Effects of Prescribed Fire on Understory Vegetation in Mixed-Conifer Forests of the Southern Sierra Nevada, California

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Abstract

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Nearly a century of fire suppression has changed fundamental aspects of the structure and functioning of many fire-adapted forest ecosystems. Many studies of these forests focus on the restoration of overstory structure and forest-floor fuels through reintroduction of fire or by mechanical means, without considering other important ecosystem attributes. In this study, I use 20 years of data from permanent plots in mixed-conifer forests of Sequoia and Kings Canyon National Parks, California, to explore changes in understory plant diversity and structure following reintroduction and repeated use of prescribed fire. Data on overstory structure, fuel loading, fire severity and heterogeneity, and the richness and abundance of plant growth forms were collected on 51 permanent plots for as many as 20 yr after treatment. Nonmetric multidimensional scaling showed distinct compositional changes over time in first- and second-entry burns despite considerable within-treatment variation. Ten years after fire, burned plots supported more than twice as many species as controls, with first-entry plots showing a nearly threefold increase in richness by year 20. Nonnative species occurred in only three plots at low abundance. Shrubs showed greater increases in richness in burned than in unburned plots, with burned plots supporting four to five times as many species as controls 5-10 yr after burning. Total understory cover increased significantly in first-entry plots, but exceeded that of the controls only after 20 yr; cover was dominated by perennial forbs and shrubs, but was highly variable among plots. In contrast, in second-entry burns, increases in plant cover were not significant (although post-treatment sampling extended to only 10 yr). Higher severity fires, regardless of treatment, led to greater numbers of species and to greater plant cover. Species richness was negatively correlated with burn heterogeneity in first-entry burns, but positively correlated with heterogeneity in second-entry burns. Long-term observations, which are rare in similar natural ecosystems, suggest that reintroduction of fire can gradually enhance the diversity and abundance of understory species. Moreover, repeated burning, which may be necessary to achieve structural and fuel-reduction objectives, does not appear to have detrimental effects on diversity and may enhance the distribution and abundance of species that have been affected by nearly a century of fire exclusion. More than two decades of plant community data from Sequoia and Kings Canyon National Parks suggest that multiple resource and ecological objectives can be met through the reintroduction of fire. However, viewing fire as critical to ecosystem restoration also requires that fire is maintained as a frequent and spatially dynamic process on the landscape.

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INTRODUCTION

Fire plays an important role in many forest ecosystems (Payette et al. 1989, Bond and Van Wilgen 1996, 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 into systems from which it has been excluded is of critical importance to resource managers (Stephenson 1999, Bond and Archibald 2003).

Historically, frequent fire regulated the successional dynamics, fuel accumulation, and nutrient cycling of Sierran mixed-conifer forests (Kilgore 1973, Stephenson 1991). Nearly a century of fire suppression, however, has changed fundamental aspects of the structure and functioning of these and other western forests (Covington and Moore 1994, Harrod et al. 1998, van Wagtendonk and Fites-Kaufman 2006, Abella et al. 2007). Most notably, fire exclusion has led to unprecedented increases in the density of shade-tolerant conifers and surface fuels, resulting in increasing potential for large stand-replacing fire (Agee et al. 1978, Vankat and Major 1978, Arno and Brown 1991, Agee 1993, Minnich et al.1995). In response to these changes and 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 accumulations of fuels (McRae et al. 2001, North et al. 2007, Schwilk et al. 2009, Vaillant et al. 2009). To varying degrees, these approaches have been successful in achieving structural and fuel-reduction objectives (Harrod et al. 2009, Schwilk et al. 2009, Valliant et al. 2009). However, the consequences for other ecosystem attributes, e.g., understory structure and diversity, have not been critically evaluated. Instead, it is implicitly assumed that by restoring structure and reducing fuel levels, recovery of other ecosystem components and processes will follow (Sierra Nevada Ecosystem Project 1996, Stephenson 1999). Historical data providing reference conditions on understory composition and structure are lacking and thus limit testing of this assumption. Nevertheless, an understanding the broader consequences of reintroducing fire is critical as land managers seek to balance ecological values, societal needs, and the logistical and operational constraints of prescribed burning.

In this paper, I explore the long-term dynamics of forest understories following reintroduction (and repeated use) of fire into previously unmanaged, mixed-conifer forests of Sequoia and Kings Canyon National Parks (SEKI), California. These understories support more than half of California's vascular plant species, with the greatest number of endemic and rare species occurring in the southern Sierra Nevada (Shevock 1996). Initiated in the late 1960s, the fire management program in SEKI is the first in the U.S. system of National Parks. It allows for natural ignitions and increasingly employs prescribed fire to achieve diverse ecological, cultural, and societal objectives (Kilgore and Briggs 1972, Rothman 2007). Data for the current study come from a system of permanent vegetation plots established in the 1970s as part of the fire-effects monitoring program in SEKI. This National Park Service-wide program is designed to ensure that resource management goals are met, to detect unanticipated trends, and to identify future research needs.

Previous studies of forest understory responses to fuel reduction treatments have compared effects of mechanical thinning vs. burning (Collins et al. 2007, Wayman and North 2007, Dodson et al. 2008), silvicultural manipulations without fire (Battles et al. 2001), and season 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. Longer term responses can differ (Bataineh et al. 2006, Moore et al. 2006), as can responses to repeated entries (multiple burns), which may be necessary to achieve structural or fuel-reduction objectives (North et al. 2007). Long-term studies in SEKI are unprecedented, exploring understory responses over multiple decades and to repeated use of fire. Published studies of comparable nature in other natural forest ecosystems do not exist.

Fire can have both direct and indirect effects on understory plant communities. Direct effects can 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 can include changes in microclimate (e.g., light and temperature) and soil resources (moisture and nutrient) resulting from reductions in tree density or consumption of coarse woody debris or forest-floor litter and duff (Wan et al. 2001, North et al. 2005, Fites-Kaufman et al. 2006, Ma et al. 2010). The relative importance of these direct and indirect effects can be mediated by the severity, frequency, or spatial heterogeneity of burning. Moreover, plants with different growth forms, life histories (e.g., annuals/biennials, herbaceous perennials, and shrubs), and sensitivities to burning can differ in their responses to fire and to variation in its severity or frequency. Numerous strategies of plant persistence and regeneration have evolved in fire-dependent communities. These range from species that are 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 those inhibited by fire (e.g., herbs with shallow root systems whose perennating structure are consumed by fire) (McLean 1968, Gill 1980, Rowe 1983, Brown and Smith 2000, Fites-Kaufman et al. 2006).

Fire severity can have a large effect on understory response (Halpern 1988, Halpern and Spies 1995, Schimmel and Granstrom 1996). At low severity, plant mortality is low, but fire-dependent species (e.g., seed-banking shrubs) 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 is high, but fire-dependent or fire-enhanced taxa are more likely to establish (Keeley 1987, Halpern 1988, Wang and Kemball 2005, Kerns et al. 2006). Effects on richness, abundance, and composition should be greater. Spatial variation (or heterogeneity) in burn severity can also affect understory response (Rocca 2009). Greater spatial variability in burn severity should produce greater heterogeneity of microclimates (gaps of varying size/openness) (Ma et al. 2010), substrates (mineral soil vs. duff) (Robichaud and Miller 1999), and soil nutrient availabilities, at least in the short term (e.g., Antos et al. 2003). These, in turn, should facilitate greater diversity of plant functional groups, comprised of species with differing environmental requirements and sensitivities to fire.

Many factors may contribute to variation in burn severity or heterogeneity. These include the amount, type, and spatial continuity of fuels; season of burning; and weather conditions at the time of ignition (Whelan 1995, Agee 2003). For example, fuel characteristics can differ markedly in forests that have, or have not, experienced recent fire. In mixed-conifer forests of the Sierra, long-term suppression of fire has allowed uncharacteristically high levels of surface fuels to accumulate. As a result, “first-entry” fires can burn at higher severity (Knapp et al. 2007). Fuel continuity also tends to be greater, resulting in greater homogeneity of burn severity (Miller and Urban 2000, Knapp and Keeley 2006). In contrast, in stands previously treated with fire, fuel loads tend to be lower, but patchier, reflecting the accumulation of branches and boles of small trees killed during initial entry (Skinner 2005, Stephens and Moghaddas 2005, Keifer et al. 2006, Schwilk et al. 2009). As a consequence, understory responses to prescribed fire may depend on how recently an area has burned (Bowles et al. 2007, Peterson and Reich 2008).

Plant composition and structure at the time of burning may also be important. 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 given the local availability of seed or negatively depending on their regenerative traits (ability to resprout) or whether sufficient time has passed for soil seed banks to have been replenished (Keeley and Fotheringham 2000).

In this study, I use two decades of data from permanent experimental plots in mixed-conifer forests of SEKI to explore the nature of plant community responses to prescribed fire, including repeated burning, and to variation in the severity and heterogeneity of fire. I address the following questions: (1) Does reintroducing fire to mixed-conifer forests affect the composition, diversity, and abundance of understory plants? (2) How does community composition and the diversity or abundance of major growth forms (annual herbs, graminoids, perennial herbs, shrubs, and understory trees) change with time following burning? (3) Do these responses differ after first- and second-entry burns? (4) How do fire severity and heterogeneity affect patterns of richness and abundance? Do relationships with severity and heterogeneity 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 mountains in Sequoia and Kings Canyon National Parks, California, USA (SEKI) (Fig. 1). Climate is characterized by cold, wet winters and warm, dry summers. Average minimum air temperatures range from -6.7°C in February to 11.8°C in August; average maxima range from 3.4°C in December to 27.4°C in 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 consisting of *Abies concolor* (white fir), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (ponderosa pine), *Calocedrus decurrens* (incense cedar), *Pinus jeffreyi* (Jeffrey pine), and *Quercus kellogii* (black oak). Additional plots occur in groves of giant sequoia (*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).

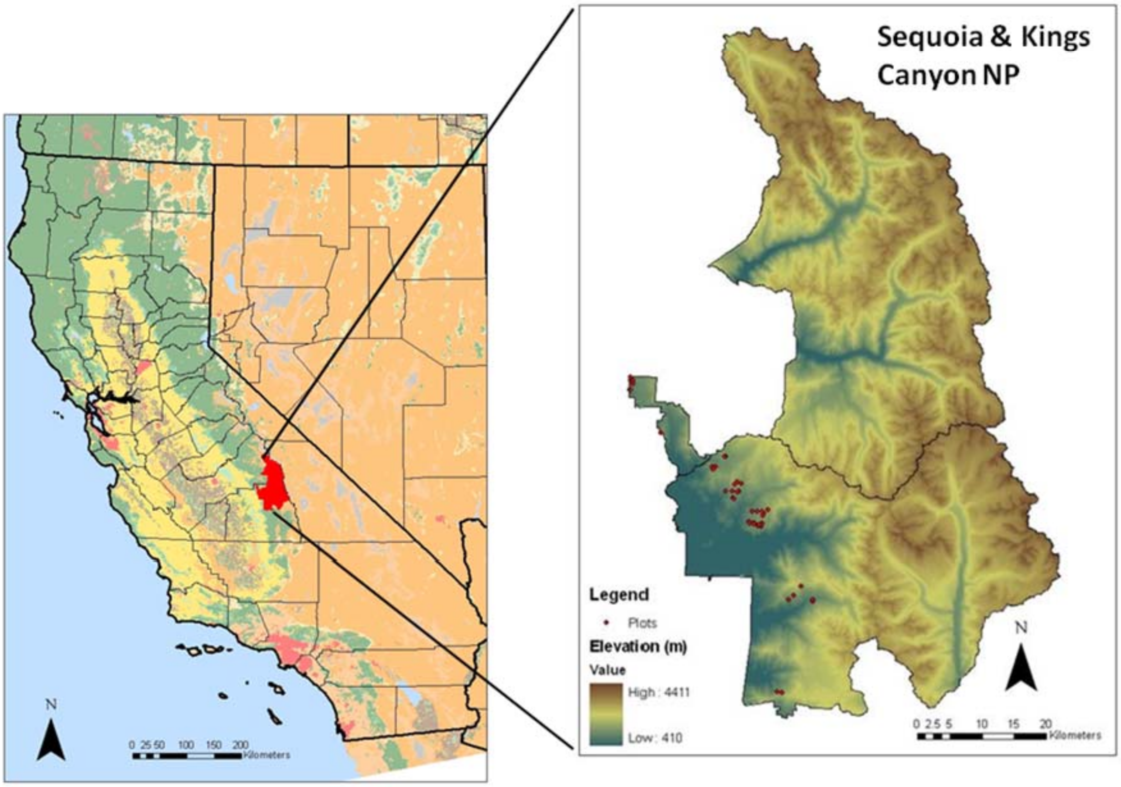

Fig. 1. Location of Sequoia and Kings Canyon National Parks.

Data collection

I used data from 51 fire-effects monitoring plots (0.1 ha, 20 x 50 m) established prior to treatment (burned or control). Plot locations were determined using a stratified randomized design. All areas scheduled to be burned were stratified by vegetation type (Sequoia and Kings Canyon National Parks 1998). Within each type, sample points were randomly placed within burn units using ESRI GIS software. Sample points were then located in the field. From each sample point, a random azimuth and distance were used to establish plot center and a random azimuth was used to define the 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 average time between first- and second-entry burns was 13 yr with a 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) (Figs. 2 and 3). Control plots were established in a manner similar to burned plots, in adjacent unburned areas or in 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 NPS 2003). Data used in this study included cover and richness of understory plants, loading of fine and coarse fuels, density and basal area of live and dead overstory trees ($\geq$1.37 m diameter at breast height, dbh), and measures of burn severity. For each plot, cover of bare ground and 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 x 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).

Fig. 2. Examples of first-entry burns.

Fig. 3. Examples of second-entry burns.

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. At each sampling date, all live and dead overstory trees in each 0.1 ha plot were tallied and measured for diameter. Burn severity of organic substrates (litter, duff, and woody debris) was assessed within 3 mo of treatment along each fuel transect (ten 2 x 2 dm quadrats at ~1.5 m spacing). Each quadrat was rated by severity class, with scores ranging from heavily burned (1) to unburned (5). In addition, 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 on the following schedule: 0-2 yr before burning; immediately after burning (for severity and heterogeneity); and 2, 5, 10, and 20 yr after burning. If a plot was burned a second time (i.e., second-entry burn) the sampling schedule was reset. For this analysis, however, first- and second-entry plots were distinct; only the second set of temporal samples was included for the latter. Controls were sampled on the same schedule as burned plots.

Data manipulation

Prior to analyses, all species were assigned to one of five plant groups based on growth form and longevity (henceforth, growth form): annual/biennial 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; see *Methods: Data collection*). Total and growth form cover were computed as the sums of individual species within each group.

For each plot, I calculated various measures of burn severity and heterogeneity that served as potential predictors of vegetation response to burning (see *Methods: Statistical analyses*, below). For severity these included: substrate burn severity class (range of 1-5; mean of 40 quadrats); post-burn duff and litter depth (cm; means of 40 points used to compute fine fuel load); 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 coefficient of variation (CV) of substrate burn severity, CV of post-burn duff and litter depth, and CV of duff and litter consumption (i.e., CV of the change in depth). For litter and duff, I considered both consumption and post-treatment depth to account for initial variation in depth and the potential for plants to show different responses 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 units they were typically >100 m apart and were often ignited on different days. In total, 34 plots were used in analyses of treatment effects on species composition, richness, and cover, and how these changed with time (questions 1-3). Sample size differed among treatments and declined with time (Table 1). Rather than limit analyses to the smaller set of plots sampled continuously through time, I retained plots with shorter sampling histories (established more recently or reburned after <20 yr) to increase replication of early years (years 2-10).

TABLE 1. Numbers of permanent plots by treatment and time since burning used in NMS and PERMANOVA tests.

	Time since burning (yr)				
Treatment	Pre	2	5	10	20
Unburned	8	8	8	8	6
First-entry burn	13	13	13	13	7
Second-entry burn	13	13	13	6	0

Prior to analyzing vegetation responses, I 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. For severity and heterogeneity, separate tests were run for each of the 17 variables (see *Methods: Data manipulation*).

I used non-metric multidimensional scaling (NMS; Kruskal 1964) to assess the effects of treatment and time since burning on species composition. Uncommon species (present in <5% of plot x 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 temporal samples (plot x time combinations) to facilitate inclusion of 41 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). All plot x time combinations were included in the ordination, but for visual clarity, I display treatment centroids (means ±1 SE) through time.

Following NMS, I used permutation-based multivariate analysis of variance

(PERMANOVA; Anderson 2001) to test for differences in species composition among treatments and sampling dates, and their interaction. PERMANOVA is a non-parametric, distance-based test that provides a pseudo-*F* statistic and associated *P*-value (Anderson 2001). The former is calculated in a manner similar to a traditional *F*-statistic, as the sum of squared distances between groups divided by the sum of the squared distances within groups. Analyses were conducted in PRIMER ver. 6 (Clarke and Gorley 2006). As with NMS, species present in <5% of the plot x time combinations were excluded, a dummy species was added to all samples, cover data were transformed (arcsine square root), 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) (Bray and Curtis 1957). Significance tests were based on 9999 permutations of the data. For significant time x 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.

I 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. ISA was implemented in PC-ORD ver. 5.0 (McCune and Mefford 2006). Three analyses were run using different sets of plots or temporal samples. The first analysis tested for associations with burning by comparing burned (first- and second-entry) vs. unburned plots. The second tested for associations with first- vs. 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 in each ISA. Species were only considered indicators if they had a significant P value and $\mathrm{IV}_{max} \geq 25$ (Dufrêne and Legendre 1997).

PERMANOVA was also used to test for differences in 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 the richness and cover of each growth form. Given the inclusion of pre-treatment data in PERMANOVA models, significant main effects were not of interest. Instead I focus on significant time x treatment interactions that imply differential responses to treatments. For significant interactions, pairwise comparisons of means were made to identify the points in time at which treatments differed.

To explore vegetation responses to burn severity or heterogeneity, and how these changed over time and with repeated entries (question 4), I developed a series of 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) (see *Methods: Data manipulation*). In addition to these burn characteristics, 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) to explore whether relationships with severity or heterogeneity differed with repeated entry or with time since burning. 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: $n = 19$ for first-entry burns (both years) and $n = 20$ (year 2) and $n = 6$ (year 10) for second-entry burns. Cover data were arcsine square root transformed prior to analysis. Predictors were retained in the models at $P < 0.05$ and excluded at $P > 0.1$ (Neter et al. 1996). Regressions were run using SPSS ver. 12.0 (SPSS 2003).

RESULTS

Overstory structure

As intended, prescribed burning had a significant effect on overstory structure. Density of live trees (primarily *Abies concolor*) declined by >50% after first-entry burns, but much less so after second-entry burns (Fig. 4a; Table 2). Subsequent changes in density were small in both treatments. Significant mortality of *A. concolor* during first-entry burns produced more than a threefold increase in density of dead trees (Fig. 4c; Table 2) although most of these stems fell by year 10. In contrast, second-entry burns resulted in minimal mortality (Fig. 4c).

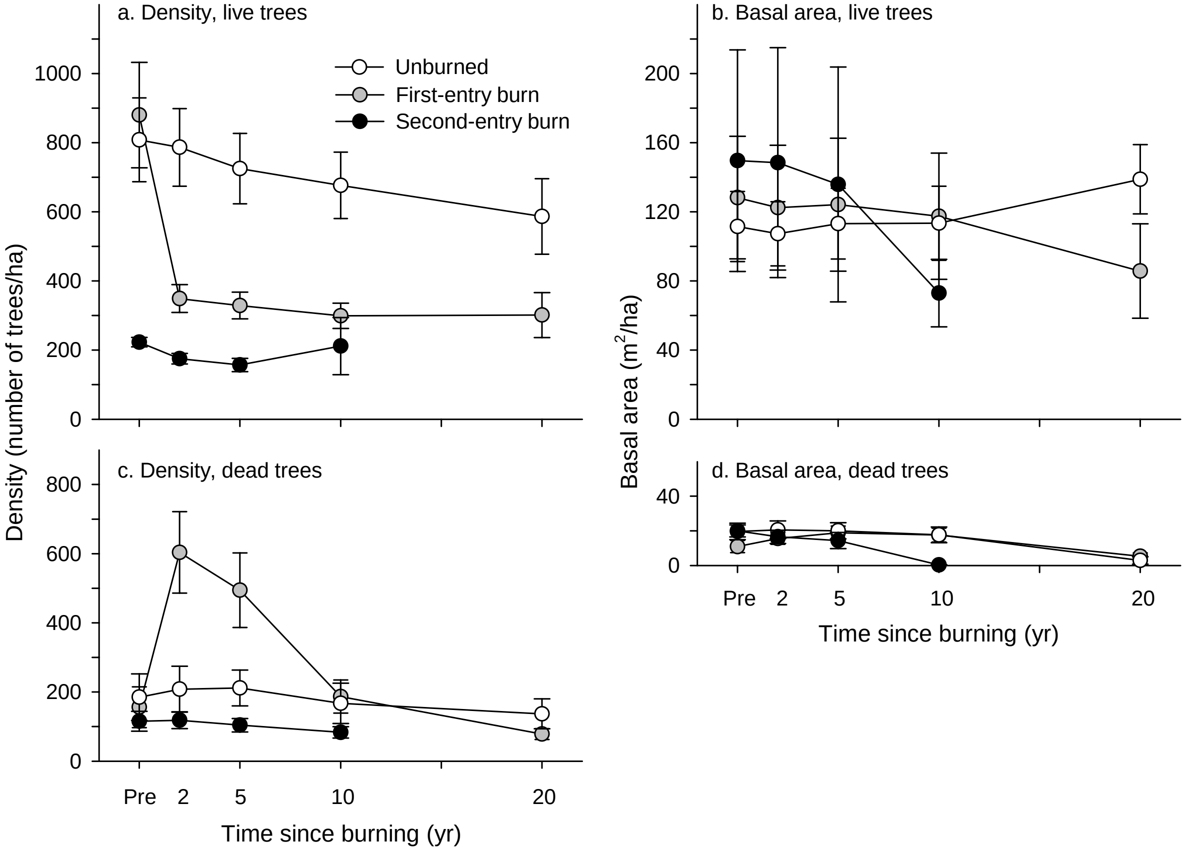

Fig. 4. Trends in density and basal area of live and dead overstory trees (≥1.37 m DBH). Values are means ± 1 SE.

TABLE 2. Results of *t*-tests comparing measures of severity and heterogeneity for first- and second-entry burns. Sample sizes (n_1, n_2) vary. Significant differences are in bold.

		First entry		Second entry			
Variable	n_1, n_2	Mean	SE	Mean	SE	*t*-statistic	*P*
Measures of severity							
Substrate burn severity (1-5)*	4,13	2.6	0.5	3.8	0.2	-2.488	**0.03**
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	0.47
Scorch height (m)	11,13	2.8	1.1	3.6	1.0	-0.552	0.59
Char height (m)	12,13	1.4	0.6	1.6	0.3	-0.309	0.76
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	0.73
Dead basal area, year 2 (m^2/ha)	13,13	15.6	3.3	16.5	3.9	-0.191	0.85
Measures of heterogeneity							
CV substrate burn severity	4,13	0.40	0.02	0.37	0.04	0.465	0.65
CV duff depth	13,13	1.70	0.39	1.43	0.42	0.474	0.64
CV litter depth	13,13	1.70	0.20	1.30	0.30	1.113	0.28
CV change in duff depth	13,13	1.55	0.54	1.19	1.73	0.202	0.84
CV change in litter depth	13,13	0.53	0.41	0.21	5.80	0.056	0.96

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

In contrast to density, basal area of live or dead trees was not affected by burning (Figs. 4b, d; Table 2). Plots within each treatment showed considerable variation in basal area (reflecting presence/absence of *Sequoiadendron giganteum*) and no detectable temporal trends. In burned treatments, apparent declines in basal area in years 10 and 20 are artifacts of a reduced sample size (6 or 7 vs. 13 initial plots; Table 1); the subset of plots sampled continuously had considerably lower basal area than those for which there were no measurements after year 5.

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 after second-entry burns (63.0% ± 10.8 vs. 27.9% ± 4.2, $t = 3.032$, $p = 0.012$). Within 2 yr, however, cover of mineral soil declined dramatically and did not differ between treatments (2.6% ± 1.2 vs. 5.6% ± 1.2, $t = -1.669$, $p = 0.108$).

Burning had a significant effect on forest-floor fuel mass and on the relative contributions of duff, litter, and wood (1-1000 hr fuels) (Fig. 5). First-entry burns reduced total mass by ~75% (Fig. 5a), with greater consumption of fine (litter and duff; Figs. 5c, d) than of coarse (woody; Fig. 5b) fuels. 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 considerably lower than in control plots (Fig. 5a) and composed primarily of woody debris (Fig. 5b). Second-entry burns reduced total mass by ~25%, mainly through consumption of this wood.

For measures based on forest-floor substrates, burn severity was significantly greater for first- than for second-entry burns (Table 2). However, for measures based on crown scorch or scorch or char height, severity did not differ between treatments. None of the five measures of burn heterogeneity differed between first- and second-entry burns (Table 2).

Floristics

In total, 204 plant species (45 families and 112 genera) were recorded over the period of study (1986-2005). Families with the greatest diversity of taxa included Poaceae (18), Scrophulariaceae (18), Asteraceae (15), Hydrophyllaceae (14), and Rosaceae (11). Diversity varied markedly among growth forms: 34 annual/biennial forbs, 112 perennial forbs, 23 graminoids, 22 shrubs, and 14 trees. The vast majority (88%) of species were present in <5% of plots x 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).

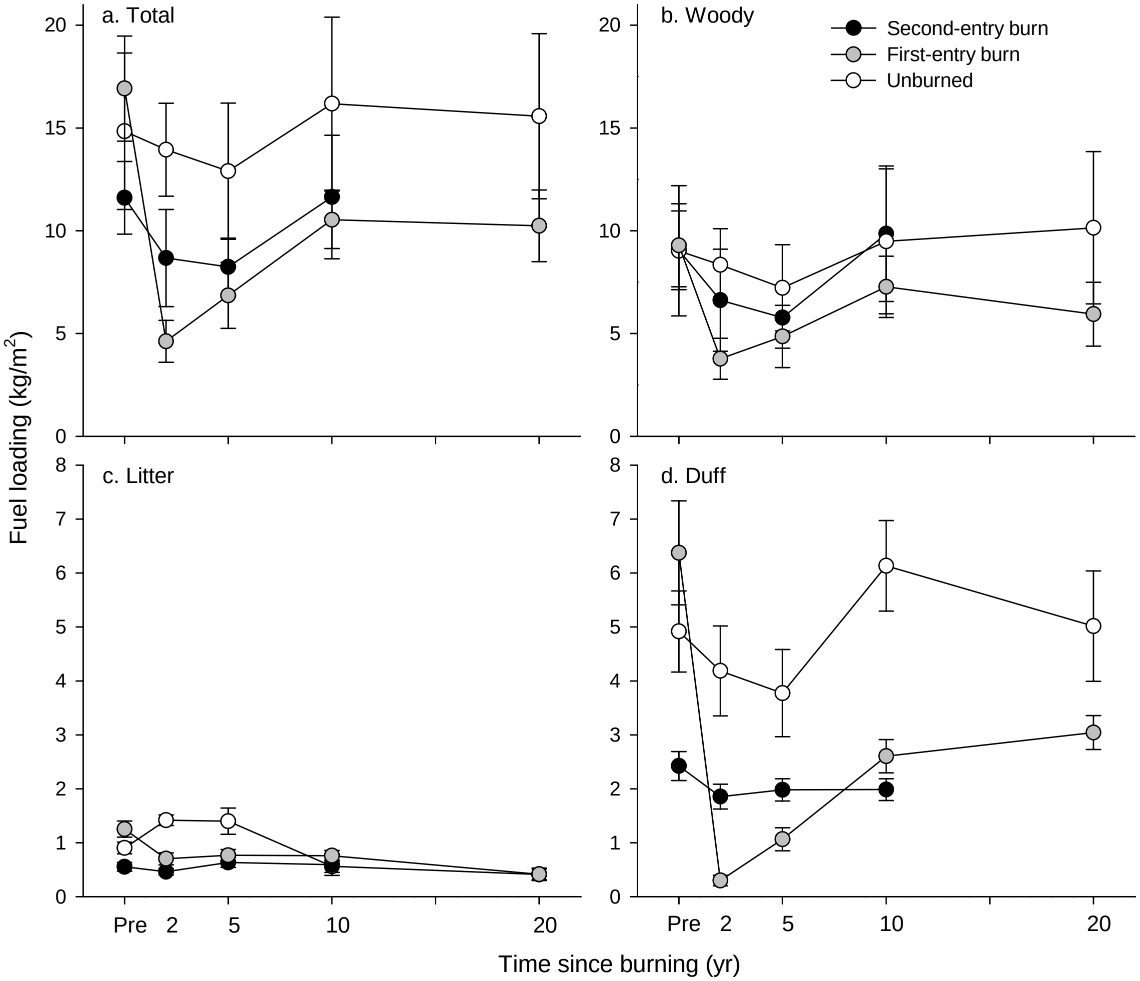

Fig. 5. Trends in (a) total fuel loading and the contributions of (b) woody fuels (1-1000 hr), (c) litter, and (d) duff. Values are means ±1 SE,

Compositional changes

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. 6a) despite considerable within-treatment variation (Fig. 6b). Sample scores generally increased with time along NMS1 and NMS2 (Fig. 6a) 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. 6c). 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 associations with NMS2.

Species composition showed a significant time x treatment interaction (PERMANOVA, $P = 0.005$), consistent with patterns evident in the NMS. Plots representing first- and second-entry 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 ($0.05 < P \leq 0.10$) differences in composition and only in year 2.

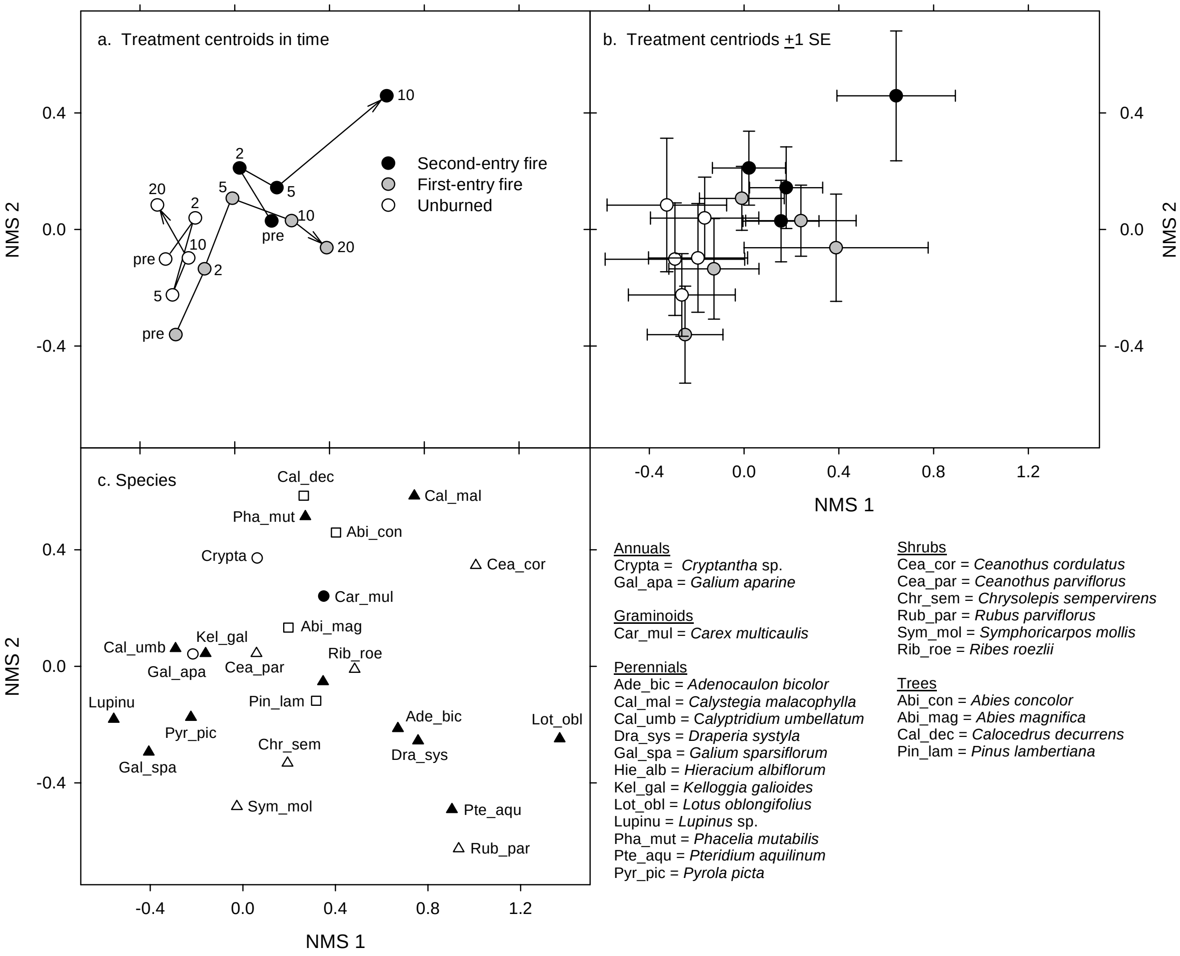

Fig. 6. Results of NMS ordination illustrating (a) trajectories of treatment centroids through time, (b) the same treatment centroids ±1 SE emphasizing compositional variation within treatments x sampling dates, and (c) scores of the 25 species present in >5% of plot x time combinations. Species are coded by growth form (annual/biennial forbs = open circles, graminoids = closed circles, perennial forbs = closed triangles, shrubs = open triangles, and trees = open squares).

Indicator species analysis

Many species showed significant associations with treatments (burned vs. unburned, first- vs. second-entry burns) or successional stages (times since burning). However, indicator values (IV_{max}) for most of these species were low (<25, Table 3). Among the strongest indicators were *Abies concolor* (associated with 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 species were largely restricted to second-entry burns (Appendix A). There were no species with high indicator values for first-entry burns or particular times since burning (Table 3).

Changes in species richness

Understories were relatively poor in species. Pre-treatment richness in previously unburned plots (controls and first-entry) averaged <10 species per plot (Fig. 7a) with perennial forbs the most diverse group (Fig. 7d). First- and second-entry burns resulted in significant increases in richness (significant treatment x time interaction), but not until year 5 (Fig. 7a). 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.

Annual/biennial forbs were uncommon before treatment averaging <1 species per plot (Fig. 7b). Lack of a significant time x treatment interaction suggests no effect of burning, despite several-fold increases in richness in burned plots. Graminoid richness was also low before treatment ($\leq$1 species per plot; Fig. 7c) and showed a non-significant time x treatment interaction. Despite the absence of significant treatment effects, 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. 7d). Although trends for first-entry burns suggest a positive response to fire (doubling of richness by year 20), small increases among controls limited detection of a treatment effect. Shrubs showed significantly greater increases in richness in burned than in unburned plots (significant treatment x time interaction; Fig. 7e). After 5-10 yr, burned plots supported four to five times as many shrub species as controls. Many of these were new to the forest understory (Appendix A).

Understory trees showed significant increases in diversity in all treatments (significant effect of time; Fig. 7f). However, differences prior to burning were maintained after treatment (significantly greater richness in second-entry than in first-entry or control plots).

TABLE 3. Results of indicator species analyses (ISA) comparing subsets of plots to assess species' affinities for burned vs. unburned sites, first- vs. second-entry burns, and time since burning. All species were included, but only those with significant ($P \leq 0.05$) indicator values (IV_{max}) are shown.

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 burns				
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

Changes in cover

Pre-treatment plant cover was low (<10-15%; Fig. 8a), comprised mostly of perennial forbs, shrubs, and understory trees (Figs. 8d-f). Total cover showed a highly significant treatment x 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 in response within treatments was high.

Cover of annuals was very low prior to treatment (<0.6%) and changed little after first-entry burns (Fig. 8b). Although trends in second-entry plots suggest a positive response to fire, variation among plots was high, limiting detection of a significant time x treatment interaction. Graminoids were also sparse before treatment (<0.5% cover; Fig. 8c). 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 (Fig. 8d), resulting in a significant treatment x time interaction (Fig. 8d). 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 community as a whole (Figs. 8e and a, respectively). Cover showed a significant treatment x time interaction, with a large order-of-magnitude increase in first-entry plots, but not in second-entry nor control plots. Cover of understory trees showed a marginally significant treatment x time interaction; post-treatment trends suggest an increase in burned, but not in control plots (Fig. 8f).

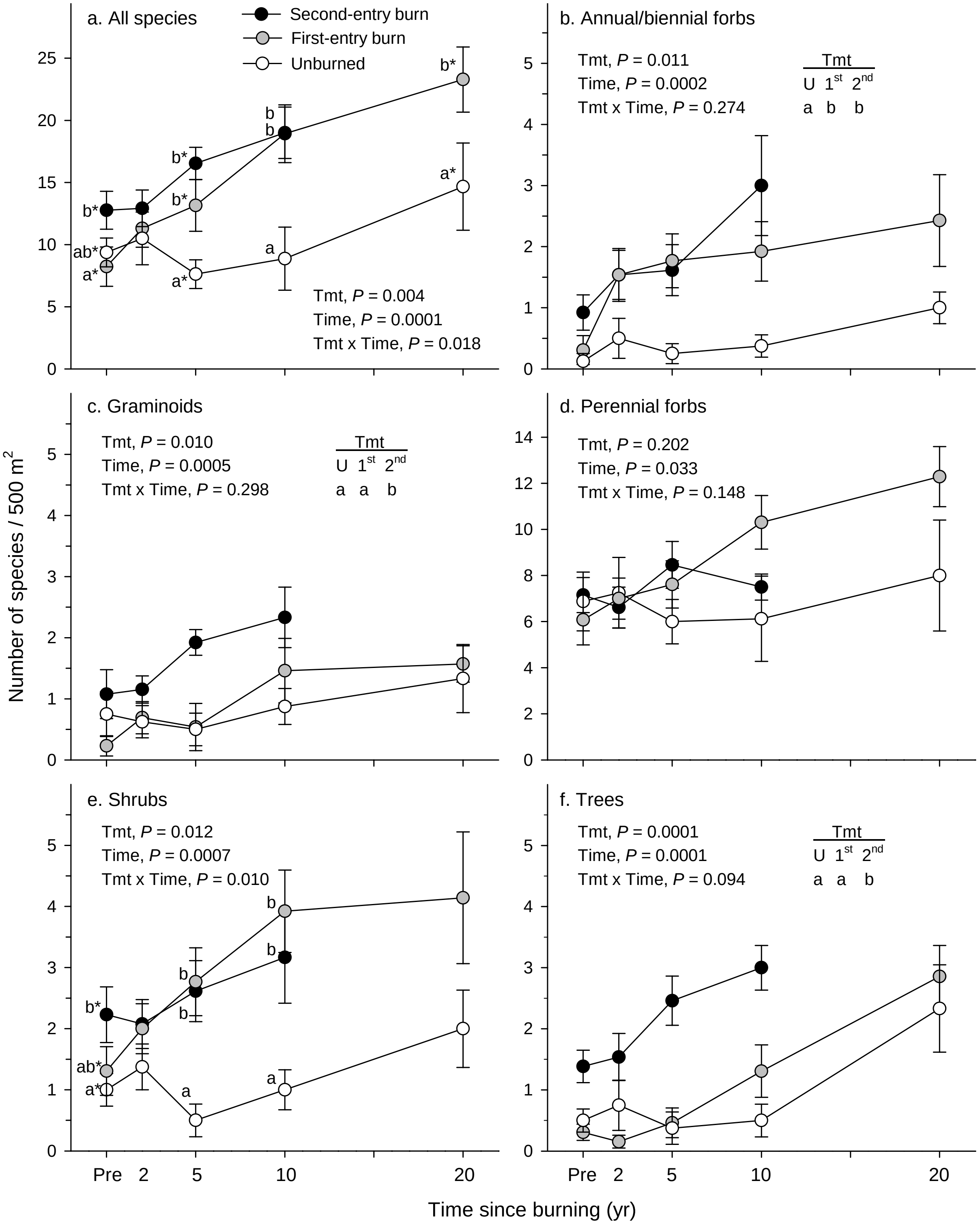

Fig. 7. Trends in species richness for all species and growth forms. Values are means ±1 SE. Where there are significant time x treatment interactions, different letters indicate significant differences ($P \leq 0.05$) among treatments within years; asterisks denote marginal significance ($0.05 < P \leq 0.10$). Elsewhere, significant main effects are coded under Tmt.

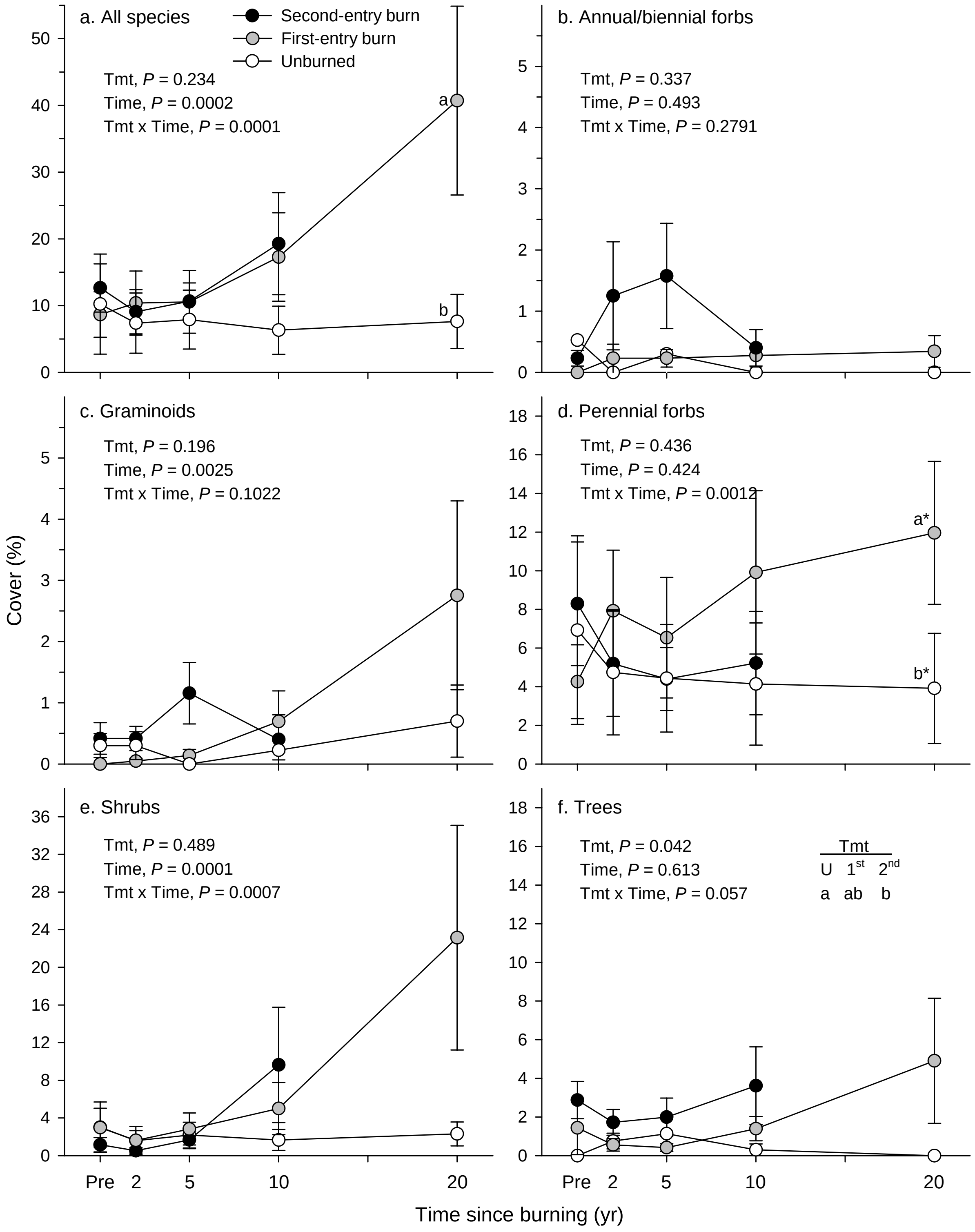

Fig. 8. Trends in cover for all species and growth forms. Values are means ±1 SE. Where there are significant time x treatment interactions, different letters indicate significant differences ($P \leq 0.05$) among treatments within years; asterisks denote marginal significance ($0.05 < P \leq 0.10$). Elsewhere, significant main effects are coded under Tmt.

Relationships with burn severity

Species richness.—For ~50% of regression models, I detected a significant positive relationship between species richness and one or more measures of burn severity (Table 4). Patterns varied among growth forms, however. Severity was a significant predictor of richness for the full community and for annual/biennial forbs, but not for perennial forbs. In contrast, pre-treatment richness was a significant predictor of post-treatment richness in <20% of models. No measure of burn severity was consistently selected as a predictor. Many predictors were correlated, with particularly strong correlations in second-entry burns (data not shown).

Severity explained greater variation in total (community) richness in second- than in first-entry burns, but less so for individual growth forms (Table 4). Time since burning did not have a large or consistent effect on the relationship between severity and community richness. For most growth forms, significant correlations were observed both early and late (years 2 and 10), although predictors and strengths of models changed.

Plant cover.— For ~50% of regression models, I detected a significant positive relationship between plant cover and burn severity (Table 5). As with richness models, relationships differed among growth forms. Severity was a significant predictor in all models of total plant cover and in three of four models for annual/biennial forbs, but in none for graminoids (Table 5). In contrast to richness, pre-treatment cover was a frequent predictor of post-treatment response (50% of models).

As with richness models, severity tended to explain greater variation in total (community) cover in second- than in first-entry burns, although patterns varied for individual growth forms (Table 5). Pre-treatment cover was more often a predictor of post-treatment response in second-entry burns. Time since burning did not have a consistent effect on severity-cover relationships among growth forms.

Relationships with heterogeneity of burning

Relationships between richness and measures of burn heterogeneity were highly variable. In first-entry burns, heterogeneity was a significant predictor in 6 of 12 models, but correlations were mostly negative (Table 6). In second-entry burns, correlations with heterogeneity were less frequent (4 of 12 models), but consistently positive. Community richness was negatively correlated to heterogeneity in first-entry burns, but not correlated to heterogeneity after second entry. For both treatments, some growth forms showed significant relationships with heterogeneity either in year 2 (annual/biennial forbs) or in year 10 (perennial forbs), but others relationships were less predictable (shrubs and trees). Pre-treatment richness was more often a predictor of post-treatment richness in second- than in first-entry plots (Table 6).

TABLE 4. Stepwise multiple regression models relating species richness of growth forms to measures of burn severity and pre-treatment richness for plots representing first- and second-entry burns 2 and 10 yr after treatment. 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).

Model	Full model		Live tree density	Dead tree basal area	Litter depth	Char height	Scorch height	Pre-treatment richness
	R^2	P						
All species								
First entry								
Year 2	0.33	0.013	-0.574					
Year 10								
Second entry								
Year 2	0.69	<0.001				-1.146, $p<0.001$	1.506, $p<0.001$	
Year 10	0.83	0.011				0.912		
Annual/biennial forbs								
First entry								
Year 2	0.74	<0.001		0.462, $p=0.007$				0.565, $p=0.002$
Year 10	0.39	0.004			-0.623			
Second entry								
Year 2	0.60	<0.001				-0.683, $p=0.028$	1.254, $p<0.001$	
Year 10	0.98	<0.001			-0.989			
Graminoids								
First entry								
Year 2								
Year 10								
Second entry								
Year 2								
Year 10	0.87	0.006				0.349		

TABLE 4. Continued.

Model	Full model R^2	Full model P	Live tree density	Dead tree basal area	Substrate burn severity	Scorch height	Percent crown scorch	Pre-treatment richness
Perennial forbs								
First entry								
Year 2								
Year 10								
Second entry								
Year 2								
Year 10	0.72	0.032						0.850
Shrubs								
First entry								
Year 2	0.62	<0.001				0.667, *p*=0.001		0.349, *p*=0.039
Year 10	0.40	0.006				0.637		
Second entry								
Year 2	0.61	<0.001						0.780
Year 10								
Trees								
First entry								
Year 2								
Year 10	0.24	0.032					0.494	
Second entry								
Year 2	0.48	0.001			-0.692			
Year 10	0.66	0.050		0.811				

TABLE 5. Stepwise multiple regression models relating cover of growth forms to measures of burn severity and pre-treatment cover for plots representing first- and second-entry burns 2 and 10 yr after treatment. See Table 4 for other details.

Model	Full model		Dead tree basal area	Live tree basal area	Litter depth	Substrate burn severity	Scorch height	Percent crown scorch	Pre-treatment cover
	R^2	*P*							
All species									
First entry									
Year 2	0.72	<0.001	0.426, *p*=0.007						0.790, *p*<0.001
Year 10	0.81	<0.001						0.655, *p*<0.001	0.680, *p*<0.001
Second entry									
Year 2	0.78	<0.001		-0.476, *p*=0.001					0.777, *p*<0.001
Year 10	0.99	0.002					0.512, *p*=0.006		1.011, *p*=0.001
Annual/biennial forbs									
First entry									
Year 2									
Year 10	0.64	<0.001			-0.359, *p*=0.031		0.672, *p*<0.001		
Second entry									
Year 2	0.64	<0.001			-0.377, *p*=0.024				0.748, *p*<0.001
Year 10	0.77	0.022				-0.876			
Graminoids									
First entry									
Year 2									
Year 10									
Second entry									
Year 2	0.39	0.003							0.627
Year 10									

TABLE 5. Continued.

Model	Full model		Dead tree basal area	Live tree basal area	Litter depth	Substrate burn severity	Scorch height	Percent crown scorch	Pre-treatment cover
	R^2	*P*							
Perennial forbs									
First entry									
Year 2	0.71	<0.001	0.310, *p*=0.041						0.810, *p*<0.001
Year 10	0.68	<0.001							0.822
Second entry									
Year 2									
Year 10	0.94	0.001							0.968
Shrubs									
First entry									
Year 2	0.53	0.002			-0.584, *p*=0.004				0.427, *p*=0.024
Year 10	0.57	<0.001						0.756	
Second entry									
Year 2	0.88	<0.001							0.939
Year 10	0.71	0.035						0.843	
Trees									
First entry									
Year 2	0.60	0.001	0.812, *p*<0.001			0.408, *p*=0.027			
Year 10	0.51	<0.001						0.716	
Second entry									
Year 2	0.63	<0.001							0.796
Year 10									

TABLE 6. Stepwise multiple regression models relating richness of growth forms to measures of burn heterogeneity and pre-treatment richness for plots representing first- and second-entry burns 2 and 10 yr after treatment. See Table 4 for other details.

Model	Full model R^2	*P*	CV duff depth	CV litter depth	CV change in duff depth	CV change in litter depth	Pre-treatment richness
All species							
First entry							
Year 2	0.46	0.011	-0.669, *p*=0.005				0.525, *p*=0.022
Year 10	0.23	0.044	-0.480				
Second entry							
Year 2							
Year 10							
Annual/biennial forbs							
First entry							
Year 2	0.49	0.007	-0.411, *p*=0.043				0.541, *p*=0.011
Year 10							
Second entry							
Year 2	0.29	0.014					0.54
Year 10							
Graminoids							
First entry							
Year 2							
Year 10							
Second entry							
Year 2							
Year 10	0.75	0.025		0.867			

TABLE 6. Continued.

Model	Full model R^2	Full model *P*	CV duff depth	CV litter depth	CV change in duff depth	CV change in litter depth	Pre-treatment richness
Perennial forbs							
First entry							
Year 2							
Year 10	0.45	0.009		0.631, *p*=0.005		-0.444, *p*=0.035	
Second entry							
Year 2							
Year 10	0.94	0.015				0.474, *p*=0.047	0.761, *p*=0.014
Shrubs							
First entry							
Year 2							
Year 10	0.43	0.004				-0.659	
Second entry							
Year 2	0.78	<0.001			0.260, *p*=0.042		0.873, *p*<0.001
Year 10							
Trees							
First entry							
Year 2	0.49	0.006		-0.431, *p*=0.035	0.618, *p*=0.005		
Year 10							
Second entry							
Year 2	0.65	<0.001		0.770, *p*<0.001			0.448, *p*=0.010
Year 10							

DISCUSSION

In most studies of restoration in fire-dependent forests of the western U.S., emphasis has been placed on changes in stand structure and reductions in surface fuels as mechanisms for reducing fire risk (e.g., North et al. 2007, Harrod et al. 2009, Schwilk et al. 2009). The consequences of reintroducing fire for other ecosystem attributes, including understory abundance and diversity, have received little attention. This study begins to address these gaps in knowledge using long-term measurements of vegetation response to the reintroduction and repeated use of fire in mixed-conifer forests of Sequoia and Kings Canyon National Parks. Our results provide strong evidence that repeated burning in areas 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 species richness and abundance in the understory. Studies of short-term responses to fire suggest similar benefits (e.g., Knapp et al. 2007, Wayman and North 2007), but none have considered longer term effects or the consequences of repeated burning.

The absence of quantitative information on forest understory composition prior to suppression poses a challenge in assessing the efficacy of restoration treatments (cf. Keith et al. 2010). However, photographic and written accounts suggest many fewer, but larger trees, and lower accumulations of surface fuels (LeConte [1875] 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 seems reasonable to infer that understories evolved within the context of a more open, patchier overstory, lighter fuel loading, and more frequent, lower intensity fire (Falk 1990, Moore et al. 1999)—conditions likely to support a greater diversity and abundance of plant species. By extension, creation of comparable conditions through prescribed burning should also promote greater diversity and abundance provided that fire behavior is similar and species colonization is not limited by dispersal.

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, marked reductions in depth and mass of fine fuels, and exposure of mineral soil—effects that have been documented in previous studies (Knapp et al. 2005, Zald et al. 2008, Vaillant et al. 2009). Reductions in the density of understory trees and consumption of surface fuels are also likely to have affected understory microclimates—increasing light availability, temperature, 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). However, 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, e.g., increases in understory light or mulching of the forest floor, are likely to be missed in short-term studies of vegetation response because it may take a decade or more for the small snags to fall (Stephens and Moghaddas 2005). By contrast, effects of second-entry burns were subtle, moderated 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.

Long-term effects on vegetation

Prescribed burning promoted significant increases in species richness and cover in forest understories that were initially characterized by low species density and abundance. However, rates of increase were very gradual for most plant groups. As a result, differences between treated and control plots were not apparent for as many as 5-20 yr after burning. Initial effects of fire thus appear consistent with those observed in short-term (2- to 3-yr) studies of understory response in other fire-dependent forests (e.g., Metlen et al. 2006, Knapp et al. 2007, Dodson et al. 2008). However, longer term changes, which have rarely been documented (Moore et al. 2006), suggest greater potential for fire to enhance diversity and abundance in the understory. These contrasts underscore the importance of long-term measurements for capturing ecological responses to fire that may play out over decades.

A diversity of processes, biotic and abiotic, may contribute to the protracted nature of these responses. The gradual development of most plant groups coupled with the 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 thus appears critical.

The comparative responses of annuals and graminoids to first- and second-entry burns suggest that development of both groups was limited by seed availability. Both growth forms 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 burns, despite more complete consumption of surface fuels and significant (>60%) exposure of mineral soil. Repeated burning promoted greater establishment in some sites, but at considerably lower levels of soil disturbance (<30% cover). Thus, populations that established after initial entry or in adjacent areas that had burned may have provided local sources of seed (Halpern 1989, Turner et al. 1998). These positive feedbacks suggest that further use of prescribed fire in this landscape could increase both the local and broader distributions of fire-enhanced species that may have declined during extended periods of suppression (Keeley et al. 2003).

Temporal lags in the development of other growth forms may also be shaped by patterns of dispersal in time and space. Shrubs played a minor role in the pre-treatment understory, and post-burning trends suggest a pattern of gradual colonization (i.e., increasing richness) and growth (cover). Two processes may underlie these trends. For a variety of taxa that produce large fruits (e.g., *Ribes, Rubus,* and *Sambucus*), seed dispersal is commonly facilitated by frugivorous birds and small mammals (e.g., Quick 1954, Crane et al. 1983). The accumulation of these species over time may reflect the stochastic nature of animal-mediated dispersal, or gradual changes in the structure or suitability of forest habitats that increase the likelihood of dispersal (e.g., McDonnell and Stiles 1983). Trends in cover, however, reflected the dynamics of the dominant seed-banking shrub, *Ceanothus cordulatus*. Fire stimulates seed germination via heating of the soil (Gratkowski 1962) and emergence occurs soon after burning (Orme and Leege 1976). However, seeds are not widely dispersed (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 resulting in little development of the shrub layer on many sites. However, repeated burning did not appear to have an adverse effect on either the richness or cover of shrubs. Once established, most species have the ability to resprout from root crowns or rhizomes (Quick and Quick 1961, Keeley 1987, Kaufmann and Martin 1991, Keeley 1991, Stickney and Campbell 2000). 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 decades of 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 abundance, although this was highly variable and only marginally significant after 20 yr. These positive effects were subsequently erased by second-entry fires, although future measurements of these plots will reveal the potential for further expansion given sufficient time. Previous studies of dry coniferous forests illustrate significant variation in the short-term responses to fire of perennial forbs (e.g., Collins et al. 2007, Dodson et al 2007, 2008, Knapp et al. 2007, Wayman and North 2007). This is not surprising given the wide variety of growth forms and reproductive strategies, and the potential for complex interactions with fire behavior and weather conditions (e.g., Moore et al. 2006). Despite significant variation in time and space, long-term trends in the current study suggest the 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 (*C. cordulatus* and *C. parvifolius*) whose long-lived seeds are stimulated by fire (Quick and Quick 1961, Kaufmann and Martin 1991, Keeley 1987, 1991) and *Abies concolor,* which establishes preferentially on mineral substrates (Stark 1965, Kilgore 1973). Moreover, frequent cone production in *A. concolor* (Laacke 1990) increases the probability of recruitment when the timing of disturbance and the availability of suitable germination sites are unpredictable (Keeley and van Mantgem 2008, Schwilk et al. 2009). For *A. concolor*, prescribed fire represents a tradeoff: burning can remove significant numbers of subcanopy trees, but at the same time initiate new cohorts of seedlings. Similar effects of prescribed fire on the size structure and density of understory trees 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 promote 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 following restoration burning or the combined application of thinning and prescribed burning in a diversity of coniferous forest types (e.g., 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 rarely observed (two species in three plots), but there was no indication of an increase in their distribution or abundance over 20 yr of observation. This contrasts, to some degree, with the low levels of invasion (3.4% of the flora) observed in a broader survey of mixed-conifer forests in the park (Keeley et al. 2003). Low-level invasions in the park may be a consequence of multiple factors acting in concert: elevational constraints on species' distributions (Keeley et al. 2003), low densities of roads that serve as dispersal corridors (Trombulak and Frissell 2000), minimal use of mechanical equipment (vectors for transport), active eradication, and long-term suppression of fire which has limited establishment of source populations (Keeley et al. 2003). As with native species that are enhanced by burning, increasing use of fire has the potential to encourage the establishment of aliens. Integrating active monitoring (and removal) of source populations into landscape management plans seems critical for minimizing future introductions (Keeley et al. 2003, Jones et al. 2010).

Relationships with burn severity

Knowledge of the regenerative strategies of species is useful in understanding vegetation responses to fire severity (Halpern 1988, Schimmel and Granstrom 1996, Wang and Kemball 2005, Pyke et al. 2010). Greater fire severity can have negative effects on community cover or richness if it results in consumption or mortality of perennating structures, or extirpation of rare or uncommon taxa that are more susceptible to fire by virtue of low population densities. In contrast, greater fire severity can have positive effects on cover and richness if it enhances resource availability (light, soil moisture, and nutrients), creates openings for recruitment of new species, or stimulates germination in fire-dependent species.

In this study, one or more measures of severity 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 these models, but the distinctions may not be critical; measures of severity were often correlated, particularly in second-entry fires where measures of residual fuel depth and fire intensity showed high correlations. Higher severity fires, regardless of treatment, led to greater numbers of species and to greater plant 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 on the relatively few 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 elicit strong gradients in community response. In fact, fire severity explained comparable, if not more, variation in community response in second- than in first-entry plots. Greater seed availability in areas that had previously burned may facilitate greater colonization of areas of higher severity. Moreover, for both treatments, effects of severity were evident early and changed little with time. The dynamics of individual growth forms provide insight into the broader patterns of community response.

Annual/biennial forbs showed consistently greater richness and cover at higher severities. Litter depth was a frequent predictor of both measures of performance. Deeper accumulations of litter may limit recruitment of species that preferentially establish on mineral substrates (Facelli and Pickett 1991, North et al. 2005). Greater severity may also promote greater resource availability by removing small trees (reducing root densities; North et al. 2005) and enhancing conversion of organic to mineral N (Prieto-Fernandez et al. 1993, Pietikainen and Fritze 1995, Grogan et al. 2000). Annuals, which possess strategies for long-distance dispersal and rapid growth, have the potential to quickly occupy 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 (seeds vs. established plants). For seed-banking taxa such as *Ceanothus*, increasing severity typically leads to greater germination (provided seeds are present in the soil; Biswell 1961, Orme and Leege 1976, Halpern 1989). However, mature plants have the ability to resprout after fire, and unless intensities exceed lethal thresholds, variation in severity during subsequent burning may have little effect on survival or abundance (Huffman and Moore 2004). Persistence through fire can be similar for *Ribes* and *Rubus* (Quick 1954, Kilgore 1973, Volland and Dell 1981, 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, particularly in forests in which there has been long-term suppression of fire. Resident species are likely to exhibit a diversity of regenerative strategies and to show contrasting responses to burning (e.g., McLean 1968, Halpern 1989, Schimmel and Granstrom 1996, Knapp et al. 2007). Many may be tolerant of fire; however, others that are adapted to shade or deep accumulations of litter (e.g., *Pyrola picta*, *Chimaphila menziesii*; North et al. 2005) may be more sensitive to burning (e.g., Halpern 1989) or to higher levels of light or moisture stress (e.g., Nelson et al. 2007) in 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 contributed to initial variation in abundance (stand structure, microclimate, and soils; North et al. 2005).

A combination of factors may contribute to the absence of significant relationships between severity and graminoid performance. As a group, graminoids contributed minimally to cover and diversity, with most species sparsely distributed among plots. In addition, unlike annuals which have mechanisms for long-distance transport, seed dispersal in grasses and sedges is more restricted (Cheplick 1998). The dominant sedge in these forests, *Carex multicaulis*, showed greatest development in second-entry burns late in succession (Table 3, Appendix A). Indeed, it was only in second-entry plots in year 10 that graminoid performance (richness) was correlated with fire severity. Thus, in systems for which the pool of potential colonists is poor and dispersal is limited, relationships between growth form performance and severity may reflect the disturbance dynamics of the dominant species. Effects may be unpredictable, however: studies from a diversity of systems suggest that graminoids may show little consistency in response to disturbance (see discussion in Dodson et al. 2008).

Relationships with heterogeneity of burning

It is commonly assumed that greater spatial heterogeneity in resource availability or physical environment allows for greater diversity of species with differing resource or environmental requirements (Tilman 1984, Huston 1994, Rosenzweig 1995). By extension, disturbances that increase resource or environmental heterogeneity should also promote diversity. Depending on fuel characteristics, fire has the potential either to homogenize or to increase heterogeneity of understory resources (e.g., 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 (CV) in fire severity. However, burn heterogeneity did not differ between treatments—nor did the resulting richness of species. It is possible that fuel characteristics were as variable within treatments (among replicate plots) as between them. Differences in elevation and inherent variation in forest structure or disturbance history may have contributed to this variability. In addition, understory plots may have been too small (0.1 ha) to capture the variation in structure and fuel characteristics that typify these forests at larger spatial scales (e.g., North et al. 2007).

Within treatments, relationships between burn heterogeneity and species richness revealed a diversity of patterns, but few supported theoretical expectations. In first-entry burns, community richness (and that of most growth forms) was negatively correlated to heterogeneity, counter to previous observations (e.g., Rocca 2009). In contrast, in second-entry burns, community richness was unrelated to heterogeneity, but several growth forms responded positively. These results may be explained, in part, by differences in the magnitude, (but not heterogeneity) of burn severity. First-entry fires were of higher severity, but exhibited little spatial variation, resulting in a relatively homogeneous, but highly modified forest floor. Annuals and conifers (*A. concolor*) that prefer mineral seedbeds, and seed-banking shrubs that benefit from intense soil heating, responded negatively to variation in these conditions. Second-entry fires also imposed little spatial variation but were of lower severity. Although individual growth forms responded positively to burn heterogeneity, effects were either short-lived (limited to year 2) or delayed until year 10; moreover they did not translate into greater community richness. In combination, these results suggest that strategies to enhance diversity by manipulating resource or environmental heterogeneity will first require significant reductions in surface fuels. Yet, even repeated burning may not achieve this goal, or only minimally so—at least at the spatial scale of this study. It is possible that at larger spatial scales (e.g., Turner et al.1994, Schoennagel et al. 2008) burn heterogeneity may yield different outcomes for diversity.

Management implications

Fire is increasingly used as a tool for restoration in forests of the western United States and elsewhere (Stephens and Ruth 2005, Dale 2006, Vanha-Majamaa et al. 2007). On federal lands in the U.S., fire is often used in combination with mechanical methods (thinning and mastication; Schwilk et al. 2009) to return forest structure and fuel levels to within their historical ranges of variation (Landres et al. 1999, Allen et al. 2002). In National Parks, prescribed and wildland fire are often exclusively used for restoration offering a unique opportunity to explore ecological responses to fire in systems that have been minimally impacted by past management (logging) or other resource extraction. Understanding the consequences of reintroducing fire in these systems is of critical importance in the context of existing constraints (air quality regulations, fiscal limitations) and future threats (non-native species, climate change).

Understory communities are critical components of western forest ecosystems. They support the majority of plant species and provide important habitat and food resources for wildlife (Lindenmayer and Franklin 2002, Bock and Block 2005, Converse et al. 2006). Long-term suppression of fire has changed fundamental aspects of forest structure and environment (stand densities, light, and fuels) with profound consequences for the abundance and diversity of understory plants. Prior to reintroducing fire, it was implicitly assumed that changes in forest structure and reductions in fuel mass would naturally lead to increases in the abundance and diversity of understory species—particularly those dependent on fire. Long-term studies from Sequoia and Kings Canyon National Parks provide strong evidence that prescribed burning enhances understory richness 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 actually 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 lower severity) appears to effect more subtle changes in environment, but provides opportunities for the spread of newly established populations. Reintroduction of fire 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 (Kinlock and Scheuner 1990, van Mantgem et al. 2004). *Sequoiadendron* is highly restricted in its distribution and has specific germination requirements (higher severity fires that create canopy gaps and bare mineral soil; Harvey et al 1980, Stephenson 1991). Repeated burning appears to be critical for regeneration and persistence of these tree species.

At the same time, prescribed burning may pose challenges to the management of shade-tolerant tree species, principally *Abies concolor*. Although a basic objective of burning is to reduce the density of subcanopy and understory trees (National Park Service 2005, Schwilk et al. 2009), *A. concolor* is both 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 the goals of restoration. Timing of fire 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 densities are high, additional burning may be necessary, conducted at a time when trees are small and more susceptible to fire (Kilgore 1973).

In contrast to the response of native species, non-natives were extremely restricted in time and space. In forests characterized by a sparse and species-poor native community, invasion resistance is likely to be low (Levine 2000). Moreover, high severity fires provide ideal substrate and resource conditions for establishment and spread of weedy aliens. It appears that low propagule pressure (Lonsdale 1999), interactions with physical environment, and until recently, the exclusion of fire from these forests, has contributed to low-level invasions (Keeley et al. 2003). Establishment is more likely to occur near roads, trails, and riparian areas, and where human and pack-stock use is high. Because alien invasions in the backcountry are uncommon in areas that have burned, limited resources for monitoring can be most effectively used in areas that support source populations or serve as conduits (Rew et al. 2006).

Burning not only enhances the abundance and diversity of species locally, but it creates variation at larger spatial scales. Fires of varying severity differentially affect species that are more sensitive to or enhanced by burning, and stimulate the emergence of species whose long-dormant seed banks are patchily distributed across the landscape. Long-term monitoring of plant community responses—rare outside of the National Park Service—suggests that full expression of this variation may take decades, thus management decisions based on short-term responses may be misguided. Given the depauperate nature of the understory and the slow pace of succession, it seems reasonable to vary fire frequency across the landscape, mimicking historical patterns of fire (Swetnam 1993). This would allow for expression of different plant groups in time and space, and for a greater variety of understory communities. Sites in the current study were reburned within 8 to 17 yr of initial treatment; unless the timing of re-entry is dictated 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 2005). More than two decades of plant community data from Sequoia and Kings Canyon National Parks suggest that multiple resource and ecological objectives can be met through the reintroduction of fire. Yet, viewing fire as critical to ecosystem restoration also requires that fire is maintained as a frequent and spatially dynamic process on the landscape. Likewise, maintaining programs for long-term monitoring and analysis of ecological responses to fire are critical to understanding its future role and management.

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APPENDIX A. Frequency (Fr, % of plots) and mean cover (Cv, %) of plant species observed in unburned, and first- and second-entry burns.

	Unburned										First entry										Second entry							
	Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10	
	(*n*=8)		(*n*=8)		(*n*=8)		(*n*=8)		(*n*=6)		(*n*=13)		(*n*=13)		(*n*=13)		(*n*=13)		(*n*=7)		(*n*=13)		(*n*=13)		(*n*=13)		(*n*=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Annual forbs																												
Allophyllum gilioides																	8	0.1										
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	0.2	31	0.1	15	0.1	14	-					8	-	17	-
Collinsia childii															8	0.1									8	-		
Collinsia heterophylla																	8	-										
Collinsia parviflora											8	-	15	-	8	-			29	0.3								
Collinsia torreyi																							15	-	8	-		
Collinsia sp.																											17	-
Cordylanthus rigidus																											17	-
Cryptantha affinis																			23	-			15	-	23	-	50	-
Cryptantha intermedia																							8	-				
Cryptantha simulans																			8	-			8	-	23	0.1	50	-
Cryptantha sp.			13	-							8	-			8	0.1	39	0.1			15	0.1	23	0.4				
Galium aparine							38	0.2	67	0.7			15	-	46	0.1	23	0.1	57	0.1	8	0.1	-		23	-	17	-
Galium triflorum			13	-							15	0.1					8	-			8	-	8					
Gayophytum diffusum													31	-	15	-	8	-	8	-			8	0.2	23	0.6	50	0.1
Gayophytum eriospermum			13	-	13	0.3	13	-							8	-	39	-	14	-	23	-	39	0.5	15	0.1		
Gayophytum sp.																					8	-						
Gilia capitata	13	-																										
Linanthus ciliatus															8	-					8	-	15	0.1	31	0.6	50	0.3
Linanthus montanus													8	-			15	-			15	-	8	-				
Linanthus sp.											8	-							14	-								
Mentzelia dispersa																							8	-				
Mimulus floribundus															8	-	8	-			8	-						

APPENDIX A. Continued.

	Unburned										First entry										Second entry							
	Pre (*n*=8)		Year 2 (*n*=8)		Year 5 (*n*=8)		Year 10 (*n*=8)		Year 20 (*n*=6)		Pre (*n*=13)		Year 2 (*n*=13)		Year 5 (*n*=13)		Year 10 (*n*=13)		Year 20 (*n*=7)		Pre (*n*=13)		Year 2 (*n*=13)		Year 5 (*n*=13)		Year 10 (*n*=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Annual forbs (cont.)																												
Mimulus guttatus													8	-			8	-			15	-						
Mimulus sp.											8	-	8	-	8	0.1												
Nemophila pulchella																									8	0.4		
Nemophila sp.																	8	-										
Phacelia eisenii													8	-							8	0.1						
Phacelia humilis													8	-														
Perennial forbs																												
Adenocaulon bicolor	50	1.2	25	0.2	25	0.2	25	-	33	0.6	23	0.4	15	-	31	0.1	39	0.1	43	-	8	0.1	31	-	31	-		
Agoseris elata																									8	-		
Agoseris retrorsa																							8	-	8	-		
Anaphalis margaritacea																					8	-	8	-			17	-
Antennaria rosea																			14	-								
Apocynum androsaemifolium	38	0.3									23	0.1					15	-	29	-			8	-	8	-		
Arabis glabra																	8	-									17	-
Arabis holboellii																	8	-							8	0.1		
Arabis repanda									33	-	8	-	8	-			8	-	57	-	15	0.1	31	0.1	54	0.1	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	0.1															15	0.2			31	0.2	15	0.4			17	-
Calystegia malacophylla					13	-	13	0.1			23	-	39	0.2	39	0.2	39	0.1	43	1.6	15	0.7	15	0.7	15	0.6	50	2.2
Campanula prenanthoides									17	0.6			8	-			8	-										
Castilleja applegatei											23	-	23	-	23	-	23	0.1	57	0.2					15	-	17	-

APPENDIX A. Continued.

	Unburned										First-entry										Second-entry							
	Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10	
	(n=8)		(n=8)		(n=8)		(n=8)		(n=6)		(n=13)		(n=13)		(n=13)		(n=13)		(n=7)		(n=13)		(n=13)		(n=13)		(n=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Perennial forbs (cont.)																												
Castilleja lemmonii							13	-																	8	0.1		
Castilleja sp.																							8	-	8	-		
Chimaphila menziesii	13	-	38	-	63	0.2	38	0.1	17	-	31	-	8	-	8	-					31	-	23	-	39	-	33	-
Chimaphila umbellata																							8	-	15	-		
Circaea alpina									17	-			8	-	8	0.1	15	0.1			8	0.2						
Cirsium andersonii													8	-														
Cirsium sp.	8	0.1															8	-					8	-				
Corallorrhiza maculata			25	-			25	-	17	-			8	-			8	0.1			8	0.1					17	-
Cynoglossum occidentale											8	0.2					15	-	14	0.1	8	-	15	-	15	-	50	-
Delphinium polycladon													8	-														
Disporum hookeri			50	0.8			38	0.5	50	0.8	8	0.1			8	0.1			14	0.6								
Draperia systyla	25	0.6	13	0.8	25	0.7	25	0.8	17	1.2	23	0.1	46	0.3	62	0.7	54	1.0	43	0.1	62	0.5	54	0.5	39	0.6	67	0.7
*Dryopteris arguta***															8	0.1	8	0.3										
Epilobium angustifolium													8	-														
Epilobium glaberrimum																	15	-										
Epilobium sp.													15	-														
Eriogonum nudum			13	-	13	0.2	13	0.1					15	-	8	-	31	-	29	-					8	-	50	-
Eriogonum umbellatum							13	-																				
Eriogonum sp.	25	-																					8	-				
Eriophyllum lanatum													8	-	8	-	8	-	14	-								
Erysimum capitatum													8	0.1	8	-	8	-			8	-			15	-		
Galium bolanderi									17	-											8	-	23	-	23	-		
Galium sparsiflorum	25	0.1	38	-	63	0.5	50	0.1	50	0.1	46	0.6	39	1.3	46	0.1	77	0.3	86	0.6	54	0.1	15	-	31	0.1	17	-
Galium trifidum			2	-													8	0.1										
Galium sp.	25	0.3	13	0.1	13	0.2					8	0.1			15	-							8	-				
Gnaphalium canescens																	8	0.3							23	0.1	50	-
Goodyera oblongifolia					13	-	13	-	17	-																		
Hackelia mundula					13	-			17	-	8	-	15	0.4	8	0.2	15	-	43	0.1	8	-	8	0.1	23	0.2	17	0.2

APPENDIX A. Continued.

	Unburned										First-entry										Second-entry							
	Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10	
	(n=8)		(n=8)		(n=8)		(n=8)		(n=6)		(n=13)		(n=13)		(n=13)		(n=13)		(n=7)		(n=13)		(n=13)		(n=13)		(n=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Perennial forbs (cont.)																												
Hackelia sp.	13	-			13	-																	8	-				
Hieracium albiflorum	50	0.1	88	0.1	38	-	50	0.2	50	0.1	15	-	46	0.1	62	0.1	85	0.9	100	1.2	69	0.7	54	0.6	62	0.4	67	2.0
Hulsea heterochroma																							8	-	8	-	17	-
Hydrophyllum occidentale													15	0.2	8	0.5					8	-						
Hydrophyllaceae sp.													8	0.1														
Iris hartwegii													15	0.1	15	0.1	15	0.1										
Kelloggia galioides	13	-	38	0.1	38	-	25	-	33	-	15	-			15	0.2	31	0.2	43	0.5	15	-	8	-	39	0.3		
Ligusticum grayi																											17	-
Lilium kelleyanum											8	0.1																
Lilium pardalinum													8	-							8	-						
Lotus crassifolius													15	-	15	-	23	-	29	0.1								
Lotus nevadensis																	8	-										
Lotus oblongifolius					13	-							15	0.1	8	0.2	8	1.7	14	1.8	8	1.0						
Lotus sp.													8	-														
Lupinus albicaulis																									8	-		
Lupinus covillei																							8	-				
Lupinus fulcratus							13	-													15	2.1	8	2.2	15	1.1		
Lupinus latifolius			13	-							8	-	8	-	8	0.1	15	0.1	14	0.6	8	-	8	-				
Lupinus polyphyllus																	8	0.1	14	0.5	8	0.3			8	0.1		
Lupinus sp.	13	0.3	25	0.2	38	0.2	13	-	17	-	15	0.5	15	0.1	15						8	0.1	8	0.1				
Mimulus moschatus			13	-									8	0.1														
Monardella odoratissima			13	-	13	-	13	-									23	-	43	-								
Nama rothrockii																							8	0.1				
Osmorhiza chilensis	38	-	50	0.4	38	0.5	50	-	17	-	23	-	39	0.1	39		39	-	71	0.1	8	-	8	-				
Osmorhiza sp.	13	-									8	-																
Pedicularis semibarbata	13	-	13	-			13	-			15	-	8	-			8	-	14	-	23	-	31	0.1	23	-	17	-
Penstemon newberryi																					8	-			15	-	17	-
Penstemon parvulus																					8	-	8	-				

APPENDIX A. Continued.

	Unburned					First-entry					Second-entry			
	Pre	Year 2	Year 5	Year 10	Year 20	Pre	Year 2	Year 5	Year 10	Year 20	Pre	Year 2	Year 5	Year 10
	(n=8)	(n=8)	(n=8)	(n=8)	(n=6)	(n=13)	(n=13)	(n=13)	(n=13)	(n=7)	(n=13)	(n=13)	(n=13)	(n=6)
Species	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv	F r Cv
Perennial forbs (cont.)														
Penstemon sp.	13 -													
Phacelia hastata													8 0.1	
Phacelia heterophylla										29 -			8 -	
Phacelia hydrophylloides				13 -	17 -	8 -	8 -	8 -	8 -	29 -	8 -	15 -	31 0.1	
Phacelia mutabilis	13 -		25 -	13 -	50 -		23 0.1	39 0.1	23 -	14 -	8 0.3	23 0.1	15 0.2	33 0.1
Phacelia ramosissima								8 -		43 0.2		15 -		17 -
Phacelia sp.	25 -	25 -				23 -	8 -	8 -	31 -	14 0.1	39 -		8 -	17 -
Pityopus californicus						8 -								
Potentilla glandulosa							8 0.1	8 -	8 -	29 0.1				
Potentilla sp.						8 -								
Pseudostellaria jamesiana				13 -			15 1.1	8 -		29 1.0				
*Pteridium aquilinum***	25 3.7	25 2.2	25 1.5	13 2.1	17 0.2	31 1.4	23 3.3	46 2.9	39 3.9	29 2.4	8 1.2	15 0.5	15 0.5	
Pterospora andromedea	25 -	13 -			17 -	23 0.1			8 -					
Pyrola picta	63 0.2	50 -	63 0.2	38 0.1	67 0.1	54 0.1	31 -	39 -	62 0.1	57 0.1	77 0.1	54 -	69 0.1	67 -
Rosa bridgesii										14 -				
Rosa californica		13 -						8 -						
Rosa pinetorum										14 -				
Rosa woodsii			13 -	13 -					15 -					
Rosa sp.	13 -					8 0.1	15 -							
Rubus leucodermis					17 -									
Sarcodes sanguinea		25 -			17 -				8 -		8 -	8 -	15 -	
Senecio triangularis		13 -									8 -		8	
Silene lemmonii				25 -	50 -	15 0.5		31 0.2	31 0.1	43 -	31 -	31 0.1	31 -	33 -
Silene sp.	25 -	13 -												
Smilacina racemosa	38 -	38 -	13 -		50 -	8 -	23 0.3	15 0.3	15 0.2	29 -			8 -	
Smilicina stellata			25 0.1			8 0.1								
Solanum xanti							15 0.1	15 0.1	23 0.1	29 0.3				

APPENDIX A. Continued.

	Unburned										First-entry										Second-entry							
	Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10	
	(n=8)		(n=8)		(n=8)		(n=8)		(n=6)		(n=13)		(n=13)		(n=13)		(n=13)		(n=7)		(n=13)		(n=13)		(n=13)		(n=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Perennial forbs (cont.)																												
Stachys albens																					8	0.5			8	-		
Stellaria sp.													8	-														
Streptanthus sp.					13	-	13	-																				
Viola adunca																					8	0.1	8	-	8	-		
Viola glabella									17	-							8	-										
Viola lobata	13	-	38	-	25	-	13	-	33	0.2	23	0.1	23	-	23	-	23	0.1	29	-	8	-	15	-	15	-	17	-
Viola purpurea	13	-	13	-			13	-	17	-									14	-								
Viola sp.	25	-	13	-	25	0.1					8	-																
Wyethia mollis																					8	-						
Unknown forb sp.					13	-									31	0.1	15	-			8	-						
Graminoids																												
Achnatherum occidentale									17	-	8	-									8	-	15	0.1	31	0.3		
Achnatherum sp.	13	-																										
Agrostis scabra																	8	-										
Bromus carinatus					13	-	13	0.1					8	-			15	-										
Bromus laevipes									17	-											8	-			15	-	17	-
Bromus orcuttianus																			57	0.8					15	-	33	-
Bromus suksdorfii															8	-	23	0.5					8	-				
*Bromus tectorum**																	8	-					8	-	8	-	17	-
Bromus sp.											8	-	8	-	8	-	15	-			8	0.1	15	0.1	8	-		
Carex multicaulis			13	-	25	-	25	-	50	0.1			8	-	8	-	31	-	43	0.4	23	-	39	0.3	77	0.8	67	0.4
Carex rossii																											17	-
Carex specifica													8	-														
Carex sp.	25	0.2	25	0.2	13	-	25	0.2	17	-	15	-	8	0.1	8	0.1	8	0.2			15	-	15	-				
Deschampsia elongata																	8	-										

APPENDIX A. Continued.

	Unburned										First-entry										Second-entry							
	Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10		Year 20		Pre		Year 2		Year 5		Year 10	
	(n=8)		(n=8)		(n=8)		(n=8)		(n=6)		(n=13)		(n=13)		(n=13)		(n=13)		(n=7)		(n=13)		(n=13)		(n=13)		(n=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Graminoids (cont.)																												
Elymus glaucus	25	-					13	-	17	0.6									29	-	8	-	8	-			17	-
Festuca occidentalis	13	0.2															8	-										
Glyceria elata																									8	-		
Juncus effusus													8	-			8	-										
Koeleria macrantha																											17	-
Melica aristata	13	-	13	-					17	-			8	-					29	1.6					15	-	50	-
*Poa pratensis**															8	-	8	-										
Poa sp.			13	-													8	-										
Poaceae sp.													15	0.1	8	-	8	-			15	-						
Shrubs																												
Acer glabrum	13	-							17	-																		
Arctostaphylos patula											8	-			8	-	23	0.1	43	-	31	-	23	-	39	-	67	-
Arctostaphylos viscida																					8	-						
Arctostaphylos sp.																							8	-				
Ceanothus cordulatus											8	-	15	-	8	0.1	46	2.0	43	15	23	0.1	39	0.4	46	1.6	50	7.9
Ceanothus integerrimus															23	0.2	15	-			8	-	8	-				
Ceanothus leucodermis																					15	0.6						
Ceanothus parvifolius													23	-	39	0.5	31	0.4			15	0.2	8	-	23	-	50	0.8
Chamaebatia foliolosa	13	-	13	-																					8	-	17	-
Chrysolepis sempervirens	38	3.0	50	1.6	25	2.1	25	1.3	33	1.8	23	0.1	15	-	15	0.1	8	-	14	-	31	-	15	-	39	-		
Corylus cornuta	25	-	25	-	13	-	25	0.2	33	-	8	0.5	23	-	15	0.2	39	0.2	29	-								
Keckiella breviflora											8	-																
Prunus emarginata							13	-			15	-			15	-	15	0.1	14	-					15	-		
Ribes cereum													8	-							8	0.1						
Ribes montigenum																					8	-						
Ribes nevadense									17	-							8	0.1	86	2.4			8	-	15	-	33	0.1

APPENDIX A. Continued.

	Unburned										First-entry										Second-entry							
	Pre (n=8)		Yr 2 (n=8)		Yr 5 (n=8)		Yr 10 (n=8)		Yr 20 (n=6)		Pre (n=13)		Yr 2 (n=13)		Yr 5 (n=13)		Yr 10 (n=13)		Yr 20 (n=7)		Pre (n=13)		Yr 2 (n=13)		Yr 5 (n=13)		Yr 10 (n=6)	
Species	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv	Fr	Cv
Shrubs (cont.)																												
Ribes roezlii	13	-	13	-					67	-	23	0.1	39	-	54	0.1	54	0.3	100	3.4	31	0.1	5	-	46	0.1	67	0.8
Ribes viscosissimum									17	0.4							15	0.1	29	0.5	3	-	8	-	15	-		
Ribes sp.			25	-	13	0.1	13	-					15	-	46	0.1	23	0.1			15	0.1	23	-				
Rubus parviflorus	13	-	13	-					17	-	31	-	23	-	31	-	39	-	29	-								
Sambucus mexicana													8	-	8	0.1	23	0.1	14	0.9	15	-	8	-	8	-	17	-
Symphoricarpos mollis			13	-			38	0.2			15	0.8	31		15	-	23	-	43	0.6	8	0.1	23	0.1	31	0.1		
Trees																												
Abies concolor	13	-	38	0.2	13	0.2	13	0.1	83	-			8	0.3	15	0.2	46	0.5	86	3.4	46	1.0	69	1.0	85	0.9	100	3.1
Abies magnifica											8	1.4	8	0.1			8	0.1	29	0.8	8	0.5	8	0.4	39	0.7		
Abies sp.																									8	0.1		
Calocedrus decurrens							13	0.3	33	-	8	0.1			8	0.1	8	0.1	43	-	8	0.4	15	0.1	15	0.1	33	0.3
Cornus nuttalli	13	-			13	0.9	13	-	17	0.1					15	0.1	15	0.1					8	0.1	8	0.1		
Pinus jeffreyi																			29	-								
Pinus lambertiana			13	0.1	13	0.1											23	0.1	57	0.2	39	0.4	31	0.1	62	0.1	83	0.1
Pinus ponderosa																			14	-					15	-	17	-
Pinus sp.																							8	-				
Quercus chrysolepis	13	-	13	-					17	-									14	-								
Sequoiadendron giganteum																	15	0.4	8	0.5	15	0.6	15	0.1	39	0.1	67	0.1
Umbellularia californica							13	-																				

Notes: dashes (-) for cover indicate species not encountered with the point-intercept method, but present in the 50 x 10 m belt (500 m^2 plot).

* non-native species, ** fern species.