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Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments

Rebecca Bewley Wayman [a], Malcolm North [b,*]

[a] Department of Plant Sciences, University of California, Davis, CA 95616, United States
[b] USFS Sierra Nevada Research Center, 2121 2nd Avenue, Suite A-101, Davis, CA 95616, United States

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Abstract

Mechanical thinning and prescribed fire are widely used to restore western forests after a century of fire suppression, yet we know little about how these treatments affect understory communities where plant diversity is highest. We followed understory plants and environmental factors in old-growth, Sierran mixed conifer for two pre-treatment and three post-treatment years using a full-factorial combination of burning and thinning treatments. Treatments significantly changed species composition through a highly localized combination of disturbance intensity interacting with pre-treatment vegetation patches. Pre-treatment richness was most significantly associated with soil moisture; after treatments additional variables became associated with richness and cover. Neither burning nor thinning alone significantly increased richness or cover. Species that increased significantly in cover were associated with conditions of burn/thin combinations: increased light and soil moisture caused by thinning, and burning's reduction of litter, slash, and shrub cover. Our study suggests that the means by which forests are restored affects understory diversity and cover. Prescribed fire was most effective for increasing understory diversity and reducing shrub cover, but when applied off-season, additional fuels provided by mechanical thinning increased burn area and intensity, reducing litter and slash and increasing herb richness and abundance.

Keywords: Fire suppression; Plant diversity; Sierra Nevada; Slash; Teakettle Experiment

1. Introduction

Restoration of western forests after a century of fire suppression has become a management priority due to recent increases in fire size and severity. Many forests have a high density of small trees and extensive ladder fuels which can change fire regimes from their historic low-intensity pattern to stand-replacing crown fires. While several restoration treatments are possible, Stephenson et al. (1999) suggest they can generally be grouped into two approaches: structural restoration, which emphasizes first restoring historic stand structure and composition through mechanical thinning, and functional restoration, which prioritizes restoring ecological processes such as fire. In spite of their widespread use, there is little research on the different effects of thinning and burning treatments on understory communities, which contain most of the plant diversity in conifer forests (Shevock, 1996; Palik and Engstrom, 1999). Maintaining biodiversity in temperate forests has become a goal of forest managers (Hunter, 1999) and requires a focus on more than the tree overstory. Some restoration plans (Verner et al., 1992; Sierra Nevada Forest Plan Amendment, 2001) have implied that if forest overstory structure is well-managed, other components of biodiversity will inherently be affected in a positive manner (Lindh and Muir, 2004). Understanding the different effects of fire, thinning, and their combined use on plant diversity is important as more aggressive forest restoration is implemented (e.g., www.healthyforests.gov; Sierra Nevada Forest Plan Amendment, 2001).

Several studies have used chronosequence (comparison of different stands that vary in time since disturbance) (e.g., Duffy and Meier, 1992; Halpern and Spies, 1995; Battles et al., 2001; Keeley et al., 2003; Kerns et al., 2006) and repeated measures following manipulation (Halpern et al., 2005; Nelson and Halpern, 2005; Heithecker and Halpern, 2006) to examine differences in understory diversity after thinning and/or burning. A review covering a range of forest types, time since

* Corresponding author. Tel.: +1 530 754 7398; fax: +1 530 752 4604.
E-mail addresses: rbewleywayman@yahoo.com (R.B. Wayman), mpnorth@ucdavis.edu (M. North).

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disturbance, and harvesting intensities in temperate forests, found understory richness response to thinning was variable; decreases, increases, and no changes were reported (Battles et al., 2001). Some understory studies lack pre-treatment data making it difficult to determine how much of the response of diversity is due to fire or thinning treatments and how much was present in initial differences between sites.

Over 50% of California's vascular plant species are found in the Sierra Nevada (Davis and Stoms, 1996; Potter, 1998), and within montane conifer forests most of the diversity is contained in the understory community. Recent management plans call for extensive use of prescribed fire and thinning, yet there have not been any permanent plot field studies that followed understory response to these treatments through time, nor studies on potential mechanisms (e.g., water, nutrients, and light) affected by treatments and their influence on the forest understory. In 1998, we established permanent sample quadrats in replicated mixed-conifer plots scheduled for fire and thinning treatments in 2000 and 2001 in the southern Sierra Nevada, which has the highest vascular plant species richness and the most endemic and rare species in the Sierra (Shevock, 1996). Our objective was to use an experimental approach to address three questions: (1) How are environmental conditions and understory habitat affected by restoration treatments? (2) How do burning and thinning treatments affect initial summary measurements of understory plant species such as richness and cover, and how do their effects differ? (3) How do treatments alter plant community structure and composition? We tried to account for understory heterogeneity in our design by incorporating pre-treatment data and repeated measurements of permanent plots that were followed through time.

2. Materials and methods

2.1. Study site

The study was conducted within the Teakettle Experimental Forest, a 1300 ha reserve of old-growth (i.e. no prior history of logging or known history of stand-replacing disturbance) on the north fork of the Kings River within the Sierra National Forest. Elevations in the study area range from 1900 to 2200 m, and annual precipitation of approximately 125 cm falls almost entirely as snow between November and April (North et al., 2002). Teakettle's most common soil is mapped as a well-drained, mixed, frigid Dystric Xeropsamment, formed from decomposed granite, typical of many southern Sierra forests (Anonymous, 1993).

The forest type in the study area is mixed-conifer, which characteristically contains white fir (*Abies concolor*), black oak (*Quercus kelloggii*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), and Jeffrey pine (*P. jeffreyi*) (Rundel et al., 1988). An analysis of fire scars in Teakettle's mixed conifer indicates that the fire return interval was 12–17 years prior to European settlement (Fiegener, 2002; North et al., 2005a), and there have not been any sizeable (>3 ha) fires since 1865. Stem maps of aged trees indicate that 20th century fire suppression has increased overall stand density, particularly of smaller diameter shade-tolerant species such as white fir and incense-cedar, but that the increase in density is concentrated in tree clusters separated by persistent gaps (North et al., 2005a).

2.2. Treatments and data collection

Our research focused on a mixed-conifer area with relatively similar soils (all mapped as the Cagwin series) derived from decomposed granite. In this watershed, 18 permanent 4 ha plots were established (Fig. 1). Plot size was established using variogram analysis to estimate an area sufficiently large enough to include the range of variable forest conditions found at the site. An analysis of forest structure and composition found no significant pre-treatment differences between the 18 plots (North et al., 2002).

Treatments were randomly allocated on 15 plots, but National Forest operational constraints limited treatments to three options for three of the plots. Within this constraint, plots were randomly assigned to one of six treatments determined by the experimental design, a full factorial crossing two levels of burning treatments (burn and no burn) and three levels of thinning treatments (none, understory and overstory) (Fig. 1). The understory prescription followed guidelines in the California spotted owl (CASPO) report (Verner et al., 1992), which removes trees 25–76 cm (10–30 in.) diameter at breast height (dbh) while retaining at least 40% canopy cover. The overstory prescription (shelterwood) removes trees >25 cm (10 in.) dbh while leaving 22 regularly spaced large diameter trees per hectare. At Teakettle this marking approximated a prescription of cutting trees up to 100 cm (40 in.) dbh. The thinnings were applied in fall of 2000 (thin and burn plots) and early spring of 2001 (thin only), and the prescribed fire was lit in fall of 2001 after fuels had 1 year to dry.

In this experiment we cannot distinguish indirect and direct effects of treatments on the plant community because we did not survey mortality immediately after treatments. The thinnings were carried out in late summer and fall when almost all Teakettle herbs were dead or senesced, and 3 days after the prescribed fire the study site was blanketed by snow. Mortality from mechanical damage and fire may not be immediate. In this study we can only present how the plant community changed after treatments and by quantifying differences in environmental conditions infer some of the factors that may be associated with these changes.

Using a surveyor's total station, nine permanent gridpoints were mapped and marked on a 50 m × 50 m grid within two replicates of each treatment, while one 'intensive' plot in each treatment had 49 gridpoints on a 25 m × 25 m grid, for a total of 402 gridpoints (Fig. 1). Gridpoints (random) are nested within treatments (fixed) following a mixed-effect design (n = the 18 plots). At each gridpoint a 10 m^2 circular plot was established (hereafter referred to as "gridpoint") where all understory herbs, graminoids, and shrubs were identified to species (Hickman, 1993). Percent cover was estimated visually

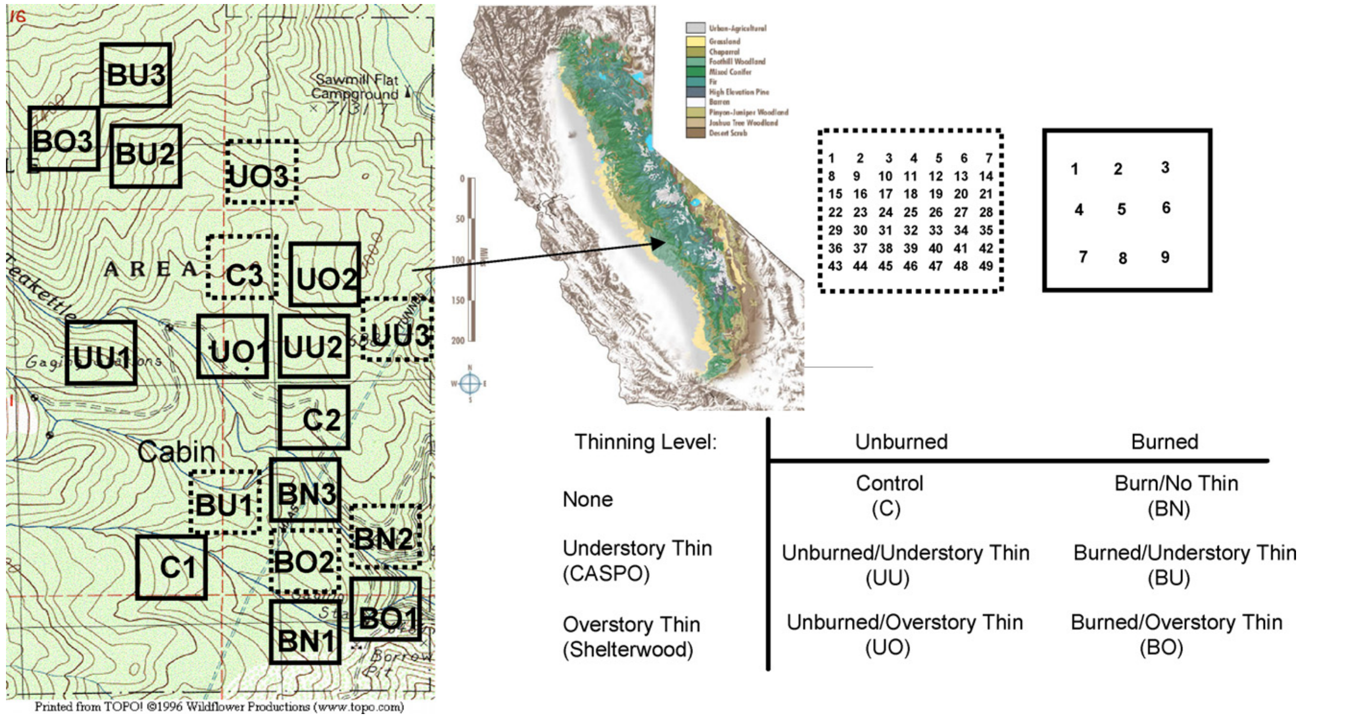

Fig. 1. Map of California showing the location of the Teakettle Experimental Forest, and a detail of the study site. The 18 4 ha plots are identified by code. For each treatment combination, plots are numbered 1–3 starting from the south. Plots outlined in a dashed line have 49 internal grid points (25 m ground distance spacing with a 25 m buffer) for intensive spatial sampling. The solid outlined plots have nine grid points (50 m spacing with a 50 m buffer).

during the peak bloom in early summer, prior to treatment application (1998 and 1999) and annually after completion of treatments (2002, 2003, and 2004). In 2000 and 2001, treatments were being implemented and no vegetation data were collected.

Environmental data were collected at all gridpoints ($n = 402$), but soil nutrient and deep (15–40 cm) soil moisture data were collected at only nine gridpoints in every plot ($n = 162$). We measured environmental variables that several studies have suggested may influence understory richness, cover, or composition: slope, aspect, slash, rock cover, percent bare ground (no litter layer), and coarse woody debris cover (all woody pieces ≥20 cm diameter) by two decay categories: 1–3 (relatively intact) and 4–5 (highly decayed) (Maser et al., 1988), slash, rock cover, and percent bare ground (no litter layer). We defined slash as all woody debris less than 20 cm in diameter excluding litter and duff. Litter depth at each gridpoint was averaged from three random measurements. In plots treated with the prescribed burn, the percent cover of ash was visually estimated in 5% increments. Soil depth over competent bedrock was determined using the three greatest depths recorded by a probe hammered into the ground at five random locations at each gridpoint. This method had been developed after testing the probe's measurement of bedrock depth against actual depth determined by digging a soil pit, and proved to be accurate with the sandy soils found throughout the 18 plots.

Volumetric soil water content was collected monthly during snow-free months for the 0–15 cm and 15–45 cm layers using time domain reflectometry (TDR; model No. 1502C, Tektronix Inc., Beaverton, OR). To assess canopy cover and understory light levels, a digital hemispherical photograph was taken from each gridpoint before and after treatments, at dawn or dusk using a level tripod, with the top of the photo oriented to true north. To facilitate detecting relative differences between plots, canopy cover photographs and soil moisture measurements were taken within a 3 week and a 3 day period, respectively.

Preliminary micro- and macro-nutrient analyses of soils were conducted in 2002 to identify potentially important nutrients from 100 core samples, each divided into organic, 0–10 cm, and 10–30 cm layers. In 2003, three 2 cm diameter soil cores were taken from 9 gridpoints per plot, compiled by 0–10 cm and 10–30 cm layers, kept on ice for no more than 10 h, and air dried to constant weight. Soils from these cores were passed through a 2 mm sieve, then analyzed for total N and C (AOAC-International, 1997), Bray P (the recommended method for low pH soils: Horneck et al., 1989), and nitrate and ammonium (flow injection analyzer method: Hofer, 2003; Knepel, 2003). Because nitrate and ammonium can fluctuate throughout the growing season (Cain et al., 1999), soils were collected during the peak bloom in June when nutrient limitations may be most apparent. Analyses were conducted by DANR analytical lab at the University of California, Davis.

2.3. Analyses

Hemispherical photographs were analyzed using Gap Light Analyzer version 2.0 (Frazer et al., 1999). For each photograph we used four metrics calculated by the program: percent canopy cover and direct, diffuse, and total transmitted light (mol m^{-2} day^{-1}). Aspect, slope, and latitude were used to estimate direct incident radiation following the procedure of McCune and Keon (2002).

TDR trace measurements were analyzed with an automated algorithm and volumetric water content estimated using the analysis procedure and ''low-C'' calibration equation from Gray and Spies (1995). Because a calibration for the Teakettle soils has not been developed yet, the actual calculated moisture values may be somewhat biased, but the relative differences among probes should be accurate since most existing TDR calibration equations have almost identical slopes (Gray and Spies, 1995).

Data were divided into two sets: plant cover and environmental variables. Each of these data categories were further divided into two sets, with one containing all 402 gridpoints, and the other containing only data for 9 gridpoints per plot (soil nutrient data and 15–45 cm soil moisture were collected only on 9 gridpoints per plot). Nonmetric multidimensional scaling (NMS), multi-response permutation procedures (MRPP), cluster analysis, and indicator species analysis (ISA) were completed using PC-ORD (MjM software design) following guidelines in McCune and Grace (2002). NMS is an ordination analysis suited for nonnormal data that places plots or plant species along Cartesian axes. MRPP is a nonparametric test of differences between grouped entities (in our case plant communities in plots with different treatments). Correlation analyses, Dunnett's C post hoc comparisons of a mixed-effects analysis of variance (ANOVA), and linear contrasts of means (LCM) were performed in SPSS 10.0 (SPSS Inc.).

To assess how treatments changed growing conditions, we compared mean environmental variables between the six treatments using a Dunnett's C post hoc analysis of a mixed-effects ANOVA. In this analysis we treated gridpoints as a random factor nested within treatments (fixed factor) of which there were three replicates. Because we did not have pre-treatment data for all environmental variables, we ran this procedure on 2003 data comparing treatments and controls.

To identify post-treatment habitats we used hierarchical cluster analysis to group individual gridpoints with similar environmental characteristics, using a Euclidian distance measure and Ward's linkage method. This analysis focused on how environmental conditions vary between gridpoints across all plots. The cluster dendrogram was inspected and parsed to four groups, while retaining at least 33% of the data information.

Using the plant cover data averaged by plot for each of the six treatments, we calculated alpha (average species richness per gridpoint) and gamma (total species) richness, Shannon's (H) and Pielou's J ((Pielou, 1969) a measure of evenness) for each treatment. To detect trajectories over time in richness, herb cover, shrub cover, evenness, and H, we used linear contrasts of means (LCM), comparing a pre-treatment (1999) value to each post-treatment year (2002–2004) value using gridpoint averages per plot. To assess differences between treatments at the same point in time, we compared mean alpha richness, herb cover and shrub cover in 2003 using a mixed-effects ANOVA.

To identify the most significant associations between environmental conditions and the plant community response across all treatments, we used nonparametric bivariate correlation analysis comparing environmental variables and selected plant diversity and cover measures: % shrub cover, % herb cover, Shannon's diversity index, evenness, and richness, using Spearman's rho. We used the 2003 plant dataset for this analysis because it was collected in the same year as soil data and other environmental variables.

We used cluster analysis and indicator species analysis (Dufrêne and Legendre, 1997) to identify the community structure of the post-treatment understory among all 402 gridpoint samples. Rare species (occurring <8 times, i.e., present on <2% of gridpoints) were deleted, leaving 42 species, and indicator species analysis was used to determine the optimal number of groups for pruning the cluster dendrogram. The 42 understory species were repeatedly clustered using a Sörensen distance measurement and flexible beta linkage ($\beta = -0.25$) into 2–15 groups. For each run, indicator values for each species were summed and the cluster step with the smallest average p-value was selected as the most informative number of clusters (McCune and Grace, 2002).

We used multi-response permutation procedure (MRPP (Mielke and Berry, 2001; McCune and Grace, 2002)) to test for differences in species composition within treatments before and after application (1999 versus 2003). A more conservative analysis, distance-based redundancy analysis, could also be used to test for differences between species composition groups (Dufrêne and Legendre, 1997). With MRPP, we used a Sörensen distance measure and n/sum(n) as the weighting function.

Nonmetric multidimensional scaling (NMS) was used to investigate indirect gradients associated with species distribution and how communities by treatment changed through time. Plant cover values were log-transformed accounting for the lowest nonzero value (McCune and Grace, 2002) because their distribution was highly skewed and a majority of cells contained zero values. To adjust for scale differences between the different measurements, environmental measurements were relativized by adjusting values to the standard deviation of each variable's mean value. To better understand the relation between the plant community and environmental conditions, a joint plot of significant ($r^2 \geq 0.1$) environmental variables was overlaid on the ordination of plots.

NMS was also used to detect trends in species distributions through time, beginning with the pre-treatment data of 1999. A vegetation matrix was created using the 39 species that occurred at least 8 times in every sampling year (1999 and 2002–2004). The percent cover values of each species were totaled for each treatment/year combination (6 treatments $\times$ 4 years = 24 ''year-plots''). An environmental matrix was created using average values for each treatment/year combination, and was used in a joint plot overlay of significant ($r^2 \geq 0.2$) variables.

Table 1
Mean 2003 environmental variables for each of the six treatments ($n = 3$)

	Control	Unburned/ understory thin	Unburned/ overstory thin	Burn/ no thin	Burn/ understory thin	Burn/ overstory thin
Ground cover						
Bare ground (no litter layer; %)	9.3 a	19.9 a	18.2 a	18.4 a	31.2 b	67.0 c
Coarse woody debris (%)	4.7 a	9.8 b	8.2 b	3.1 a	3.1 a	7.0 b
Litter depth (cm)	2.9 a	2.7 a	3.5 b	1.7 c	1.6 c	0.6 d
Ash cover (%)	–	–	–	11 a	52 b	71 c
Canopy and light						
Canopy cover (%)	79.8 a	72.5 b	62.7 c	80.0 a	71.3 b	58.0 c
Transmitted direct light (mol $m^{-2}d^{-1}$)	24.9 a	31.8 b	42.4 c	21.9 a	32.7 b	45.6 c
Transmitted diffuse light (mol $m^{-2}d^{-1}$)	2.3 a	3.0 b	3.9 c	2.2 a	3.1 b	4.4 c
Soil moisture						
June soil moisture 0-15 cm (%)	12.8 a	15.9 b	19.3 c	13.2 a	15.6 b	13.2 a
September soil moisture 0–15 cm (%)	10.3	10.9	11.8	10.6	12.1	11.5
June soil moisture 15–45 cm (%)	15.5	18.8	21.4	17.0	18.4	16.5
September soil moisture 15-45 cm (%)	11.7	13.2	13.6	12.2	12.6	12.3
Soil nutrients						
Total N, 0–10 cm (%)	0.23	0.25	0.22	0.19	0.24	0.19
Total N, 10–30 cm (%)	0.10	0.11	0.10	0.09	0.12	0.11
Total C, 0–10 cm (%)	5.42	6.33	5.28	4.36	4.94	4.24
Total C, 10–30 cm (%)	1.97	2.53	2.07	1.86	2.06	2.37
NH_4, 0–10 cm (ppm)	7.3	11.2	8.9	5.6	8.0	8.6
NH_4, 10–30 cm (ppm)	2.3	4.0	3.3	2.5	2.8	3.8
NO3, 0–10 cm (ppm)	1.1 a	2.5 ab	3.5 b	0.9 a	3.5 b	4.2 b
NO3, 10-30 cm (ppm)	0.1 a	0.4 a	0.6 a	0.1 a	0.4 a	1.6 b
P (Bray method), 0–10 cm (ppm)	117.9	73.2	124.9	119.8	127.5	116.6
P (Bray method), 10-30 cm (ppm)	92.4	41.9	109.6	73.6	84.4	59.0

Values in a row are not significantly different ($p < 0.05$) unless they have different letters (Dunnett's C post hoc analysis of the mixed-effects ANOVA).

3. Results

3.1. Treatment effects on environmental conditions and understory habitat

Treatments had significant, predictable effects on environmental variables such as litter depth, canopy cover, and coarse woody debris, although effects on soil moisture and nutrients were less straightforward. Differences in environmental variables between treatments and controls largely reflected the nature and intensity of each treatment's prescription (Table 1). Dunnett's C post hoc analysis of the mixed-effects ANOVA ($n = 18$, d.f. = 5) revealed significant differences in ground cover conditions, with both burn/thin treatments having significantly more bare ground and less coarse woody debris and litter than the other treatments. There were also significant differences in canopy cover and light between treatments with cover decreasing and light increasing with thinning intensity. June soil moisture at 0–15 cm increased with thinning intensity except in the burn overstory treatment. Other measures of soil moisture and all of the soil nutrients except for NO_3 did not significantly differ between treatments (Table 1).

Cluster analysis of environmental conditions using all gridpoint plots ($n = 402$) identified four major habitat types within the post-treatment forest: (1) high light, shallow soil; (2) low light, thick litter layer; (3) low light, deep soil; (4) high light, wet (Table 2). Significant differences in light, soil moisture, and slash (litter and CWD) distinguished the habitats. Habitat types did not align closely with particular treatments. All habitat types were found in almost all treatments, and no more than 34% of gridpoints belonged to a single habitat type within any treatment.

3.2. Treatment effects on cover, diversity, and individual plants

The post-treatment understory community contained 121 species: 12 graminoids, 17 shrubs, and 92 herbs (compared to 16 shrubs and 89 herbs in the pre-treatment sample; graminoids were not separated to species). Comparing plant and environmental measures ($n = 402$) from 2003, we found total richness, Shannon's diversity index, evenness, and herb cover were positively correlated with bare ground, direct and diffuse light, and soil moisture (Table 3). These variables were negatively correlated with litter depth, and richness, diversity, and herb cover were also negatively correlated with soil depth, slash, and coarse woody debris. In addition, herb cover was correlated with P at both depths, and negatively associated with total N, total C, and NH_4 at 0–10 cm. Shrub cover was positively correlated with total N and NO_3 at 0–10 cm, and negatively correlated with coarse woody debris classes 1–3, soil depth, and deep soil moisture.

Linear contrasts of means revealed that alpha richness and herb cover did not significantly change until the second post-treatment season (2003) (Fig. 2a). In 2003 and 2004 alpha richness tended to increase but only significantly in the burn/

Table 2
Major habitat types as identified by cluster analysis of the environmental variables

	High light, shallow soil	Low light, thick litter layer	Low light, deep soil	High light, wet
Percentage of total gridpoints (# of gridpoints)	43 (172)	32 (130)	18 (73)	7 (27)
Environmental conditions: % bare ground	45 a	0.5 c	25 b	29 ab
Litter depth (cm)	0.8 c	4.4 a	2.4 b	1.5 bc
% cover coarse woody debris	6.1 b	12.8 a	4.4 b	10.5 ab
Canopy cover (%)	66 c	77 a	74 b	68 c
Direct light (mol m^{-2} day^{-1})	40 a	25 c	29 b	37 a
Diffuse light (mol m^{-2} day^{-1})	3.6 a	2.4 c	2.8 b	3.4 a
Soil depth (cm)	56 c	77 b	119 a	95 ab
June soil moisture (%)	13 b	14 b	14 b	29 a
September soil moisture (%)	10 b	9 c	11 b	22 a
Plant cover and richness: herb cover (%)	13.5 a	3.6 b	7.6 ab	12.8 ab
Shrub cover (%)	7.5 b	15.0 a	10.6 ab	2.0 c
Richness (#species per gridpoint)	4.3 a	2.5 b	4.0 a	4.8 a
Percentage of habitat type in each treatment	32% BO	27% Control	34% BU	30% UO
	18% BN	25% UU	25% UU	22% UU
	16% BU	22% UO	11% Control	22% BU
	14% UO	21% BN	11% BO	11% BO
	13% Control	5% BU	10% UO	7% Control
	6% UU	0% BO	10% BN	7% BN

The four habitats are identified by mean values of their most significant environmental conditions. Vegetative characteristics of each habitat type are shown for reference but were not used in clustering habitat types. Values in a row with different are significantly different ($p < 0.05$). UU = unburned/understory thin; UO = unburned/overstory thin; BN = burned/no thin; BU = burn/understory thin; BO = burn/overstory thin.

overstory thin ($p = 0.001$ in 2003 and $p = 0.000$ in 2004). Herb cover significantly increased over 1999 levels by 2003 in the burn/thin combinations. Decreases in shrub cover occurred largely by the first post-treatment season, with little further change observed in 2003 (Fig. 2b) and 2004.

Comparing treatments in 2003, herb richness was significantly higher ($p < 0.1$, mixed-effects ANOVA) in the burn/understory thin compared to all other treatments except the burn/overstory thin (Fig. 2a). There was no significant difference in shrub cover between the treatments, but herb cover was significantly higher in the burn/understory and burn/overstory treatments compared to the others (Fig. 2b).

Herbs that significantly increased in cover and frequency are associated with bare soils and all dramatically increased in burn

Table 3
Significant post-treatment correlations (Spearman's rho) between environmental variables and plant cover, richness, diversity, and evenness calculated across treatments using all gridpoints ($n = 402$)

	Herb cover	Shrub cover	Richness	Shannon's diversity	Evenness
Ground cover					
Bare ground	+++		+++	+++	++
Litter depth	− − −		− − −	− − −	− − −
Slash	− − −	− −	− − −		
Coarse woody debris classes 1–3		− −	− −		
Canopy and light					
Direct light	+++		+++	+++	++
Diffuse light	+++		+++	+++	+++
Canopy cover	− − −		− − −	− − −	− −
Mean soil depth	− − −	− −	−	− − −	
Soil moisture					
June, 0–15 cm	+		+++	+++	+++
June, 15–45 cm	++	−	+++	+++	+++
Soil nutrients					
Total N, 0–10 cm	− − −	+			
Total C, 0–10 cm	− − −				
NH_4, 0–10 cm	− − −		−		
NO_3, 0–10 cm		++			
P, 0–10 cm	++				
P, 10–30 cm	++				− −

Only environmental measures with significant ($p < 0.1$) correlations are shown. Levels of significance are indicated as: $p < 0.01$ +++/− − −; $p < 0.05$ ++/− −; $p < 0.1$ +/−.

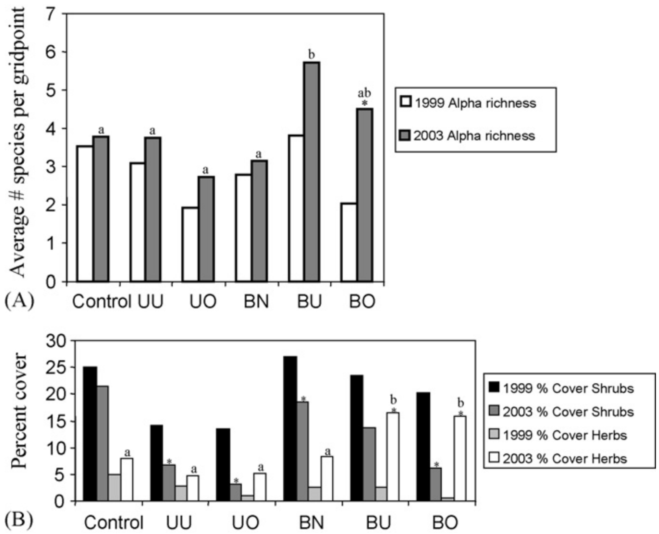

Fig. 2. (A) Average plant species richness per gridpoint (averaged by plot then by treatment) in 1999 (pre-treatment) and 2003 (second year post-treatment). Significant changes between years, found only in the burn/overstory thin, are indicated with an asterisk ($p < 0.1$ using linear contrasts of means, $n = 3$, d.f. = 3). Significant differences between treatments within 2003 are indicated by different superscript letters (Dunnett's C of mixed-effects ANOVA, $n = 18$, d.f. = 5). (B) Percent cover of herbs and shrubs by treatment in 1999 (pre-treatment) and 2003 (second year post-treatment). Significant changes between years are indicated with an asterisk ($p < 0.10$ using linear contrasts of means, $n = 3$, d.f. = 3). Significant differences between treatments within 2003 are indicated by different superscript letters (Dunnett's C of mixed-effects ANOVA, $n = 18$, d.f. = 5).

treatments. Most of the herbaceous species that decreased markedly in cover and frequency were either significant indicators of the control (*Hieracium albiflorum*, *Pyrola picta*) or were eliminated from any treated plot (*Corallorhiza maculata* and *Pterospora andromedea*) (Table 4). *C. maculata* was present in five of the six treatment areas in 1999 and was eliminated from all manipulation treatments, and *P. andromedea* had six occurrences in 1999 in four treatments (no occurrences in the control), and was absent from all post-treatment surveys. Several of the most common shrubs showed divergent trends in their frequency versus cover (Table 4). For many species, shrub cover was reduced while frequency counts remained similar or increased.

3.3. Treatment effects on plant communities

The cluster analysis of post-treatment community structure, using the 42 most common species and all 402 gridpoint plots, identified seven understory plant communities. The environmental variables that significantly differed between communities (not shown) were related to litter depth and bare ground, understory light, and soil moisture. For the NMS ordination of current conditions the greatest reduction in stress was achieved with three axes. The proportion of variance (the fit between distance in the ordination and the original space) represented by the first three axes was 0.145, 0.140, and 0.229, respectively (cumulative 0.514). The NMS ordination (Fig. 3, axes 2 and 3 are clearest display of factors of interest (McCune and Grace, 2002)) shows that there is little correlation between treatment and plant community, as the treatments are spread relatively

Table 4
Changes by species in the total number of occurrences over the 402 gridpoints, and in total percent cover summed over all gridpoints

Species	Frequency (number of occurrences)		Abundance (sum of % cover per gridpoint)		Treatments most abundant in
	1999	2003	1999	2003	
Increase					
Allophyllum integrifolium	2	33	0.2	76.6	BU, BO
Collinsia torreyi	32	96	31.3	264.7	BN, BU
Cryptantha simulans	16	91	1.7	245.5	BO, BN
Gayophytum eriospermum	53	162	18.4	1620.7	BO, BU
Lotus crassifolius	1	10	0.5	60.8	BO, BU
Phacelia hastata	3	30	0.4	42.3	BU, BO
Decrease					
Chrysolepis sempervirens	17	14	581.6	306.7	UU, BN
Corallorhiza maculata	7	1	0.7	0.1	Control
Hieracium albiflorum	31	13	82.5	25.6	Control, UU
Poaceae (*family*)	71	55	104.2	58.5	UU,
Pterospora andromedea	6	0	0.7	0	Eliminated
Pyrola picta	61	28	11.8	5.4	UU, Control
Divergent trend in frequency vs. percent cover					
Arctostaphylos patula	41	43	836.9	350.4	BN, Control
Ceanothus cordulatus	122	155	4441.2	2115.7	Control, BN
Corylus cornuta	13	14	602.4	396.5	BN, Control
Prunus emarginata	27	26	264.5	129.8	BU, Control
Ribes roezlii	20	80	93.6	80.3	BU, BO

For each species the two treatments in which it was most abundant are listed, with the treatment of greatest abundance listed first. Treatment code definitions are listed in Fig. 1. Only species with marked increases or decreases in frequency (≥2-fold) and/or abundance (≥30%) are shown. All five species with divergent trends are the most common shrubs at Teakettle.

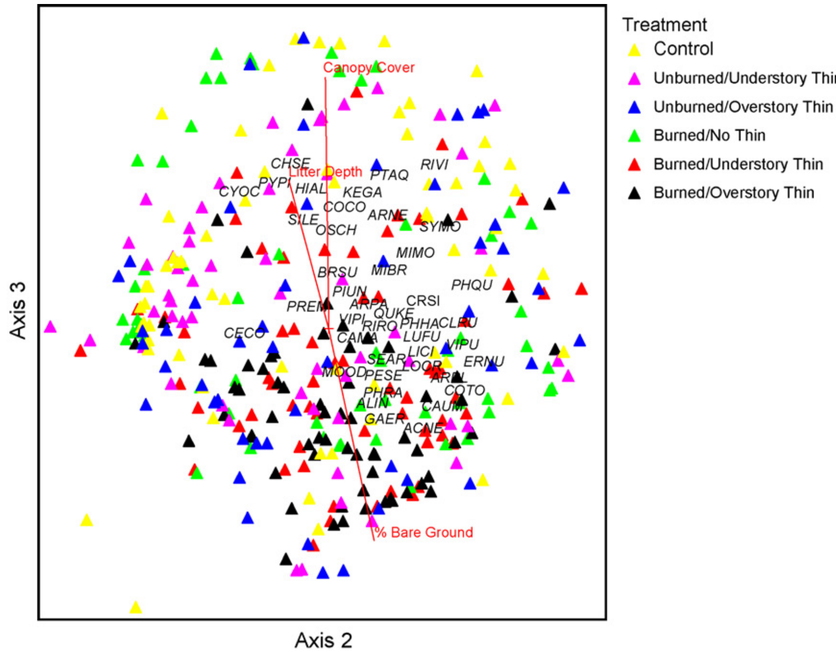

Fig. 3. Nonmetric multidimensional scaling ordination of the 42 most common plant species (see Appendix A) and the 356 plots that had plant cover of these species. Plots are shown with six symbols indicating their treatment. Significant ($r^2 \geq 0.2$) environmental variables, and the magnitude and direction of their gradient, are shown in the joint plot. The most important environmental variables identified are bare ground, litter depth, and canopy cover.

evenly throughout the ordination space. Bare ground, canopy cover, and litter depth were identified as the most significant environmental conditions associated with the ordination's gradients.

Species composition changed significantly between pre- (1999) and post-treatment (2003) in the burn/overstory thin ($p = 0.025$, $A = 0.243$ [chance-corrected within-group agreement]), burn/understory thin ($p = 0.082$, $A = 0.118$), and unburned/overstory thin ($p = 0.035$, $A = 0.135$) (MRPP analysis).

Following changes in overall plant composition, the NMS ordination (two axes cumulative proportion of variance = 0.897) showed patterns of treatment effects on community composition ($n = 24$) (Fig. 4). All pre-treatment plots in 1999 are clustered together and associated with greater litter depth, canopy cover and abundance of course woody debris decay classes 4 and 5. In

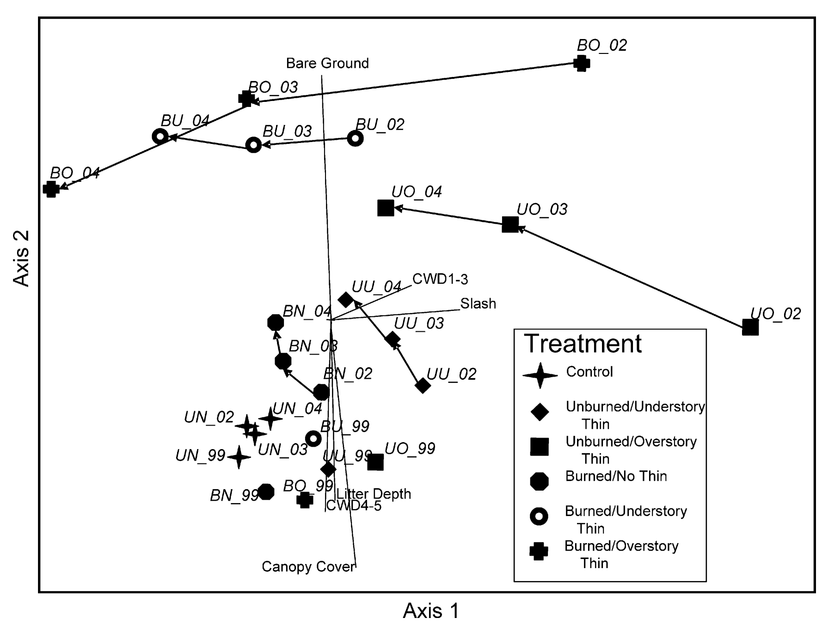

Fig. 4. Nonmetric multidimensional scaling ordination of the treatments through time. Cover values for the 39 species that occurred at least 8 times in every sampling year were totaled by treatment/year combination for 24 "year-plots". Pre-treatment data are from 1999 and post-treatments years are 2002–2004. Significant ($r^2 \geq 0.2$) environmental variables, and the magnitude and direction of their gradient, are shown in the joint plot.

subsequent years treatments follow different community trajectories, while the control plots remain in the original ordination space locale. The five manipulation treatments all show a similar pattern of divergence from pre-treatment composition in the first year after treatment, followed by smaller yet substantial changes over the next 2 years. The burn/no thin remained the most similar to pre-treatment plots. After the first year composition did not continue to move further away from pre-treatment composition, except in the burn/no thin and the unburned/understory thin. All thinning treatments were negatively associated with canopy cover, and the burn/thin combinations were associated with bare ground. Both unburned/thinned treatments were associated with fine coarse woody debris and slash.

4. Discussion

The understory community constitutes almost all of the plant diversity and provides habitat and food for many wildlife species in western conifer forests (Lindenmayer and Franklin, 2002). In our study, fire was crucial for restoring richness and herb cover of the mixed-conifer understory community because it reduced litter depth and coarse woody debris, providing more bare ground which may favor herb germination. Based on species succession patterns in logged and burned sites, Rees and Juday (2002) also concluded that early burn dominants responded to fire in particular and not to disturbance in general. We found thinning increased richness and cover but only when followed by fire. The importance of thinning before prescribed burning may be that it increased the extent and intensity of the fire. The percent of ash and blackened ground were significantly greater in the burn/understory thin (52%) and burn/overstory thin (71%) plots than in the burn/no thin (11%) plots, which lacked thinning slash (Heather Erickson, unpublished data). As is typical in the Sierra Nevada, our prescribed fire was lit in late October after the natural lightning season for easier containment and when air quality regulators allow more burning. Fires may not burn as hot or consume as much fuel in this condition of lower temperatures and higher humidity without the addition of thinning slash to fuel fire intensity and increase burn coverage.

Our results should be viewed with caution because we cannot separate whether treatments directly altered the understory community or indirectly influenced it by changing environmental conditions. We suspect shrubs may be more affected by the mechanical effects of the treatments (i.e., crushing or burning) because of their woody stems, larger stature and the fact that they are established and possibly better buffered from environmental change. In contrast, herbs may respond more to changes in environmental conditions because when treatments were implemented at Teakettle (late summer and fall), almost all herbs were dead or senesced. Determining the mechanisms that affect individual species may require more tightly controlled greenhouse experiments. Our intent is to quantify how plant communities were affected by treatments and infer factors that may possibly be influencing those changes.

4.1. Changes in environmental and edaphic conditions

Cluster analysis of the pre-treatment forest found it was characterized by patches of closed canopy, partial canopy, and dry gaps (i.e., open canopy) (North et al., 2005b). The highest richness and cover were associated more with soil moisture than with light levels, and light was not thought to be a limiting resource for the understory community (North et al., 2004). This relationship may be common in areas of summer drought, and in fire-suppressed forests where soil moisture can be a significant control on understory plants (Coomes and Grubb, 2000; Lindh et al., 2003).

Cluster analysis of the post-treatment forest found that influences of environmental conditions on richness and cover involved more than water. Soil moisture was still a main site factor associated with high richness and cover (Table 3), but other site conditions (soil and litter depth, diffuse light) were also identified as potential post-treatment influences on the understory community. Depth to bedrock was strongly associated with vegetation, with trees often occupying deep soil pockets and shrubs occupying shallower soils and open gaps where soils were less than 40 cm deep (Andrew Gray, unpublished data). The high herb richness on very shallow soils may reflect the absence of competing shrubs or dense tree cover. While these sites can have sufficient soil moisture in May and June when most herbs are at their peak of growth and blooming, the shallowest soils may not hold enough water to support trees and shrubs late in the growing season. Litter depth was negatively associated with herb cover and richness (Table 3), and decreases in herb cover were dramatic in localized areas of thinned plots with heavy slash. Thinning treatments that leave substantial logging residue may significantly depress herb cover and richness until fire or decomposition reduce slash and litter thickness.

Most soil nutrients were not strongly correlated with herb or shrub cover (Table 4). This may be because there was high spatial variability in pre-treatment soil nutrients (Erickson et al., 2005) as in other forests (Homann et al., 2001), and this is now coupled with fine-scale variability in disturbance intensity. Herb cover was correlated with P, but this correlation may be an artifact of P depletion at *Ceanothus cordulatus* sites. Nitrogen fixers are heavy P users (Uliassi et al., 2000; Pearson and Vituosek, 2002), and patches of *C. cordulatus*, the most dominant shrub at Teakettle, rarely have any herbs due to their complete occupancy of a site. Shrub cover was positively correlated with total N and NO_3 in the upper horizon, probably due to enriched *C. cordulatus* litterfall (Zavitoski and Newton, 1968). Studies in Mediterranean climates (e.g., Pausas and Austin, 2001) have suggested water can often be the most limiting resource, masking or overriding soil nutrient influences on herbaceous plants.

4.2. Fire and thinning effects on plant cover and diversity

We expected the thinning to affect the forest understory more by reducing competition for surface soil moisture (i.e., removing small trees that deplete surface soil moisture), than by increasing light levels through canopy cover reduction. Although pre-treatment richness was concentrated in wet areas, in the post-treatment environment a second area of high richness and herb cover emerged: high light, low moisture, shallow litter habitats common in burn/thin treatments (Table 2). The species with the most substantial increase in cover, *Gayophytum eriospermum*, grows in high light environments with shallow litter layers and low soil moisture (Potter, 1998), as do all of the species that substantially increased in cover and frequency, except *Phacelia hastata* (Table 4). Our study does not demonstrate a causative mechanism for the relationship of richness and cover with bare ground and shallow litter, but other studies have found similar correlations (Battles et al., 2001). Seedling germination of many understory species is dependent on bare soil. Although these seedbed conditions are frequently produced in burn areas when fire consumes much of the surface litter, they are generally reduced in thinning operations because of the increase in slash volume. This important area of high richness and cover that emerged in the post-treatment environment was not created in the thin-only plots.

The largest decrease in shrub cover occurred in the burn treatments. Shrubs directly compete with herbs for space, light, and soil moisture. Richness increases (largely accounted for by herbs, which were 92 of the 121 species) may have been greatest in burn/thin combinations partially because of the release from competition with shrubs.

Although the treatments created habitat conditions that could be conducive to exotic plant invasion, no infestation was observed. Other studies have documented an increase in non-native species in post-treatment forest communities (North et al., 1996; Battles et al., 2001; Crawford et al., 2001; Griffis et al., 2001; Keeley et al., 2003; Kerns et al., 2006). At our study site the only known non-native species was *Rumex acetosella*, which was limited to roads and skid trails, and was not widespread. Exotics can take several years to invade a treated area (Keeley et al., 2003; Kerns et al., 2006), so our study may have been too early to detect this change. Teakettle, however, is relatively isolated, closed to public vehicles, and only accessible from one dirt road 6 km from a lightly used paved road. These factors make it an unlikely site for major exotic infestation, but invasion rates might be higher if similar treatments were applied at more accessible sites.

Four species, *H. albiflorum*, *P. picta*, *P. andromedea* and *C. maculata* declined significantly in cover and/or frequency (Table 4). These species are common in red fir and mixed-conifer forests and are associated with denser tree cover and a deeper litter layer (Potter, 1998). The orchid, *C. maculata*, and the ericaceous *P. andromedea* disappeared in all treated plots. Because these declines were observed over all treatments except the controls, both thinning and burning may be detrimental to these species. The Sierra Nevada has several other chlorophyll-lacking, semi-parasitic species, including *Sarcodes sanguinea*, which are associated with old-growth conditions and may be sensitive to logging or fire disturbance. Halpern (1989) found that some species associated with old-growth forest in the Pacific Northwest do not noticeably recover from thinning and burning. A consistent trend in many studies is that untreated forest plots contain some species not found in any treated plots (North et al., 1996; Battles et al., 2001; Scheller and Mladenoff, 2002), although their numbers are usually few. To retain these species, a patchy array of treated and untreated areas may be necessary.

Two growing seasons after treatment completion, we saw increases in average species richness per gridpoint in those treatments that combined thinning with burning. Thinning or burning alone did not create conditions that triggered a significant response in species richness. All of the species that showed marked increases in post-treatment cover (Table 4) were most abundant in the burn/understory thin and/or burn/overstory thin plots. This may indicate that these species were responding to the particular conditions created by both burning and thinning together such as increased understory light and soil moisture caused by thinning, and burning's reduction in litter, slash, and shrub cover. In the burn/no thin plots, canopy cover was not significantly reduced and fire consumption of fine fuels was minimal without the addition of logging slash.

4.3. Post-treatment habitat types and plant communities

The effect of restoration treatments on the understory community was a highly localized combination of disturbance intensity and extent overlaid on existing patch conditions. For example, environmental conditions at some gridpoints in a burn/understory thin plot might closely resemble either unburned/understory thin or burn/no thin gridpoints if they did not burn or have slash, respectively (Fig. 3). This increased the contrast in environmental conditions between habitat types following treatments (Table 2 compared to Table 4 in North et al. (2005b)). Plant response was influenced not only by this habitat change, but also by the interaction of the existing plant community and the treatment. A patch of shrubs might be severely altered by fire but little impacted by thinning slash, while a patch of herbs might have the opposite response. Because of this complex interaction, gridpoint plant communities were highly varied within the same treatment (Fig. 3) and treatment effects would have been difficult to understand without following fixed gridpoint samples through time. Pre-treatment patch conditions have a strong legacy effect on post-treatment understory because the vegetation influences the intensity and residue of fire and thinning effects, respectively. Although individual measures of environmental or species variables showed clear trends relating to treatments, this heterogeneity made the results of analyses that combined the variables into habitats or communities more difficult to discern.

Using identical analyses, the number of communities increased from four (North et al., 2005b) to seven following treatments. Examining the species groupings, we found new plant associations and an increase in habitat heterogeneity. The environmental variables that significantly differed between the new plant communities were litter depth and bare ground, understory light, and soil moisture. In general, treatments caused an overall shift from a shrub-dominated to an herb-dominated community, particularly in the burn/thin combinations. All treatments showed an increase in the ratio of herb cover to shrub cover, but this change was most dramatic in the burn/thin combinations. Most Sierran herbs are annuals or short-lived perennials, and should therefore respond to disturbance on a different timescale than shrubs. While a dramatic herb response was observed immediately, we would expect even fire-adapted shrubs to be slower to recover.

4.4. Implications for restoration

The ordination of treatments through time shows that the greatest changes in species composition occurred in the first year after treatment implementation, with smaller but substantial changes each year thereafter (Fig. 4). Five of the six significant environmental variables in the before and after ordination are related to reducing ground fuels, which fire treatments decrease and thinning increases. Canopy cover is the only significant variable that decreases with thinning and is negatively associated with understory diversity. There are no quantitative descriptions of pre-fire suppression forest conditions, but anecdotal (LeConte [1875] 1930) and photographic (Gruell, 2003) descriptions indicate forests may have had a more open canopy, shallower litter, and less coarse woody debris. These conditions may serve as a reference point for the evolutionary environment of mixed conifer produced by an active fire regime (Falk, 1990; Society for Ecological Restoration, 1993). This would suggest that desired restoration conditions might be toward the upper left portion of the ordination space (Fig. 4), where the burn/understory thin and burn/overstory thin plots have tracked.

Our study suggests that the means by which fuels are reduced and forest structure is restored affects understory diversity and cover. Increased understory light and reduced litter, slash, and shrub cover were most associated with increases in species richness and herb cover. Prescribed fire was the most effective means of increasing these favorable habitat conditions, but when applied off-season it had a greater positive effect if additional fuels were provided by previous mechanical thinning. If care is taken to maintain those understory species that rely on undisturbed forest patches and to prevent exotic invasion, combined thinning and fire treatments may enhance richness and cover of native plants in the understory community.

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Appendix A

Teakettle's 42 most common understory species

Four letter code	Scientific name
COTO	*Collinsia torreyi*
ERNU	*Eriogonum nudum*
VIPU	*Viola purpurea*
ARPL	*Arabis platysperma*
PESI	*Pedicularis semibarbata*
CLRU	*Claytonia rubra*
SEAR	*Senecio aronicoides*
CRSI	*Cryptantha simulans*
LICI	*Linanthus ciliatus*
CAUM	*Calyptridium umbellatum*
VIPI	*Viola pinetorum*
PTAQ	*Pteridium aquilinum*
COCO	*Corylus cornuta*
CHSE	*Chrysolepis sempervirens*
OSCH	*Osmorhiza chilensis*
PYPI	*Pyrola picta*
HIAL	*Hieracium albiflorum*
CYOC	*Cynoglossum occidentale*
CAMA	*Calystegia malacophylla*
SYMO	*Symphoricarpos mollis*
PREM	*Prunus emarginata*
SILE	*Silene lemmonii*
PIUN	*Piperia unalascensis*
MIBR	*Mimulus breweri*
ARNE	*Arctostaphylos nevadensis*
LUFU	*Lupinus fulcratus*
PHRA	*Phacelia racemosa*
KEGA	*Kelloggia galioides*
MIMO	*Mimulus moschatus*
RIRO	*Ribes roezlii*
RIVI	*Ribes viscosissimum*
PHHA	*Phacelia hastata*
PHQU	*Phacelia quickii*
GAER	*Gayophytum eriospermum*
ALIN	*Allophyllum integrifolium*
ACNE	*Achnatherum nelsonii*
LOCR	*Lotus crassifolius*
ARPA	*Arctostaphylos patula*
BRSU	*Bromus suksdorfii*
QUKE	*Quercus kelloggii*
CECO	*Ceanothus cordulatus*
MOOD	*Monardella odoratissima*

References

Anonymous, 1993. Soil Survey of the Sierra National Forest Area, California. USDA Forest Service, Clovis, CA.
AOAC-International, 1997. Method 972.43. Official Methods of Analysis of AOAC International, 16th ed. AOAC International, Arlington, VA.
Battles, J., Shlisky, A., Barrett, R., Heald, R., Allen-Diaz, B., 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. For. Ecol. Manage. 146, 211–222.
Cain, M.L., Subler, S., Evans, J.P., Fortin, M.J., 1999. Sampling spatial and temporal variation in soil nitrogen availability. Oecologia 118, 397–404.
Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70, 171–207.
Crawford, J.A., Wahren, C.H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. J. Veg. Sci. 12, 261–268.

Davis, F.W., Stoms, M., 1996. Sierran vegetation: a gap analysis. Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II, Assessments and Scientific Basis for Management Options. University of California, Centers for Water and Wildlands Resources Center Report No. 37, pp. 671–690.

Duffy, C.D., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. 6, 196–201.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Erickson, H., Soto, P., Johnson, D., Roath, B., Hunsaker, C., 2005. Soil nutrient pools and fluxes within a mixed-conifer forest: implications for an ecological restoration. For. Sci. 51, 211–220.

Falk, D.A., 1990. Discovering the future, creating the past: some reflections on restoration. Rest. Man. Notes 8, 71.

Fiegener, R., 2002. Influence of Sampling Intensity on the Fire History of an Old-Growth Sierra Nevada Mixed Conifer Forest. University of California, Davis, CA.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation.

Gray, A., Spies, T.A., 1995. Water content measurement in decayed wood and forest soils using time domain reflectometry. Can. J. For. Res. 25, 376–385.

Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. For. Ecol. Manage. 146, 239–245.

Gruell, G.E., 2003. Fire in Sierra Nevada Forests: A Photographic Interpretation of Ecological Change Since 1849. Mountain Press Publishing, Berkeley, CA, 238 pp.

Halpern, C.B., 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70, 704–720.

Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5, 913–934.

Halpern, C.G., McKenzie, D., Evans, S.A., Maguire, D.A., 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecol. Appl. 15, 175–195.

Heithecker, T.D., Halpern, C.B., 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. For. Ecol. Manage. 226, 60–71.

Hickman, J.C., 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley, CA, 1400 pp.

Hofer, S., 2003. Determination of Ammonia (Salicylate) in 2M KCl Soil Extracts by Flow Injection Analysis. QuikChem Method 12-107-06-2-A. Lachat Instruments, Loveland, CO.

Homann, P.S., Bormann, B.T., Boyle, R.J., 2001. Detecting treatment differences in soil carbon and nitrogen resulting from forest manipulations. Soil Sci. Soc. Am. J. 65, 463–469.

Horneck, D.A., Hart, J.M., Topper, K., Koespell, B., 1989. Methods of soil analysis used in the soil testing laboratory at Oregon State University. Agric. Exp. Stn. SM 89, 4.

Hunter, M., 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, 698 pp.

Keeley, J.E., Lunbin, D., Fotheringham, C.J., 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. Ecol. Appl. 13, 1355–1374.

Kerns, B.K., Thies, W.G., Niwa, C.G., 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. Ecoscience 13, 44–55.

Knepel, K., 2003. Determination of Nitrate in 2 M KCl Soil Extracts by Flow Injection Analysis. QuikChem Method 12-107-04-1-B. Lachat Instruments, Loveland, CO.

LeConte, J. [1875] 1930. A journal of ramblings through the high Sierra by the University Excursion Party. Reprint. Sierra Club, San Francisco. 152 pp.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, DC, 351 pp.

Lindh, B.C., Muir, P.S., 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? For. Ecol. Manage. 192, 285–296.

Lindh, B.C., Gray, A., Spies, T.A., 2003. Responses of herbs and shrubs to reduced root competition under canopies and in gaps: a trenching experiment in old-growth Douglas-fir forests. Can. J. For. Res. 33, 2052–2057.

Maser, C., Cline, S., Cromack, K.J., Trappe J., Hansen, E., 1988. What we know about large trees that fall to the forest floor. In: From the forest to the sea: a story of fallen trees. USFS PNW-GTR-229, Portland, OR, 153 pp.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, 300pp.

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606.

Mielke, P.W., Berry, K.J., 2001. Permutation Methods: A Distance Function Approach. Springer Series in Statistics, New York City, NY, 352 pp.

Muir, J., 1911. My First Summer in the Sierra. Houghton-Mifflin Co., Boston, MA, 353 pp.

Nelson, C.R., Halpern, C.B., 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Can. J. Botany 83, 610–620.

North, M., Chen, J., Smith, G., Krakowiak, L., Franklin, J., 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Sci. 70, 24–35.

North, M., Oakley, B., Chen, J., Erickson, H., Gray, A., Izzo, A., Johnson, D., Ma, S., Marra, J., Meyer, M., Purcell, K., Roath, B., Rambo, T., Rizzo D., Schowalter, T., 2002. Vegetation and ecological characteristics of mixed-conifer and red-fir forests at the Teakettle Experimental Forest. USFS PSW-GTR-186, 52 pp.

North, M., Chen, J., Oakley, B., Song, B., Rudnicki, M., Gray, A., 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. For. Sci. 50, 299–310.

North, M., Hurteau, M., Fiegener, R., Barbour, M.G., 2005a. Influence of fire and El Nino on tree recruitment varies by species in Sierran mixed conifer. For. Sci. 51, 187–197.

North, M., Oakley, B., Fiegener, R., Gray, A., Barbour, M., 2005b. Influence of light and soil moisture on the Sierran mixed-conifer understory community. Plant Ecol. 177, 13–24.

Palik, B., Engstrom, R.T., 1999. Species Composition. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York, NY, pp. 65–94.

Pausas, J.G., Austin, M.P., 2001. Patterns of plant species richness in relation to different environments. J. Veg. Sci. 12, 153–166.

Pearson, H.L., Vituosek, P.M., 2002. Soil phosphorus fractions and symbiotic nitrogen fixation across a substrate-age gradient in Hawaii. Ecosystems 5, 587–596.

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. John Wiley & Sons, New York, 286 pp.

Potter, D.A., 1998. Forested Communities of the Upper Montane in the Central and Southern Sierra Nevada. USDA Forest Service, PSW-GTR-169, Albany, CA, 319 pp.

Rees, D.C., Juday, G.P., 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. 155, 291–302.

Rundel, P.W., Parson, D.J., Gordon, D.T., 1988. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour, M.G., Major, J. (Eds.), Terrestrial Vegetation of California. California Native Plant Society, Sacramento, CA, pp. 559–599.

Scheller, R.M., Mladenoff, D.J., 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecol. Appl. 12, 1329–1343.

Shevock, J.R., 1996. Status of rare and endemic plants. Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II. Assessments and Scientific Basis for Management Options. University of California, Centers for Water and Wildlands Resources Center Report No. 37, pp. 691–709.

Sierra Nevada Forest Plan Amendment: Final Environmental Impact Statement, 2001. Vols. 1–6. USDA Forest Service, Pacific Southwest Region, Vallejo, CA.

Society for Ecological Restoration, 1993. Mission statement. Res. Ecol. 1, 206–207.

Stephenson, N.L., Parsons, D.J., Swetnam, T.W., Christensen, N.L., 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecol. Appl. 9, 1253–1265.

Uliassi, D.D., Huss-Danell, K., Ruess, R.W., Doran, K., 2000. Biomass allocation and nitrogenase activity in *Alnus tenuifolia*: responses to successional soil type and phosphorus availability. Ecoscience 7, 73–79.

Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould Jr., G.I., Beck, T.W., 1992. The California Spotted Owl: A Technical Assessment of Its Current Status. U.S.F.S, PSW-GTR-133 Berkeley, CA, 285 pp.

Zavitoski, J., Newton, M., 1968. Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. Ecology 49, 1134–1145.