Festuca sp.	graminoid	16.7	0.018
	Bromus orcuttianus	graminoid	16.7	0.017
	Phacelia ramosissima	perennial forb	16.7	0.017
	Ribes nevadense	shrub	15.9	0.018
	Lupinus polyphyllus	perennial forb	15.5	0.015
	Abies magnifica	tree	14.9	0.050
	Ribes viscosissimum	shrub	14.5	0.023

Note: All species were included, but only those with significant ($P \leq 0.05$) indicator values (IV_{max}) are shown. Dashes indicate the absence of species with significant indicator values.

interaction (Fig. 5D). At year 20, cover in first-entry plots was three times that of controls (marginally significant difference, post-hoc comparison of means).

Trends for shrubs mirrored those of the understory as a whole (Fig. 5E). Cover showed a significant treatment × time interaction, with an order-of-magnitude increase in first-entry plots, but not in second-entry or control plots. Cover of understory trees showed a marginally significant treatment × time interaction, increasing in burned, but not in control plots (Fig. 5F).

Relationships with severity of burning

Species richness.—Species richness and burn severity were significantly correlated (positive effect) in ~50% of regression models (Table 3). Relationships varied among growth forms, however. Severity (typically a single variable) was a significant predictor for the full community and for annual forbs, but not for perennial forbs. No measure of severity was consistently selected as a predictor, although many were correlated, particularly in second-entry burns (data not shown). Pre-treatment richness was a significant predictor of post-treatment richness in <20% of models.

Severity explained greater variation in total (community) richness in second- than in first-entry burns, but less so for individual growth forms (Table 3). Time since burning did not have a large or consistent effect on this relationship. For most growth forms, significant correlations occurred early and late (years 2 and 10), although predictors and strengths of models changed.

Plant cover.—Plant cover and burn severity were significantly correlated (positive effect) in ~50% of regression models (Table 4). As with richness models, relationships differed among growth forms. Severity (typically a single variable) was significant in all models of total cover and in three of four models for annual forbs, but in none for graminoids (Table 4). In contrast to richness, pre-treatment cover was a frequent predictor of post-treatment cover (50% of mod-

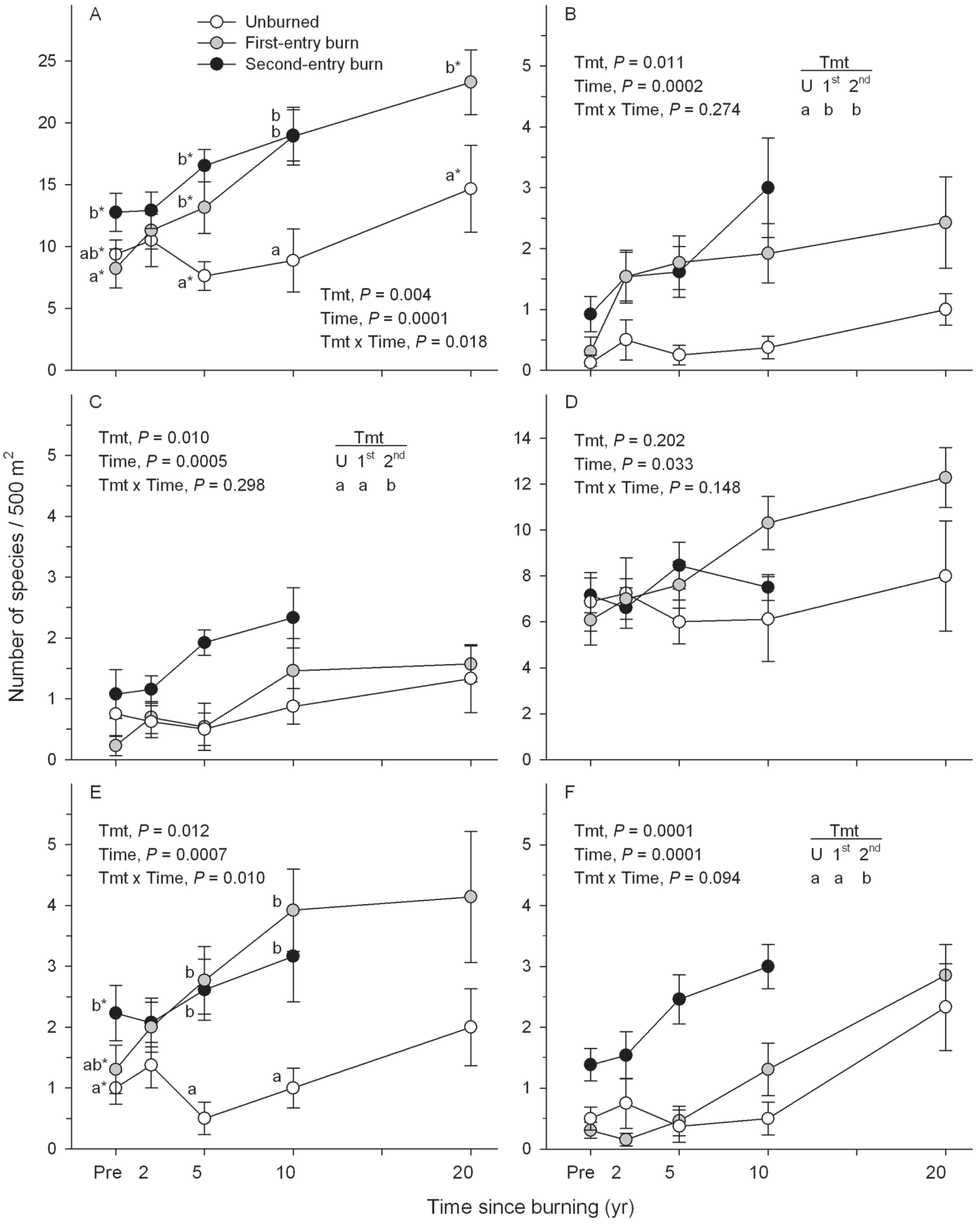

Fig. 4. Trends in species richness for (A) all species, (B) annual/biennial forbs, (C) graminoids, (D) perennial forbs, (E) shrubs, and (F) trees. Values are means ±1 SE. Where there are significant time × treatment interactions, different letters indicate significant differences ($P \leq 0.05$) among treatments within years; asterisks denote marginal significance ($0.05 < P \leq 0.10$). Elsewhere, significant main effects are coded under Tmt.

els).

As with richness models, severity tended to explain greater variation in total cover in second-entry burns, although patterns varied among growth forms (Table 4). Pre-treatment cover was more often a predictor of post-treatment re-

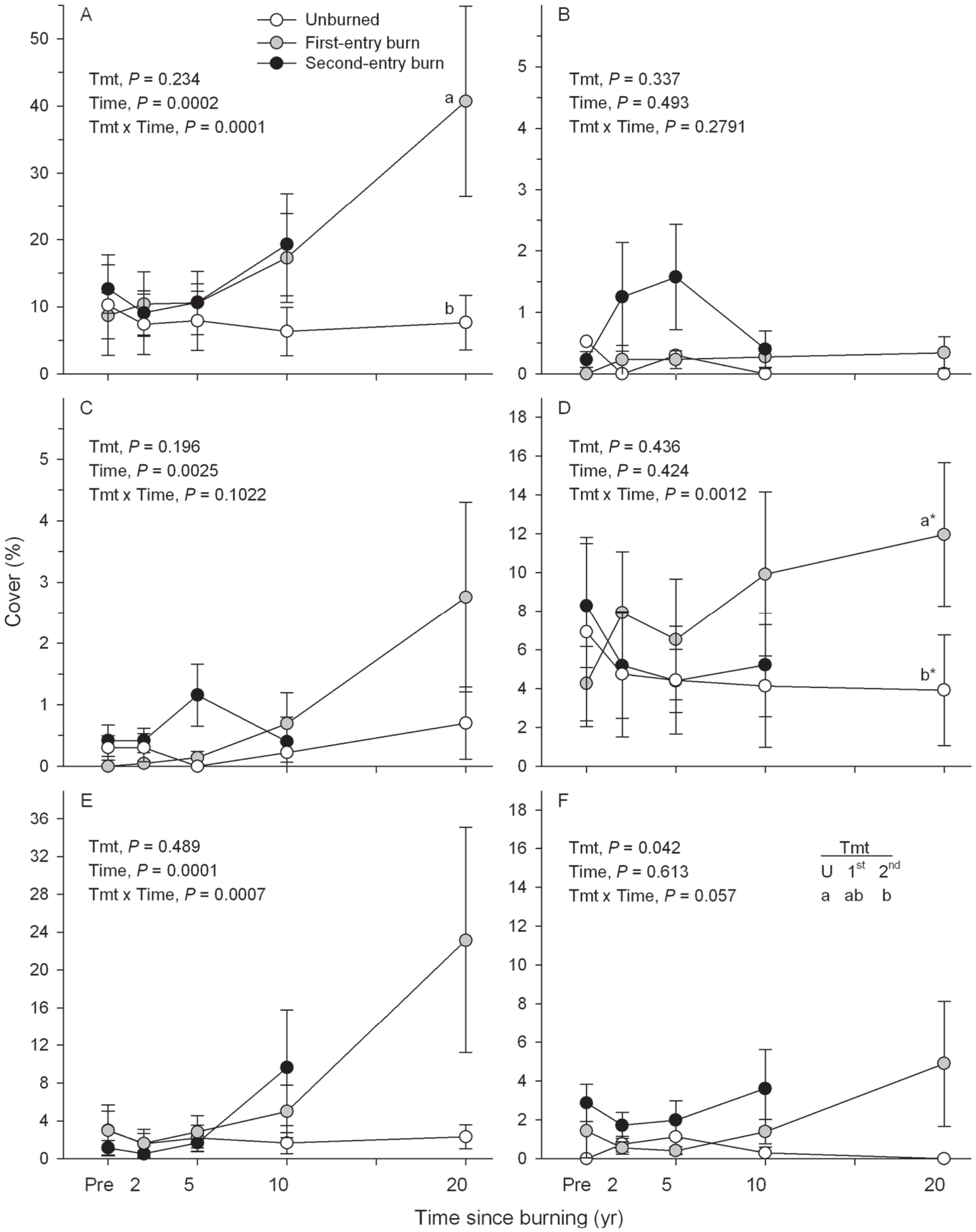

Fig. 5. Trends in cover for (A) all species, (B) annual/biennial forbs, (C) graminoids, (D) perennial forbs, (E) shrubs, and (F) trees. See Fig. 4 for details.

sponse in second-entry burns. Time since burning did not have a consistent effect on severity-cover relationships.

Relationships with heterogeneity of burning

In contrast to severity, burn heterogeneity appeared to have little effect on species richness. Heterogeneity was a significant predictor in only three of 24 regression models and in only one of

Table 3. Stepwise multiple regression models relating species richness to measures of burn severity (severity predictors) and pre-treatment richness for plots representing first- and second-entry burns 2 and 10 yr after treatment.

	Full model			
Model	R^2	P	Severity predictors (coefficient, P)	Pre-treatment richness (coefficient, P)
All species				
First entry, yr 2	0.33	0.013	live tree density (−0.574)	
First entry, yr 10	—	—		
Second entry, yr 2	0.69	<0.001	char height (−1.146, $P < 0.001$); scorch height (1.506, $P < 0.001$)	
Second entry, yr 10	0.83	0.011	char height (0.912)	
Annual/biennial forbs				
First entry, yr 2	0.74	<0.001	dead tree BA (0.462, $P = 0.007$)	(0.565, $P = 0.002$)
First entry, yr 10	0.39	0.004	litter depth (−0.623)	
Second entry, yr 2	0.60	<0.001	char height (−0.683, $P = 0.028$); scorch height (1.254, $P < 0.001$)	
Second entry, yr 10	0.98	<0.001	litter depth (−0.989)	
Graminoids				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	0.87	0.006	char height (0.349)	
Perennial forbs				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	0.72	0.032		(0.850)
Shrubs				
First entry, yr 2	0.62	<0.001	scorch height (0.667, $P = 0.001$)	(0.349, $P = 0.039$)
First entry, yr 10	0.40	0.006	scorch height (0.637)	
Second entry, yr 2	0.61	<0.001		(0.780)
Second entry, yr 10	—	—		
Trees				
First entry, yr 2	—	—		
First entry, yr 10	0.24	0.032	% crown scorch (0.494)	
Second entry, yr 2	0.48	0.001	substrate burn severity (−0.692)	
Second entry, yr 10	0.66	0.050	dead tree BA (0.811)	

Notes: Only significant predictors are shown with standardized coefficients and P values. See *Methods: Data manipulation* for full set of predictors and measurement units. Sample sizes: first entry ($n = 19$); second entry, year 2 ($n = 20$) and year 10 ($n = 6$). Dashes indicate non-significant models.

these was the correlation with richness positive (Table 5). Similar to severity models, pre-treatment richness was not a frequent predictor of post-treatment richness (significant in only three models; Table 5).

Discussion

The success of restoration practices in fire-dependent forests of the western U.S. is commonly viewed from the perspective of stand structure and surface fuels (e.g., North et al. 2007, Harrod et al. 2009, Schwilk et al. 2009). The consequences for other forest attributes, including understory composition and diversity, have been considered (e.g., Knapp et al. 2007, Wayman and North 2007), but only in the short-term (but see Harvey et al. 1980) and in response to initial, but not repeated use of fire. Long-term (multi-decadal) studies from Sequoia and Kings Canyon National Parks provide strong evidence that repeated burning in forests from which fire has been excluded for nearly a century can be used to achieve structural and fuel-reduction objectives and, at the same time, enhance understory diversity and abundance. The absence of historical data on the structure and composition of forest understories poses a challenge in that reference or target conditions cannot be identified. Photographic and written accounts suggest considerably fewer, but larger trees, and lower accumulations of surface fuels (LeConte 1930, Muir 1911, Gruell 2001). In addition, reconstructions of fire history confirm that fire was more frequent in the past (Kilgore and Taylor 1979, Swetnam 1993). Thus, it is likely that understo-

Table 4. Stepwise multiple regression models relating cover to measures of burn severity (severity predictors) and pre-treatment cover for plots representing first- and second-entry burns 2 and 10 yr after treatment.

	Full model			
Model	R^2	P	Severity predictors (coefficient, P)	Pre-treatment cover (coefficient, P)
All species				
First entry, yr 2	0.72	<0.001	dead tree BA (0.426, $P = 0.007$)	(0.790, $P < 0.001$)
First entry, yr 10	0.81	<0.001	% crown scorch (0.655, $P < 0.001$)	(0.680, $P < 0.001$)
Second entry, yr 2	0.78	<0.001	live tree BA (−0.476, $P = 0.001$)	(0.777, $P < 0.001$)
Second entry, yr 10	0.99	0.002	scorch height (0.512, $P = 0.006$)	(1.011, $P = 0.001$)
Annual/biennial forbs				
First entry, yr 2	—	—		
First entry, yr 10	0.64	<0.001	litter depth (−0.359, $P = 0.031$); scorch height (0.672, $P < 0.001$)	
Second entry, yr 2	0.64	<0.001	litter depth (−0.377, $P = 0.024$)	(0.748, $P < 0.001$)
Second entry, yr 10	0.77	0.022	substrate burn severity (−0.876)	
Graminoids				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	0.39	0.003		(0.627)
Second entry, yr 10	—	—		
Perennial forbs				
First entry, yr 2	0.71	<0.001	dead tree BA (0.310, $P = 0.041$)	(0.810, $P < 0.001$)
First entry, yr 10	0.68	<0.001		(0.822)
Second entry, yr 2	—	—		
Second entry, yr 10	0.94	0.001		(0.968)
Shrubs				
First entry, yr 2	0.53	0.002	litter depth (−0.584, $P = 0.004$)	(0.427, $P = 0.024$)
First entry, yr 10	0.57	<0.001	% crown scorch (0.756)	
Second entry, yr 2	0.88	<0.001		(0.939)
Second entry, yr 10	0.71	0.035	% crown scorch (0.843)	
Trees				
First entry, yr 2	0.60	0.001	dead tree BA (0.812, $P < 0.001$); substrate burn severity (0.408, $P = 0.027$)	
First entry, yr 10	0.51	<0.001	% crown scorch (0.716)	
Second entry, yr 2	0.63	<0.001		(0.796)
Second entry, yr 10	—	—		

Note: See Table 3 for details.

ries evolved within the context of a more open, patchier overstory; lighter fuel loads; and more frequent, lower intensity fire (Falk 1990, Moore et al. 1999)—conditions and processes that are likely to support a greater diversity and abundance of plant species. By extension, creation of comparable conditions through prescribed burning should promote greater plant diversity and abundance provided that fire behavior is similar and seed availability or dispersal are not limiting.

Changes in forest structure and fuels

Initial application of fire had large effects on forest structure, surface fuels, and ground conditions, consistent with restoration objectives. These included significant mortality of subcanopy trees, reduced depth and mass of ground fuels, and exposure of mineral soil—effects that have been documented in previous studies (Knapp et al. 2005, Vaillant et al. 2009). Direct effects on structure and fuels are also likely to have increased light availability and soil moisture, and to have stimulated at least a transient increase in nitrogen availability (Wan et al. 2001, Keeley et al. 2003, North et al. 2005, Wayman and North 2007, Peterson and Reich 2008, Ma et al. 2010). Burning also set in motion additional changes as fire-killed *A. concolor* gradually fell to the forest floor leading to patchy accumulations of woody fuels. Any consequences of this gradual redistribution of fuels (increases in light or mulching of the forest floor), are likely to be missed in short-term studies of vegetation response as it may take a decade or more for snags to fall (Stephens and Moghaddas 2005). By contrast, effects of second-entry burns were subtle, tempered by the initial effects of fire. Few additional trees were killed and consumption of litter and duff was small, as were subsequent changes in forest structure.

Table 5. Stepwise multiple regression models relating species richness to measures of burn heterogeneity (heterogeneity predictors) and pre-treatment richness for plots representing first- and second-entry burns 2 and 10 yr after treatment.

Model	Full model		Heterogeneity predictors (coefficient, P)	Pre-treatment richness (coefficient, P)
	R^2	P		
All species				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	—	—		
Annual/biennial forbs				
First entry, yr 2	—	—		
First entry, yr 10	0.29	0.017	SD litter depth (−0.540)	
Second entry, yr 2	0.29	0.014		(0.540)
Second entry, yr 10	—	—		
Graminoids				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	—	—		
Perennial forbs				
First entry, yr 2	0.22	0.042	SD change in duff depth (0.471)	
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	0.97	0.006	SD duff depth (−0.498, P = 0.017)	(0.814, P = 0.004)
Shrubs				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	0.61	<0.001		(0.780)
Second entry, yr 10	—	—		
Trees				
First entry, yr 2	—	—		
First entry, yr 10	—	—		
Second entry, yr 2	—	—		
Second entry, yr 10	—	—		

Note: See Table 3 for details.

Long-term effects on vegetation

Prescribed burning promoted significant increases in species richness and cover in forests characterized by a depauperate understory. However, rates of increase were very gradual for most plant groups. As a result, responses to treatment were not apparent for as many as 5–20 yr after burning, underscoring the importance of long-term measurements for capturing effects that may play out over decades (Moore et al. 2006). A diversity of processes may contribute to the protracted nature of response. The gradual development and sparse distributions of most species (90% of taxa were present in <5% of temporal samples) point to propagule availability and seed dispersal as critical determinants of post-fire patterns (Keeley et al. 2003). As in many coniferous forests, few understory species maintain persistent seed banks (Archibold 1989, Halpern et al. 1999, Keeley et al. 2003). Thus post-fire development is dependent either on vegetative recovery or dispersal from source populations. Given the depauperate nature of these pre-treatment understories, dispersal appears critical.

The dynamics of annuals and graminoids suggest that both groups were seed limited. Both typically benefit from soil disturbance (Laughlin et al. 2004, Moore et al. 2006) and increases in understory light (Naumburg and DeWald 1999). Yet establishment was sparse following first entry despite significant consumption of surface fuels and exposure of mineral soil (>60% cover). Establishment was greater after second entry, at considerably lower levels of disturbance (<30% cover of mineral soil). Populations that established after initial entry (or in adjacent treated areas) may have provided local sources of seed (Halpern 1989, Turner et al. 1998). These positive feedbacks suggest that repeated burning could enhance the distribution and abundance of species that have declined in the absence of fire

(Keeley et al. 2003).

Temporal lags in the development of other growth forms may also be shaped by dispersal limitations in time and space. Shrubs were sparse prior to treatment and post-burning trends suggest gradual colonization of species (increasing richness) and growth (cover). Two processes may underlie these trends. For taxa with large fruits (e.g., *Ribes, Rubus,* and *Sambucus*), seed dispersal is facilitated by frugivorous birds and small mammals (e.g., Quick 1954, Crane et al. 1983). Gradual accumulation of these species over time may reflect the stochastic nature of animal-mediated dispersal or changes in habitat suitability that increase the likelihood of dispersal (McDonnell and Stiles 1983). Trends in cover, however, were driven by the dynamics of the dominant seed-banking shrub, *Ceanothus cordulatus*. Fire stimulates germination via heating of the soil (Gratkowski 1962) and emergence occurs soon after burning (Orme and Leege 1976). However, seeds have limited dispersal (Conard et al. 1985) and presence in the post-fire community is often determined by historical distributions (e.g., Halpern 1989). In this study, *C. cordulatus* emerged in ~50% of plots restricting shrub-layer development on many sites. On the other hand, repeated burning did not have an adverse effect on shrub richness or cover: once established, most species can resprout from root crowns or rhizomes (Keeley 1987, Kauffman and Martin 1990, Keeley 1991). Long-term observations in SEKI thus confirm the potential for prescribed burning to enhance the diversity and abundance of woody species that have been reduced or locally extirpated by fire exclusion. However, they also illustrate that responses to fire can be unpredictable when the dominant species are dispersal limited.

In contrast to shrubs, burning had no apparent effect on the richness of perennial forbs, the most diverse group of understory plants. Although continuous increases in diversity following first-entry fires suggested gradual colonization, variation within controls precluded detection of a treatment effect. In contrast, burning promoted a large increase in cover, although this was highly variable and only marginally significant after 20 yr. These positive effects were subsequently erased by second-entry fires, although the post-treatment sampling period was truncated (10 vs. 20 yr following first entry).

Previous studies of dry coniferous forests illustrate significant variation in the short-term responses to fire of perennial forbs (Collins et al. 2007, Knapp et al. 2007, Wayman and North 2007, Dodson et al. 2008). This is not surprising given the variety of growth forms and reproductive strategies, and the potential for complex interactions with fire behavior and weather (Moore et al. 2006). Despite significant variation in time and space, long-term trends in SEKI suggest strong potential for fire to enhance the diversity and abundance of perennial forbs.

The results of indicator species analyses suggest that few taxa were fire obligates, although many showed an affinity for burned sites. These included shrubs in the genus *Ceanothus* whose long-lived seeds are stimulated by fire (Keeley 1987, Kauffman and Martin 1990) and *Abies concolor*, which establishes preferentially on mineral soil (Stark 1965, Kilgore 1973). Thus, for *A. concolor*, prescribed fire results in a tradeoff: burning can remove significant numbers of subcanopy trees, but simultaneously initiate a new cohort of seedlings. Similar effects of fire on the size structure and density of conifers have been observed in other systems (e.g., Schwilk et al. 2009). Other than *A. concolor*, however, few species showed strong affinity for either first- or second-entry burns. Most species present at the time of second entry persisted through, or reestablished after burning.

The potential for prescribed fire to facilitate establishment or spread of non-native species is of growing concern throughout the western U.S. (D'Antonio 2000, Griffis et al. 2001, Nelson et al. 2008) and in other in fire-dependent systems (Hobbs and Huenneke 1992). Low to moderate levels of invasion have been observed after restoration burning or combined application of thinning and prescribed fire in a diversity of forest types (Griffis et al. 2001, Dodson and Fiedler 2006, Collins et al. 2007, Knapp et al. 2007, Wayman and North 2007, Dodson et al. 2008, Nelson et al. 2008). In SEKI, however, not only were non-natives rare (two species in three plots), but there was no indication of an increase over the 20 yr of observation. This contrasts with somewhat higher rates of invasion (3.4% of the flora) observed in a broader survey of mixed-conifer forests in the park (Keeley et al. 2003).

Limited establishment of alien species may be a consequence of multiple factors: elevational constraints (Keeley et al. 2003), low densities of roads that serve as corridors (Trombulak and Frissell 2000), minimal use of mechanical equipment (vectors for transport), active eradication, and long-term suppression of fire which has limited the establishment of source populations (Keeley et al. 2003). As with native species, increasing use of fire has the potential to encourage alien establishment. Integrating active monitoring (and removal) of source populations into resource management plans seems critical for minimizing future introductions (Keeley et al. 2003, Jones et al. 2010).

Relationships with severity of burning

The regenerative strategies of species provide insights into the effects of fire severity on vegetation response (Halpern 1988, Schimmel and Granstrom 1996, Wang and Kemball 2005, Pyke et al. 2010). Greater severity can adversely affect plant cover or richness if it results in consumption or mortality of perennating structures, or in extirpation of rare or uncommon taxa that are susceptible to fire by virtue of low population densities. In contrast, greater severity can have positive effects if it enhances resource availability, creates openings for recruitment, or stimulates germination of fire-dependent species.

With any such comparison of fire effects it is critical to place "severity" in context. Prescribed burns in SEKI resulted in surface fires of low to moderate severity (as likely occurred historically), with levels of crown scorch ranging from 0 to 78%, char heights ranging from 0.3 to 8 m, and limited mortality of overstory trees. Within this context, single measures of severity (or occasionally two) explained much of the variation in community response ($R^2 \geq 0.70$ for most models of total richness and cover). It is difficult to determine why particular variables were selected in each model, but the distinctions may not be critical: measures of severity were often correlated, particularly in second-entry fires where residual fuel depth and fire intensity were strongly correlated. Higher severity fires, regardless of treatment, led to greater numbers of species and to greater cover. These effects are consistent with observations from other coniferous forests in which the benefits of burning for fire-enhanced species outweigh any detrimental effects for species that are fire-sensitive (Huisinga et al. 2005, Metlen and Fiedler 2006, Knapp et al. 2007). Even during second-entry burns—characterized by lower severity fires—there was sufficient variation to create strong and persistent gradients in community response. In fact, severity explained comparable, if not more, variation in total richness and cover than in first-entry plots. The dynamics of individual growth forms may provide insight into these broader patterns of community response.

Annual forbs showed consistently greater richness and cover at higher severities. Litter depth was a frequent predictor of performance. Deeper accumulations of litter may limit recruitment of species that preferentially establish on mineral soil (Harvey et al. 1980, Facelli and Pickett 1991, North et al. 2005). Greater fire severity can also promote greater resource availability by reducing the density of competing tree roots (North et al. 2005) and enhancing conversion of organic to mineral N (Prieto-Fernandez et al. 1993, Pietikainen and Fritze 1995). Annuals with strategies for long-distance dispersal and rapid growth have the potential to capitalize on these high-resource environments.

Shrubs also showed positive responses to severity, but only after first-entry burns. On subsequent entry, severity had limited effect on richness or cover. This contrast may reflect the importance of fire for different stages in the life history. For seed-banking taxa such as *Ceanothus*, increasing severity typically leads to greater germination (provided seeds are present in the soil; Orme and Leege 1976, Halpern 1989). However, established plants have the ability to resprout after fire, and unless intensities exceed a lethal threshold, variation in severity during subsequent burning may have little effect on survival or abundance (Huffman and Moore 2004). Methods of persistence through fire can be similar for *Ribes* and *Rubus* (Quick 1954, Kilgore 1973, Halpern 1989, McDonald 1999). Thus, in second-entry treatments, pre-treatment richness and abundance of shrubs, rather than severity, were predictors of post-burning response.

In contrast to annual forbs and shrubs, perennial forbs and graminoids showed limited response to fire severity. This may not be surprising for highly diverse groups such as perennial forbs with species that exhibit diverse regenerative strategies and responses to burning (McLean 1969, Halpern 1989, Schimmel and Granstrom 1996, Knapp et al. 2007). Many are tolerant of fire; however, others that are adapted to shade or deep accumulations of litter (e.g., *Pyrola picta*, *Chimaphila menziesii*; Harvey et al. 1980, North et al. 2005) may be more sensitive to burning (e.g., Halpern 1989) or to the higher levels of light or moisture stress (e.g., Nelson et al. 2007) that characterize the larger openings created by higher severity fire. That pre-treatment cover was a significant predictor in most models of response suggests that at least the dominant perennials are tolerant of higher severity fire and post-treatment variability is shaped by the factors that contribute to initial variation in abundance (stand structure, microclimate, and soils; North et al. 2005). In contrast, graminoids were initially uncommon and with few mechanisms for dispersal (Cheplick 1998), had limited ability to respond to variation in fire severity.

Relationships with heterogeneity of burning

It is commonly assumed that greater spatial heterogeneity of resource availability or physical environment allows for greater diversity of species with differing resource or environmental requirements (Huston 1994, Rosenzweig 1995). Depending on fuel characteristics, fire has the potential either to homogenize or to increase heterogeneity of understory resources (light, soil nutrients) and forest-floor conditions (Christensen et al. 1989, Robichaud and Miller 1999, Antos et al. 2003, Rocca 2009). Greater patchiness of woody fuels in second-entry plots was expected to yield greater variation (SD) in fire severity; however, there was little evidence of this effect. Variability in substrate burn severity, post-treatment litter depth, and litter consumption were comparable between treatments. Although duff depth varied more after second-entry burns, duff consumption varied more during first-entry, reflecting greater variation in duff depth in forests that had not burned previously. Given the lack of consistency in physical effects, it is not surprising that we failed to observe significant relationships between species richness and burn heterogeneity. In only one model (perennial forbs) was richness positively correlated with burn heterogeneity, but this was effect was short-lived, limited to year 2 in first-entry plots. Thus, in contrast to severity, burn heterogeneity appears to play a minor role in shaping patterns of plant diversity—at least for the range of severities and at the spatial scales considered in the current study. It is possible that over a greater range of severities (including higher severity patches that elicit stronger responses), or at larger spatial scales (e.g., Turner et al. 1994, Schoennagel et al. 2008), heterogeneity could yield different outcomes for diversity.

Management implications

Prescribed burning is increasingly used as a tool for restoration in forests that have evolved with fire (Stephens and Ruth 2005, Dale 2006, Vanha-Majamaa et al. 2007). On federal forestlands in the U.S., it is often used in combination with mechanical methods (thinning and mastication; Schwilk et al. 2009) to modify structure and reduce fuels to within an historical range of variation (Landres et al. 1999, Allen et al. 2002). Programs for prescribed burning in the National Parks offer unique opportunities to study effects of fire in natural ecosystems that have been minimally impacted by past management or resource extraction. For park managers, understanding the ecological consequences of fire is of paramount importance given current operational constraints (air quality regulations, fiscal limitations) and future threats (non-native species, climate change) to these systems.

Long-term studies from SEKI illustrate that prescribed fire after nearly a century of fire suppression can enhance understory diversity and cover, albeit gradually. Moreover, repeated burning, which may be critical to achieve fuel-reduction objectives (Keifer et al. 2006), does little to alter this dynamic and may enhance the abundance of some species. Fire appears to play two critical roles: stimulating germination of species that are dependent on fire, and creating resource or environmental conditions that foster establishment of fire-enhanced species. Repeated burning (at relatively low severity) appears to effect more subtle changes in environment, but provides opportunities for spread of newly established populations. The reintroduction of fire into these systems may also benefit species of concern. For example, regeneration of *Pinus lambertiana* and *Sequoiadendron giganteum* occurred almost exclusively in second-entry plots. *Pinus* is highly susceptible to white pine blister rust and to effects of fire exclusion (Kinloch and Scheuner 1990, van Mantgem et al. 2004). *Sequoiadendron* is restricted in its distribution and has specific germination requirements: higher severity fires that create canopy gaps and expose mineral soil (Harvey et al. 1980, Stephenson et al. 1991). Repeated burning appears critical for the regeneration and persistence of these tree species.

At the same time, prescribed burning may pose challenges to managing shade-tolerant tree species such as *Abies concolor*. Although a basic objective of burning is to reduce the density of subcanopy trees (National Park Service 2009, Schwilk et al. 2009), *A. concolor* is a prolific seeder and germinates preferentially on mineral soil (Stark 1965, Laacke 1990). Fire, and as demonstrated in this study, repeated burning, can initiate new cohorts of seedlings whose subsequent development runs counter to restoration. Timing of burning to be asynchronous with seed-crop production in *A. concolor* would be possible, but difficult, given the frequency of mast seed years. In areas where regeneration is high, more frequent burning may be necessary, conducted when trees are small and more susceptible to fire (Kilgore 1973).

In contrast to the responses of native species, non-natives were very uncommon. In mixed-conifer forests characterized by a sparse native community, invasion resistance is likely to be low (Levine 2000). Moreover, high severity fires provide ideal substrate and resource conditions for establishment of weedy aliens. Several factors may contribute to low rates of invasion in these forests: limited propagule pressure (Lonsdale 1999) and conduits for dispersal; environmental constraints (including a short growing season); and until recently, long-term exclusion of fire (Keeley et al. 2003). Aliens in these forests are more often found near roads, trails, and riparian areas, and where human and pack-stock use are high. Because invasions are rare in burned areas in the backcountry, limited resources for monitoring should be devoted to areas of higher use that are more likely to support source populations or to serve as conduits.

Burning not only enhances the local abundance and diversity of species, but it creates habitat variation at larger spatial scales. Long-term monitoring of fire effects on forest understory communities—rare outside of the Parks—suggests that full expression of this variation may take decades to unfold. Thus, management decisions based on short-term responses may be misguided. Given the depauperate nature of these understories and the slow pace of succession, it seems reasonable to vary fire frequency across the landscape, mimicking historical patterns of burning (Swetnam 1993). This would allow for the expression of different plant groups in time and space, and for greater variety of understory communities. Experimental plots in SEKI were reburned within 8 to 17 yr of initial treatment; unless decisions on the timing of re-entry are driven by other management concerns (e.g., fire hazard), extending the return interval in some areas could be highly beneficial.

Historically, mixed-conifer forests of the Sierra Nevada burned frequently (Kilgore and Taylor 1979, Swetnam 1993). More than a century of fire suppression has imposed dramatic changes in structure and function. A policy goal of many land management agencies is to restore the ecological integrity of these forests by reintroducing fire as a fundamental ecosystem process (Stephenson 1999, National Park Service 2009). Long-term studies in Sequoia and Kings Canyon National Parks suggest that multiple resource and ecological objectives can be met through the reintroduction of fire, even after a century of exclusion. However, viewing fire as critical to ecosystem restoration also requires that it is maintained as a frequent and spatially dynamic process on the landscape. Maintaining programs for long-term monitoring and analysis of ecological responses to fire are equally critical for managing these forests in the face of climate change and other human pressures.

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APPENDIX

Frequency of occurrence of species (% of plots) before (Pre) and 2, 5, 10, and 20 yr after treatment in unburned, first-entry, and second-entry burns.

	Unburned					First-entry burn					Second-entry burn			
Species	Pre (8)	2 (8)	5 (8)	10 (8)	20 (6)	Pre (13)	2 (13)	5 (13)	10 (13)	20 (7)	Pre (13)	2 (13)	5 (13)	10 (6)
Annual forbs														
Allophyllum gilioides									8					
Allophyllum integrifolium		13	13		33		23	8	8	43		8		17
Boraginaceae sp.							8	8			8	8		
Clarkia rhomboidea								8				8	8	17
Clarkia unguiculata														17
Clarkia sp.								8						
Claytonia perfoliata							23	31	15	14			8	17
Collinsia childii								8					8	
Collinsia heterophylla									8					
Collinsia parviflora						8	15	8		29				
Collinsia torreyi												15	8	
Collinsia sp.														17
Cordylanthus rigidus														17
Cryptantha affinis										23		15	23	50
Cryptantha intermedia												8		
Cryptantha simulans										8		8	23	50
Cryptantha sp.		13				8		8	39		15	23		
Galium aparine				38	67		15	46	23	57	8		23	17
Galium triflorum		13				15			8		8	8		
Gayophytum diffusum							31	15	8	8		8	23	50
Gayophytum eriospermum		13	13	13				8	39	14	23	39	15	
Gayophytum sp.											8			
Gilia capitata	13													
Linanthus ciliatus								8			8	15	31	50
Linanthus montanus							8		15		15	8		
Linanthus sp.						8				14				
Mentzelia dispersa												8		
Mimulus floribundus								8	8		8			
Mimulus guttatus							8		8		15			
Mimulus sp.						8	8	8						
Nemophila pulchella													8	
Nemophila sp.									8					
Phacelia eisenii							8				8			
Phacelia humilis							8							

Continued.

	Unburned					First-entry burn					Second-entry burn			
Species	Pre (8)	2 (8)	5 (8)	10 (8)	20 (6)	Pre (13)	2 (13)	5 (13)	10 (13)	20 (7)	Pre (13)	2 (13)	5 (13)	10 (6)
Perennial forbs														
Adenocaulon bicolor	50	25	25	25	33	23	15	31	39	43	8	31	31	
Agoseris elata													8	
Agoseris retrorsa												8	8	
Anaphalis margaritacea											8	8		17
Antennaria rosea										14				
Apocynum androsaemifolium	38					23			15	29		8	8	
Arabis glabra									8					17
Arabis holboellii									8				8	
Arabis repanda					33	8	8		8	57	15	31	54	17
Arabis sp.				13		8		23	8		15	8		
Asarum hartwegii							8							
Aster ascendens										14				
Aster sp.	13		13					8						
Athyrium filix-femina†											8			
Brassicaceae sp.	13	13						8				8	8	
Calyptridium umbellatum	13								15		31	15		17
Calystegia malacophylla			13	13		23	39	39	39	43	15	15	15	50
Campanula prenanthoides					17		8		8					
Castilleja applegatei						23	23	23	23	57			15	17
Castilleja lemmonii				13									8	
Castilleja sp.												8	8	
Chimaphila menziesii	13	38	63	38	17	31	8	8			31	23	39	33
Chimaphila umbellata												8	15	
Circaea alpina					17		8	8	15		8			
Cirsium andersonii							8							
Cirsium sp.	8								8			8		
Corallorrhiza maculata		25		25	17		8		8		8			17
Cynoglossum occidentale						8			15	14	8	15	15	50
Delphinium polycladon							8							
Disporum hookeri		50		38	50	8		8		14				
Draperia systyla	25	13	25	25	17	23	46	62	54	43	62	54	39	67
Dryopteris arguta†								8	8					
Epilobium angustifolium							8							
Epilobium glaberrimum									15					
Epilobium sp.							15							
Eriogonum nudum		13	13	13			15	8	31	29			8	50
Eriogonum umbellatum				13										
Eriogonum sp.	25											8		
Eriophyllum lanatum							8	8	8	14				
Erysimum capitatum							8	8	8		8		15	
Galium bolanderi					17						8	23	23	
Galium sparsiflorum	25	38	63	50	50	46	39	46	77	86	54	15	31	17
Galium trifidum		2							8					
Galium sp.	25	13	13			8		15				8		
Gnaphalium canescens									8				23	50
Goodyera oblongifolia			13	13	17									
Hackelia mundula			13		17	8	15	8	15	43	8	8	23	17
Hackelia sp.	13		13									8		
Hieracium albiflorum	50	88	38	50	50	15	46	62	85	100	69	54	62	67
Hulsea heterochroma												8	8	17
Hydrophyllum occidentale							15	8			8			
Hydrophyllaceae sp.							8							
Iris hartwegii							15	15	15					
Kelloggia galioides	13	38	38	25	33	15		15	31	43	15	8	39	
Ligusticum grayi														17
Lilium kelleyanum						8								
Lilium pardalinum							8				8			
Lotus crassifolius							15	15	23	29				
Lotus nevadensis									8					
Lotus oblongifolius			13				15	8	8	14	8			
Lotus sp.							8							
Lupinus albicaulis													8	
Lupinus covillei												8		
Lupinus fulcratus				13							15	8	15	

Continued.

	Unburned					First-entry burn					Second-entry burn			
Species	Pre (8)	2 (8)	5 (8)	10 (8)	20 (6)	Pre (13)	2 (13)	5 (13)	10 (13)	20 (7)	Pre (13)	2 (13)	5 (13)	10 (6)
Lupinus latifolius		13				8	8	8	15	14	8	8		
Lupinus polyphyllus									8	14	8		8	
Lupinus sp.	13	25	38	13	17	15	15	15			8	8		
Mimulus moschatus		13					8							
Monardella odoratissima		13	13	13					23	43				
Nama rothrockii												8		
Osmorhiza chilensis	38	50	38	50	17	23	39	39	39	71	8	8		
Osmorhiza sp.	13					8								
Pedicularis semibarbata	13	13		13		15	8		8	14	23	31	23	17
Penstemon newberryi											8		15	17
Penstemon parvulus											8	8		
Penstemon sp.	13													
Phacelia hastata													8	
Phacelia heterophylla										29			8	
Phacelia hydrophylloides				13	17	8	8	8	8	29	8	15	31	
Phacelia mutabilis	13		25	13	50		23	39	23	14	8	23	15	33
Phacelia ramosissima								8		43		15		17
Phacelia sp.	25	25				23	8	8	31	14	39		8	17
Pityopus californicus						8								
Potentilla glandulosa							8	8	8	29				
Potentilla sp.						8								
Pseudostellaria jamesiana				13			15	8		29				
Pteridium aquilinum†	25	25	25	13	17	31	23	46	39	29	8	15	15	
Pterospora andromedea	25	13			17	23			8					
Pyrola picta	63	50	63	38	67	54	31	39	62	57	77	54	69	67
Rosa bridgesii										14				
Rosa californica		13						8						
Rosa pinetorum										14				
Rosa woodsii			13	13					15					
Rosa sp.	13					8	15							
Rubus leucodermis					17									
Sarcodes sanguinea		25			17				8		8	8	15	
Senecio triangularis		13									8		8	
Silene lemmonii				25	50	15		31	31	43	31	31	31	33
Silene sp.	25	13												
Smilacina racemosa	38	38	13		50	8	23	15	15	29			8	
Smilicina stellata			25			8								
Solanum xanti							15	15	23	29				
Stachys albens							8				8		8	
Stellaria sp.							8							
Streptanthus sp.			13	13										
Viola adunca											8	8	8	
Viola glabella					17				8					
Viola lobata	13	38	25	13	33	23	23	23	23	29	8	15	15	17
Viola purpurea	13	13		13	17					14				
Viola sp.	25	13	25			8								
Wyethia mollis											8			
Unknown forb sp.			13					31	15		8			
Graminoids														
Achnatherum occidentale					17	8					8	15	31	
Achnatherum sp.	13													
Agrostis scabra									8					
Bromus carinatus			13	13			8		15					
Bromus laevipes					17						8		15	17
Bromus orcuttianus										57			15	33
Bromus suksdorfii								8	23			8		
Bromus tectorum‡									8			8	8	17
Bromus sp.						8	8	8	15		8	15	8	
Carex multicaulis		13	25	25	50		8	8	31	43	23	39	77	67
Carex rossii														17
Carex specifica							8							
Carex sp.	25	25	13	25	17	15	8	8	8		15	15		
Deschampsia elongata									8					
Elymus glaucus	25			13	17					29	8	8		17
Festuca occidentalis	13								8					

Continued.

	Unburned					First-entry burn					Second-entry burn			
Species	Pre (8)	2 (8)	5 (8)	10 (8)	20 (6)	Pre (13)	2 (13)	5 (13)	10 (13)	20 (7)	Pre (13)	2 (13)	5 (13)	10 (6)
Glyceria elata													8	
Juncus effusus							8		8					
Koeleria macrantha														17
Melica aristata	13	13			17		8			29			15	50
Poa pratensis‡								8	8					
Poa sp.		13							8					
Poaceae sp.							15	8	8		15			
Shrubs														
Acer glabrum	13				17									
Arctostaphylos patula						8		8	23	43	31	23	39	67
Arctostaphylos viscida											8			
Arctostaphylos sp.												8		
Ceanothus cordulatus						8	15	8	46	43	23	39	46	50
Ceanothus integerrimus								23	15		8	8		
Ceanothus leucodermis											15			
Ceanothus parvifolius							23	39	31		15	8	23	50
Chamaebatia foliolosa	13	13											8	17
Chrysolepis sempervirens	38	50	25	25	33	23	15	15	8	14	31	15	39	
Corylus cornuta	25	25	13	25	33	8	23	15	39	29				
Keckiella breviflora						8								
Prunus emarginata				13		15		15	15	14			15	
Ribes cereum							8				8			
Ribes montigenum											8			
Ribes nevadense					17				8	86		8	15	33
Ribes roezlii	13	13			67	23	39	54	54	100	31	5	46	67
Ribes viscosissimum					17				15	29	3	8	15	
Ribes sp.		25	13	13			15	46	23		15	23		
Rubus parviflorus	13	13			17	31	23	31	39	29				
Sambucus mexicana							8	8	23	14	15	8	8	17
Symphoricarpos mollis		13		38		15	31	15	23	43	8	23	31	
Trees														
Abies concolor	13	38	13	13	83		8	15	46	86	46	69	85	100
Abies magnifica						8	8		8	29	8	8	39	
Abies sp.													8	
Calocedrus decurrens				13	33	8		8	8	43	8	15	15	33
Cornus nuttalli	13		13	13	17			15	15			8	8	
Pinus jeffreyi										29				
Pinus lambertiana		13	13						23	57	39	31	62	83
Pinus ponderosa										14			15	17
Pinus sp.												8		
Quercus chrysolepis	13	13			17					14				
Sequoiadendron giganteum									15	8	15	15	39	67
Umbellularia californica				13										

Notes: Numbers of plots sampled are in parentheses beneath sampling years. Second-entry burns were not sampled in year 20.

† Fern species

‡ Nonnative species