FIRE DECREASES ARTHROPOD ABUNDANCE BUT INCREASES DIVERSITY: EARLY AND LATE SEASON PRESCRIBED FIRE EFFECTS IN A SIERRA NEVADA MIXED-CONIFER FOREST

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ABSTRACT

Prior to fire suppression in the 20th century, the mixed-conifer forests of the Sierra Nevada, California, U.S.A., historically burned in frequent fires that typically occurred during the late summer and early fall. Fire managers have been attempting to restore natural ecosystem processes through prescription burning, and have often favored burning during the fall in order to mimic historical fire regimes. Increasingly, however, prescription burning is also being done during the late spring and early summer in order to expand the window of opportunity for needed fuel reduction burning. The effect of prescribed fires outside of the historical fire season on forest arthropods is not known. The objective of this study was to compare the short-term effects of prescribed fires ignited in the early and late fire season on forest floor arthropods. Arthropod abundance and diversity were assessed using pitfall trapping in replicated burn units in Sequoia National Park, California. Overall, abundance of arthropods was lower in the burn treatments than in the unburned control. However, diversity tended to be greater in the burn treatments. Fire also altered the relative abundances of arthropod feeding guilds. No significant differences in arthropod community structure were found between early and late season burn treatments. Instead, changes in the arthropod community appeared to be driven largely by changes in fuel loading, vegetation, and habitat heterogeneity, all of which differed more between the burned and unburned treatments than between early and late season burn treatments.

Keywords: *Forest arthropods, community heterogeneity, prescribed fire, season of fire, Fire and Fire Surrogate Study, species richness.*

INTRODUCTION

The responses of forest arthropods to fire has not been extensively investigated and studies that have been done show variable outcomes (Bess et al. 2002, Moretti, et al. 2004). For example, mid- and late-successional species are often negatively affected by a decrease in optimal habitat following fires (Yanovsky and Kiselev 1996, Økland, et al. 1996, York 2000). Other studies have demonstrated the importance of fire in creating diverse habitat mosaics that benefit various arthropod taxa and feeding guilds (Buddle et al. 2000, Gandhi et al. 2001, Moretti et al. 2004).

A large volume of evidence points toward the influence of vegetation community traits on arthropod distribution and diversity (Root 1973, Mopper and Simberloff 1995, Fernandes and Price 1988, Waring and Cobb 1992, Hunter 1992, Marques et al. 2000), as well as to the influence of the structure and composition of the forest floor litter layer (York 1999, Moretti et al. 2004, Gibb et al. 2006). Changes in the vegetation, litter, and woody surface fuels as a result of fire are therefore likely to influence the abundance and diversity of arthropod taxa and functional feeding guilds.

In the Sierra Nevada of California, frequent fires historically maintained heterogeneous forest stands with high structural diversity (Knapp and Keeley 2006). The influence of fire in Sierra Nevada ecosystems has been reduced over the 20th century due to aggressive fire suppression policies. Excluding fire from Sierra Nevada forests has altered forest structure by increasing the abundance of shade tolerant tree species (e.g. white fir) at the expense of shade intolerant but more fire resistant species (e.g. sugar pine and ponderosa pine) (Ansley and Battles 1998, Parsons and DeBenedetti 1979, Vankat and Major 1978). Fire exclusion has resulted in higher tree densities and abundant surface fuels, enhancing the continuity between surface fuels and live canopies (Biswell et al. 1968, van Wagtendonk 1985, Skinner and Chang 1996), and greatly increasing the risk of large, intense fires (Agee and Skinner 2005).

Prescribed burning has been used since the 1960's in an effort to return the natural role of fire to the Sierra Nevada (Kilgore and Briggs 1972, Bancroft et al. 1985, NPS 2005). The historical burn season in these forests was primarily during late summer to early fall (Caprio and Swetman 1995, Schwilk et al. 2006) and prescribed fires in Sequoia and Kings Canyon National Parks are often ignited during the latter part of this period (NPS 2005). However, atmospheric inversions during the fall are often not conducive to smoke dispersal and poor air quality can lead to postponement or cancellation of planned burns (NPS 2005). As a result, interest in early season burning when atmospheric conditions are generally more favorable for smoke dispersal is increasing.

Given the diversity of arthropod life histories, direct and indirect effects of fire on the arthropods are likely to vary by species. Previous work in the Sierra Nevada has shown burning to generally reduce arthropod abundance, but also favor some previously rare species (Apigian et al. 2006). Prescribed burning in this forest has the potential to influence arthropod abundance and community structure in two major ways. First, fire may directly kill arthropods. Second, fire can alter resources by

consuming vegetation, litter, duff, and woody debris that provide shelter and food to many arthropods. Fire might also enhance some arthropod communities by producing a diversity of new habitats (Martin and Sapsis 1992), weakening tree defenses (Ehnström et al. 1995, Ganz et al. 2003, McHugh et al. 2003, Sullivan et al. 2003), creating gaps that allow for an increase in understory herbaceous vegetation (Moretti et al. 2002), or through pulse releases of nitrogen that can follow forest fires (Hungerford et al. 1991, Debano et al. 1998, Neary et al. 1999, Fisher and Binkley 2000, Wan et al. 2001). These direct and indirect effects are likely to vary with the season of fire. The timing of fires relative to the phenological stages of arthropods could alter the affects of fire on their populations. Adult insects are likely more capable of fleeing fires than the less mobile developmental stages. Differences in how fires burn in the two seasons might also influence arthropod populations. Due to higher moisture content of surface fuels, early season burns consumed less total fuel and were patchier, leaving behind a greater amount of unburned habitat (Knapp et al. 2005). The ability of arthropods to rapidly recolonize burned areas may depend on the presence of these unburned islands.

The objectives of this study were: 1) to evaluate short-term changes in arthropod abundance and diversity following prescribed fires, 2) to determine the effects of season of fire on the arthropod community structure, and 3) to investigate how environmental changes resulting from the burning season treatments may have influenced the arthropod community.

METHODS

Study sites and system

The study area was located in an old-growth mixed-conifer forest on west to northwest facing aspects adjacent to the Giant Forest sequoia grove in Sequoia National Park (California, USA), at elevations ranging from 1900 to 2150 m. Nine 15 to 20 hectare experimental units were established and three early season burn, three late season burn, and three control treatments were randomly assigned (see Knapp et al. 2005 for site map). Overstory trees within the experimental units, in order of abundance, were white fir (*Abies concolor* Gordon and Glend.), sugar pine (*Pinus lambertiana* Douglas), incense cedar (*Calocedrus decurrens* Torrey), red fir (*A. magnifica* ssp. *shastensis* Murray), Jeffrey pine (*P. jeffreyi* Grev and Balf.), ponderosa pine (*P. ponderosa* Lawson), mountain dogwood (*Cornus nuttallii* Audobon), and black oak (*Quercus kelloggii* Newb.). The pre-settlement fire return interval for forests on these sites averaged 27 years (range 7-56 years) with 89 percent of fires occurring during the late or dormant season (Schwilk et al. 2006). The last major fire in the study area occurred in 1879 (Schwilk et al. 2006).

Treatments and arthropod sampling

Early season burns were conducted on 20 and 27 June 2002. Late season burns were conducted on 28 September, and on 17 and 28 October 2001. Knapp et al. (2005) provide a detailed description of ignition procedures and weather conditions during the burns.

Arthropods active on the forest floor were sampled in reference to a system of 36 permanent points on a 50 m grid within each experimental unit. Two pitfall traps were deployed 7 m and 17 m from all odd-numbered grid points (36 traps/unit, N = 324), along randomly oriented transects placed for measuring surface fuels and coarse woody debris parameters before and after fire treatments (see Knapp et al. 2005 for description of fuel transect protocols). To ensure that fuel measurements would not be altered by pitfall trapping, the traps were set one meter to the side of the fuel transect. Pitfall traps consisted of plastic buckets, 15 cm in diameter by 13 cm in height, and were dug into the ground so that the opening of the bucket was approximately 2 cm below the ground surface. Each trap contained a 50:50 mixture of water and propylene glycol to act as a killing agent and preservative. Two post-treatment samples were taken on consecutive weeks starting on 19 August 2003. After collecting the first set of samples on 27 August, traps were reset and the final sample was collected on 3 September 2003. All samples were initially frozen, and then sorted, counted, and stored in 95 percent ethanol.

A pilot arthropod survey using the same field procedures was also completed for a single one-week sampling period prior to the burns (starting 15 August, 2001). However, only a subset of taxa (primarily large and easy to count ground-dwelling species) were sorted and identified from these samples.

Specimens were named according to the lowest taxonomic level to which they could be readily identified. In general, arthropods were identified by family membership and sorted to morphospecies (hereafter referred to as species). Voucher specimens were preserved in 95 percent ethanol or pinned, and stored at the U.S. Geological Survey Sequoia-Kings Canyon Field Station in Sequoia National Park, CA. Arthropod data were standardized by calculating the mean capture of each species per pitfall trap, per day, at each sampled grid point. Where necessary, such as in the event of pitfall traps disturbed by bears, unit level calculations were corrected for these losses by omitting those traps from calculations. Of the 324 buckets deployed, 27 were disturbed during the first week and 21 were disturbed during the second week.

Effect of fire on the abundance of arthropod species and feeding guilds

Differences in arthropod abundance following fires were assessed by testing for treatment effects on average capture rates and also by comparing the distribution of treatment cumulative abundance against assigned rank abundance. Mean capture of arthropods per trap, per day across treatments were compared with ANOVA. Unplanned pair-wise comparisons among all treatments were made using Tukey's Honest Significant Differences procedure (HSD). Cumulative abundance distributions were tested for differences using the Kolmogorov-Smirnov Test.

All taxa were assigned to one of six trophic guilds based on a variety of sources of information (e.g. Borror, et al. 1992, Arnett 2000), including observations made during the course of this work. Guilds were selected for analysis in addition to species because

Table 1. Summary of the arthropods captured across all experimental units.

Class	Order	# Morpho-species	Total # individuals	Proportion of capture
Hexapoda	Hymenoptera	100	4302	0.201
	Diptera	81	3855	0.180
	Coleoptera	63	1603	0.075
	Hemiptera	21	401	0.019
	Lepidoptera	12	64	0.003
	Orthoptera	9	5079	0.237
	Neuroptera	7	15	0.001
	Psocoptera	5	30	0.001
	Trichoptera	3	44	0.002
	Auchenoryncha	3	220	0.010
	Sternoryncha	2	197	0.009
	Thysanura	1	3	<0.001
	Siphonaptera	1	7	<0.001
	Rhapidoptera	1	13	0.001
	Blattaria	1	2	<0.001
	Microcoryphia	1	3101	0.145
	Phthiraptera	1	63	0.003
Arachnida	Araneae	26	2181	0.102
	Acari	2	149	0.007
	Scorpiones	1	1	<0.001
	Pseudoscorpiones	1	4	<0.001
	Opiliones	1	19	0.001
Diplopoda	Opisthospermophora	2	20	0.001
Chilopoda	Scolopendromorpha	2	15	0.001
	Lithobiomorpha	1	39	0.002

feeding guilds were assumed to reflect functional relationships of species to the environment. The guilds assigned were: detritivores, omnivores, parasites, predators, phytophages, and xylophages. Taxa falling into the unknown feeding category were excluded from the guild analyses. Total captures per guild, per treatment was then calculated by summing the standardized capture numbers as described above. To test for an effect of burning on guild abundance, the community structure of the combined burn treatments as represented by the trophic guild abundance counts was compared to the control using chi-square (X^2) distribution analysis. The effect of fire season on guild structure was further tested using chi-square to compare the observed abundances of the guilds between the fire treatments.

Arthropod community diversity and structure

Two community diversity statistics (species richness and the Shannon-Wiener Index (H´)) were calculated at two scales based on trapping point totals nested within units (alpha diversity) and for each experimental unit (beta diversity). The effect of treatment on alpha diversity measures was evaluated using a nested ANOVA (trapping points as subsamples within units). Treatment effects on beta diversity were analyzed as a completely randomized design with ANOVA. Comparisons among treatment and control means of species richness and H´ at both diversity scales were made using Tukey's HSD.

In addition to richness and H´, the effects of fire on arthropod pattern diversity (Magurran 1988), sometimes referred to as "community heterogeneity" (Collins 1992), was examined. Arthropod community heterogeneity was defined as the mean pairwise dissimilarity between trapping points in an experimental unit and was calculated using the methods of Bray and Curtis (1957) and Faith et al. (1987). Mean heterogeneities of the treatments were calculated from the average heterogeneity values of the experimental units and were evaluated with ANOVA.

Effect of environment on guild structure and arthropod community

To examine the possibility that vegetation heterogeneity present after the burns drove the differences in arthropod assemblages among treatments, within-unit heterogeneity of the arthropod community was tested for association with vegetation heterogeneity using Spearman's coefficient of rank correlation. Vegetation was sampled in ten 50 m x 20 m modified Whittaker plots per unit for a different study using the same experimental units (sampling details and list of most abundant herbaceous and shrub species in Knapp et al., (in press)). Heterogeneity of vegetation was defined as the mean pairwise species composition dissimilarity among vegetation plots within a unit and was calculated on presence/absence data using the method of Czekanowski (1913) (See Collins 1992, Schwilk et al. 1997).

Relationships between arthropod community structure and environmental variables were analyzed using Nonmetric Multidimensional Scaling (Mather 1976, Kruskal 1964) in PC-ORD (McCune and Mefford 1999). Two ordinations of 159 trapping points were run: the first on guild compositions (capture per trap per day of 6 guilds) and the second on individual species (capture per trap per day of 351 species). The ordinations used an iterative search for the axes positions that minimized the stress of axes configuration.

Nine environmental variables described the physical environment at each trapping point: proportion of the ground surface burned, litter depth, duff depth, percentage of ground covered by coarse woody debris (CWD) (with CWD defined as having a diameter = 7.6 cm), volume of CWD per hectare, elevation, slope, aspect, and potential solar radiation. Elevation, aspect, and slope were estimated by overlaying the spatial coordinates of the nearest gridpoint with a Geographic Information System 10 m resolution digital elevation model, using ArcMap (ESRI 2000). Potential solar radiation was estimated using formulas

Table 2. Chi-square table of observed and expected daily capture of six arthropod feeding guilds under three treatments: no burn (control), early season prescribed fire (early), and late season prescribed fire (late). Expected counts are in parentheses.

Burn treatment	Detritivore	Omnivore	Parasite	Phytophage	Predator	Xylophage	Total
Control	197.4 (184.7)	54.3 (54.2)	6.5 (13.0)	8.8 (17.0)	57.1 (54.6)	0.5 (1.0)	324.6
Early	100.3 (104.6)	30.6 (30.7)	7.2 (7.4)	10.9 (9.6)	34.0 (30.9)	0.9 (0.6)	183.8
Late	119.8 (128.1)	37.7 (37.6)	15.6 (9.0)	18.8 (11.8)	32.4 (37.9)	0.9 (0.7)	225.2
Total	417.5	122.6	29.3	38.5	123.5	2.3	733.6

of McCune and Keon (2002). Litter and duff depth, volume of CWD/ ha, and percent of ground surface covered by CWD were estimated along fuel transects placed adjacent to the pitfall traps, using methods of Brown (1974) and Bate et al. (2002). Proportion of ground surface area burned was estimated by measuring the length of burned and unburned patches along the fuel transects.

Both the guild and individual species Nonmetric Multidimensional Scaling ordinations were started with a random configuration and used the Sorenson distance measure. A total of 40 runs were done with real data, followed by a Monte Carlo test of 50 runs with randomized data. Correlations with environmental variables were tested using sequential Bonferroni-correction.

Table 3. Strength of association (r^2) between environmental variables and NMS ordination axes for ordinations based on (a) arthropod feeding guilds, or (b) individual arthropod species. Environmental variables significantly correlated with each axis (P<0.05 after sequential Bonferroni analysis) are noted in bold.

(a) Guild ordination		
Environmental variable	**Axis 1**	**Axis 2**
	---------- r^2	----------
Prop. ground burned	**0.154**	**0.211**
Litter depth	**0.071**	**0.151**
Duff depth	**0.056**	**0.091**
Elevation	**0.061**	0.003
Aspect of slope	**0.060**	0.031
Volume of logs/ha.	**0.038**	0.020
% covered by logs	0.037	0.012
Solar radiation	0.027	0.001
Slope	0.043	0.007

(b) Individual species ordination			
Environmental variable	**Axis 1**	**Axis 2**	**Axis 3**
	---------- r^2 ----------		
Prop. ground burned	0.003	**0.339**	**0.088**
Litter depth	0.001	**0.293**	0.029
Duff depth	0.003	**0.209**	0.026
Elevation	0.005	**0.106**	0.027
Aspect of slope	0.051	**0.059**	0.000
Volume of logs/ha.	0.001	0.042	0.018
% covered by logs	0.002	0.148	0.000
Solar radiation	0.006	0.042	0.012
Slope	**0.045**	**0.023**	0.001

RESULTS

Effect of fire on the abundance of arthropod species and feeding guilds

A total of 21,427 individuals representing 348 morphospecies were collected across all units over the two week post-treatment sampling period (Table 1). The mean daily capture of arthropod individuals per trap, per day in both early and late season burn treatments (3.91 and 4.85 respectively) did not differ from each other, but were significantly lower than the mean of the unburned control (6.43) ($F_{2,6}$=16.34, P=0.004). The treatments also differed in their cumulative abundance curves (P<0.001, Fig.1), with arthropods again showing greater abundance in the control than in the burn treatments.

The proportional guild structure of the combined burn treatments differed significantly from the control (X^2_{12}=21.78, P=0.042). Proportion of the community belonging to specific feeding guilds differed among treatments, with a trend toward increased representation of the less dominant guilds such as the phytophagous, parasitic, and xylophagous groups in the burning treatments (Fig.2, Table 2). The proportion of the community represented by detritivores was also less in the burn treatments**.** Little difference in the proportion of the community represented by omnivores and predators was found among treatments. No significant differences between guild proportions in the early and late season burn treatments were found (x^2_6=4.97, P=0.55). Of the 348 morphospecies, 60 were excluded from the guild analyses due to lack of information regarding their life histories. The majority of excluded species were Diptera (38), followed by Coleoptera (8), Hymenoptera (6), Hemiptera (5), and Trichoptera (3). The excluded species represented 8.9 percent of the total arthropod individuals collected.

Arthropod community diversity and structure.

Species richness at the individual trapping point level was greater in the late season burn treatment than in early season burn treatment and in the control ($F_{2,6}$=10.00, P<0.001; Fig.3a). Richness in the early season burn treatment did not differ from the control. Comparisons of the Shannon index indicated that burn treatments contained greater arthropod community diversity than the control ($F_{2,6}$=14.03, P<0.001; Fig.3b). However, H' did not differ between early and late season burn treatments.

Arthropod richness and H´ at the unit level showed a similar pattern to the trapping point level measures. Although late-season burn species richness and H´ were marginally significantly greater, and significantly greater than that of the control ($F_{2,6}$=4.97, P=0.053 and $F_{2,6}$=5.52, P=0.044, respectively), neither differed from the early season treatment. Arthropod pattern diversity as measured by community heterogeneity was significantly greater in the burning treatments ($F_{2,6}$=10.98, P=0.009; Fig. 4), but community heterogeneity did not differ significantly between the early and late season burning treatments.

Data from the pre-treatment pilot study were analyzed to investigate whether any of the diversity results could be explained by differences among treatments that existed prior to the burns. However, no significant differences in species richness or H´ were found among experimental units in the pilot study ($F_{8,143}$=0.91, P=0.450; and $F_{8,143}$=0.38, P=0.700, respectively).

Analyses conducted for this study included all species found in the pitfall traps, whether they were ground dwelling and specifically targeted by the trapping method or flying and captured incidentally by, for example, attraction to the liquid in the pitfall traps. In order to determine the extent to which the findings of this study were influenced by including species trapped incidentally (i.e. Hymenoptera, Diptera, Lepidoptera) in the analyses, we conducted the same analyses for a subset of the 2003 data, including only species commonly sampled with pitfall traps (ground-dwelling beetles, ants, Orthoptera etc. – the same species of the 2001 pretreatment pilot study). Results for all tests with the restricted data set were similar to those found for the full data set, and therefore not reported here.

Effect of environment on guild structure and arthropod community.

Following fire treatments, arthropod community heterogeneity was positively correlated with vegetation community heterogeneity (r_s=0.689, P=0.040, Fig. 5). This association between the arthropod community and environmental factors was further explored through NMS ordinations. For the ordination of the community summarized by feeding guilds, a two dimensional solution was determined to be the best final fit after 400 iterations. Axis one accounted for 48 percent of the variation in data, while axis two accounted for 42 percent. Final stress for the solution was 12.65, and final instability was 0.00003. For the ordination of the community summarized by individual species, a three dimensional solution was

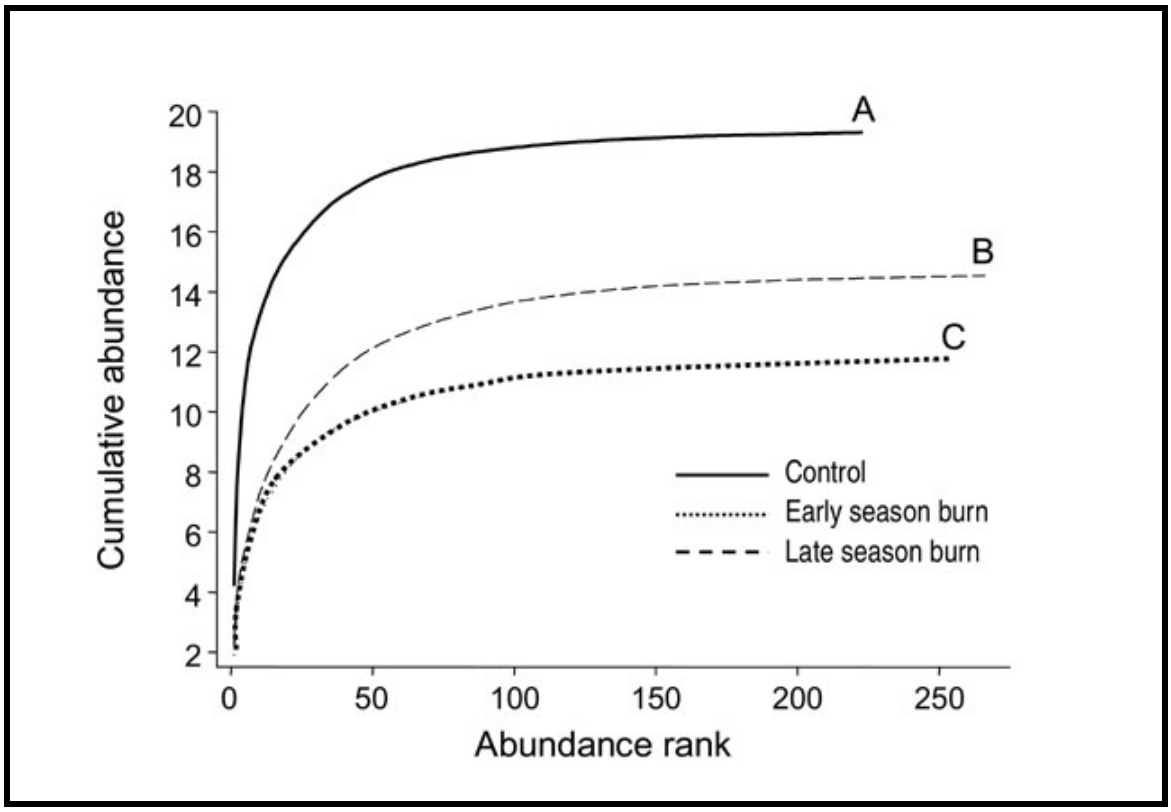

Fig. 1. Effect of fire on cumulative arthropod abundance (mean capture per day) vs. abundance ranks. Plots with different letters differ significantly in distribution (Kolmogorov-Smirnov test, $P<0.05$).

determined to be the best fit after 142 iterations. Axis one accounted for 19 percent of the variation in the data, axis two accounted for 22 percent, and axis three accounted for 32 percent. Final stress for the solution was 17.94, and final instability was 0.00001. Based on the final stress and instability, both ordinations were considered to be good fits for the data (McCune and Mefford 1999).

The feeding guild ordination identified six of the nine environmental variables (proportion of the ground surface burned by the fire treatments, litter depth, duff depth, elevation, aspect and the volume of CWD per hectare) as being significantly associated with axis one (Table 3a). Percent of the ground surface burned, litter depth, and duff depth were also significantly associated with axis two. The proportion of the plot area burned had the strongest association with arthropod guild structure in the burning treatments, while litter and duff depths were most strongly associated with guild structure in the untreated control.

The individual species ordination provides a visual depiction of differences between arthropod guild structure in the burned treatments and the controls (Fig.6), with the majority of trapping points in the control units located in the lower part of the figure. This species-based ordination also identified six of the nine environmental variables as being significantly associated in axes structure for arthropod species composition (Table 3b). The two ordinations had five variables in common. Volume of CWD per hectare

was not a significantly associated with axis structure for the species ordination, while slope was. As found in the guild ordination, the variable most strongly associated with species composition in the burn treatments was proportion of the plot area burned, while litter and duff depths were most strongly associated with species composition in the controls.

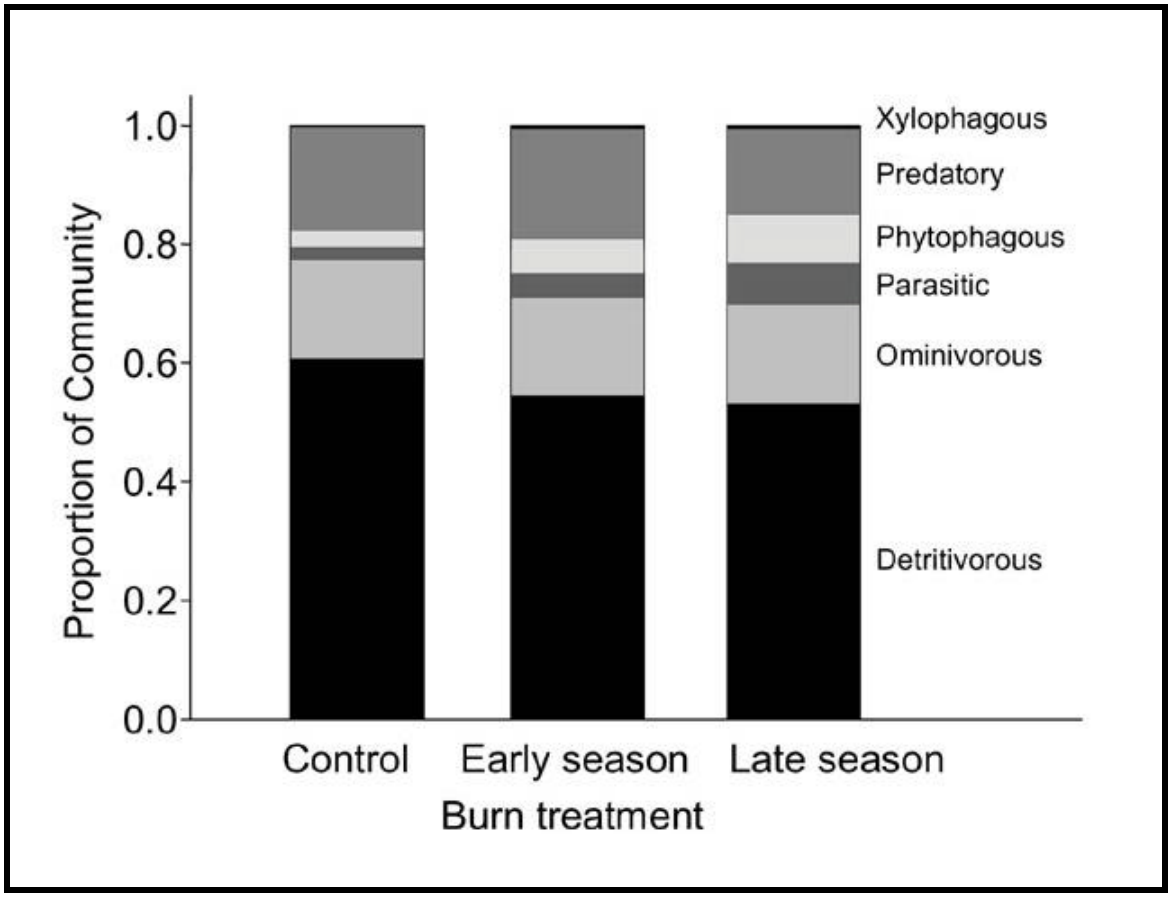

Fig. 2. Proportional abundance of six arthropod feeding-guilds in each of three prescribed burn treatments (unburned control, early season burn, and late season burn).

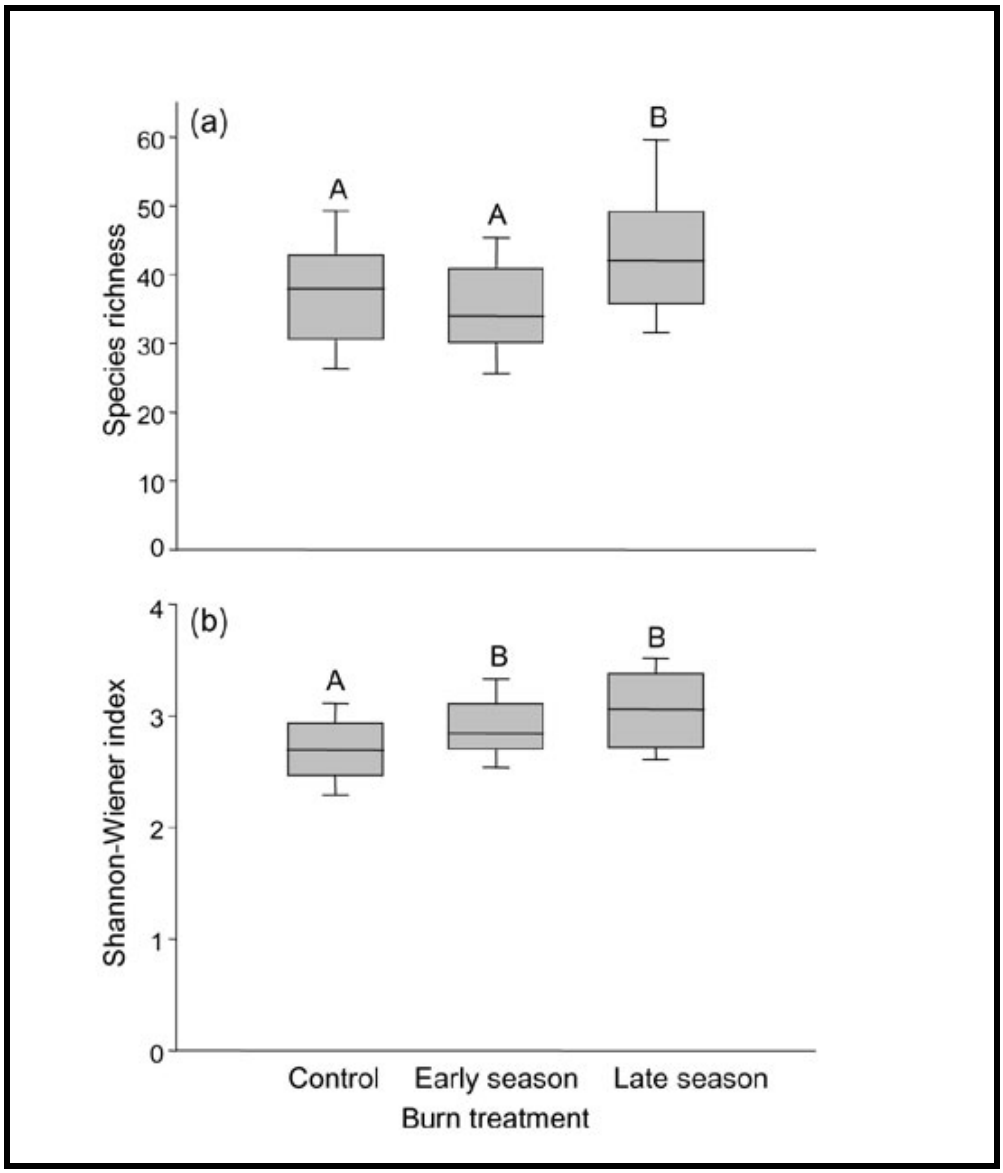

Fig. 3. Arthropod species richness (a), and Shannon-Wiener Index of arthropod diversity (b) for trapping point means, following one of three treatments: unburned control, early season burn, and late season burn. The median species richness of the treatments is shown, with the bottom and the top of the box plots representing the 25th and the 75th percentiles respectively. The bottom error bar shows the 10th percentile and the top bar shows the 90th. Boxes with different letters are significantly different (ANOVA followed by Tukey's HSD multiple comparisons, $P<0.05$).

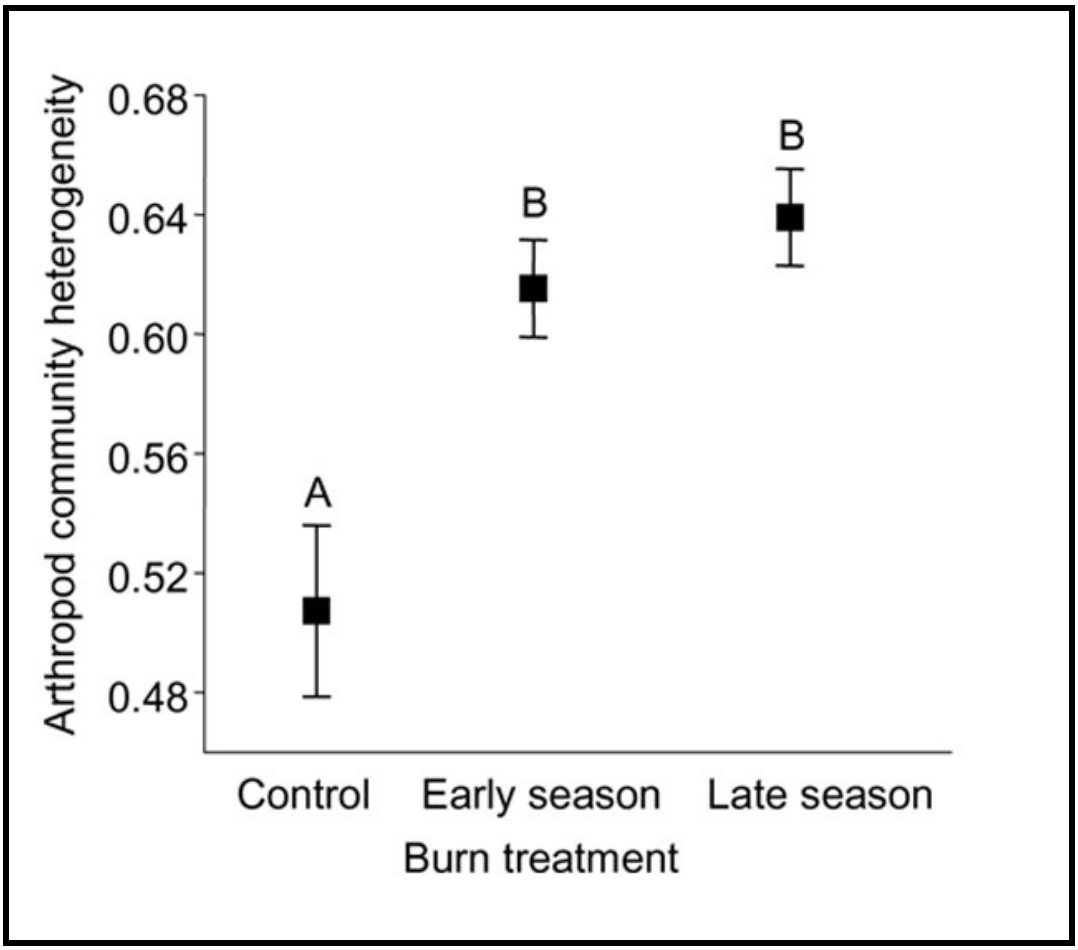

Fig. 4. Arthropod community heterogeneity following three treatments: unburned control, early season burn, and late season burn. Means (±1SE) with different letters are significantly different (ANOVA followed by Tukey's HSD multiple comparisons, $P<0.05$).

DISCUSSION

Pitfall trapping is a common and efficient means of sampling ground-dwelling arthropods (Spence and Niemela 1994, Spence et al. 1997, Abildsnes and Tommeras 2000) and has been shown to provide reasonable abundance estimates for certain arthropod groups (Baars 1979, Niemela et al. 1990, and Wang et al. 2001). However, pitfall trapping data must be interpreted cautiously because trapping efficiency varies greatly among species and there are many possible additional sources of bias (see Ulyshen et al. 2005, Work et al. 2002, Spence and Niemela 1994, Benest 1989, Digweed et al. 1995, Maelfait and Desender 1990, Adis 1979, Liebherr and Mahar 1979). While differences in response among taxa or guilds in this study may be due, in part, to our choice of sampling method, our objective was not to obtain true abundance estimates for all taxa, but to detect differences in arthropods across treatments.

Due to the effort required to sort the many samples for such a large-scale study, it was feasible to only trap for a portion of the seasonal active period for many arthropods. Short trapping

intervals may fail to capture arthropods that are present in the system but not active during the sampling period. However, the influence of trapping season length is assumed to be proportional across all experimental units, allowing useful among-treatment comparisons to be made.

The higher species richness in the late season burn treatment and the greater H´ in both burn treatments are contrary to the decrease in diversity after fire reported by Hanula and Wade (2003). However, the burning treatments in longleaf pine forests studied by Hanula and Wade (2003) involved multiple burns across many years, while this study reported results after a single burn. Our results were also somewhat surprising given that the abundance of individuals was lower in the burn treatments, which based on previous studies (Preston 1962b, Williams 1964, Rosenzweig 1995) would be expected to result in capture of fewer species. Our results, however, are in general agreement with those of Apigian et al. (2006), who found that burning in another Sierra Nevada forest that had experienced fire suppression slightly increased arthropod diversity by favoring previously rare species despite causing decreases in the abundance of common species. Greater diversity of arthropods in the burning treatments is possibly the result of greater heterogeneity in habitat, because burning produces a mosaic of burned and unburned patches (Knapp et al. 2005). In addition, the significant positive association between arthropod community heterogeneity and vegetation community heterogeneity supports the idea that fire may have influenced arthropod community heterogeneity through its effects on vegetation.

Both early and late season prescribed burns appear to have significantly altered the feeding guild structure of the arthropod community in this forest. The reduced abundance of detritivores was likely due to fire's consumption of the organic components of the litter and duff layers (Debano et al. 1998, Neary et al. 1999). A decrease in quantity and quality of available organic material, and an increase in ground surface exposed to sunlight would be expected to lead to fewer decomposers on the forest floor (Collett et al. 1993). The greater abundance of dead wood utilizing xylophages (e.g. Buprestidae and Cerambycidae) noted in burn treatments in this study was likely due to the higher number of standing dead trees. Between 2001 (preburn) and 2004 (one year after the conclusion of the sampling for this study), 6 percent of the trees in the control had died, as compared to 35 percent and 48 percent in the early- and late season burn treatments, respectively (Ferrenberg, unpublished data, Schwilk et al. 2006). Greater abundance of arthropods (particularly beetles) that utilize dead and dying wood is a widely reported trend following fires (Ehnström et al. 1995, Ganz et al. 2003, McHugh et al. 2003, Sullivan et al. 2003).

While the vegetation community responds variably to fire, many of the effects of fire on plants can be beneficial to phytophagous insects, a guild that was more abundant in the two burn treatments. Reduced forest canopy

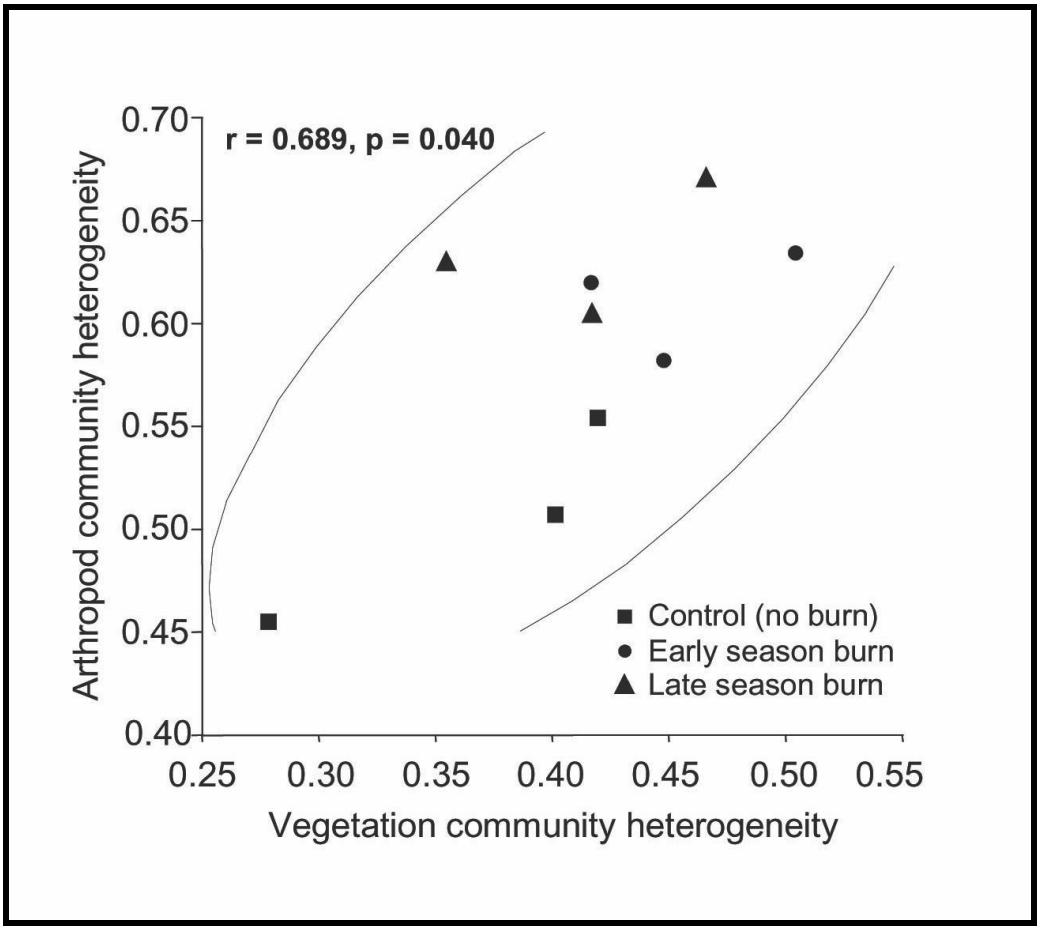

Fig. 5. Association of arthropod community heterogeneity with vegetation community heterogeneity following the burn treatments. The treatments of the experimental units are noted by symbols and the 95 percent density ellipse is illustrated with upper and lower arcs.

cover after fires often leads to an increase in herbaceous understory plant cover (Moretti et al. 2002). Fire also causes the seeds of some plant species to germinate and destroys standing vegetation, leading to a community with a greater number of resprouts and seedlings that are more palatable to insects than mature plants (Price 1997). Forest fires are also typically followed by a pulse release of nitrogen that can enhance the nutrient content of vegetation (Hungerford et al. 1991, Debano et al. 1998, Neavy et al. 1999, Fisher and Binkley 2000, Wan et al. 2001). An increase in nitrogen available for plant growth and new vegetation may have, in part, led to the increase in the number of phytophagous arthropods (Hunter and Price 1992, Denno 1983, Ferrenberg and Denno 2003). A higher number of endoparasitic insects were also found in the burn treatments. While species-specific relationships were not investigated, endoparasitic hymenoptera are frequently specialized feeders (Hawkins 1988, Hawkins et al. 1990, Price 1991) and the greater abundance of

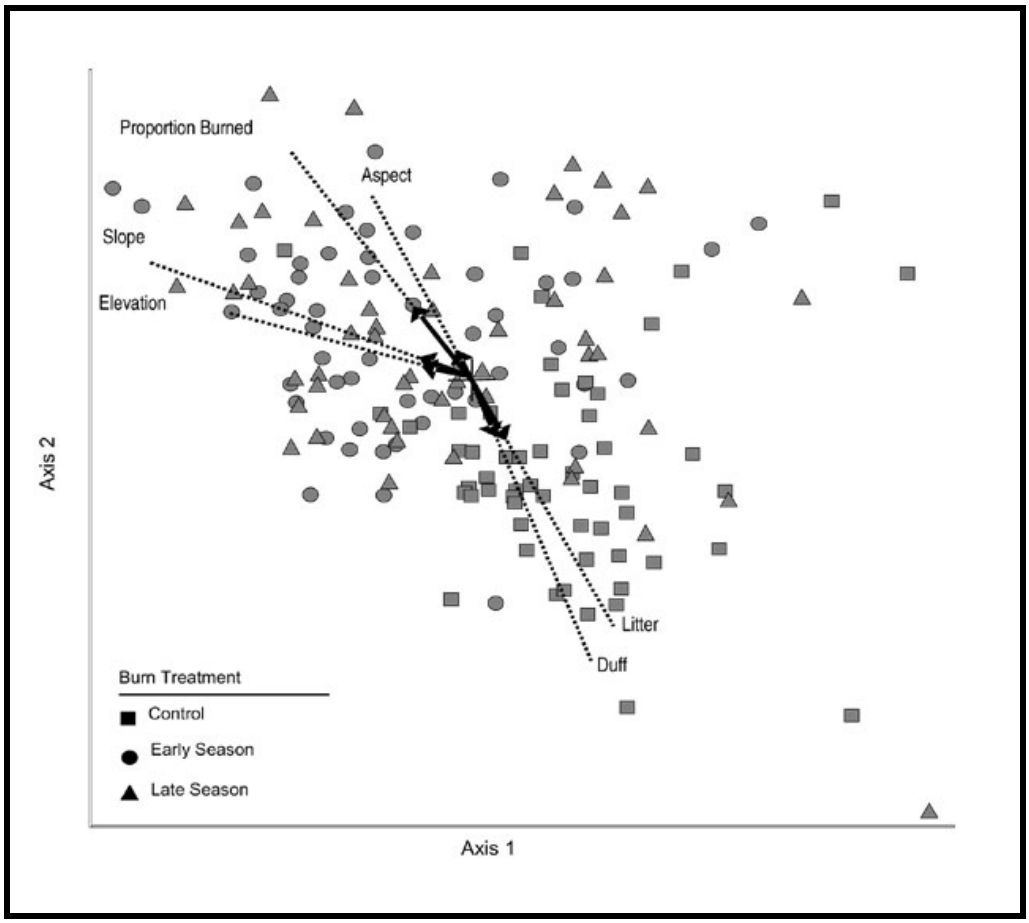

Fig. 6. Nonmetric Multidimensional Scaling ordination of arthropod trapping points (three treatments, coded with different symbols) in community space. The six correlation vectors shown as solid arrows and labeled with dashed lines are for environmental variables significantly associated with arthropod community differences (sequential Bonferroni analysis). Length of vectors is proportional to the strength of the correlation.

this guild is possibly related to the increased abundance of phytophagous species.

The stability of predator proportions in response to fire may result from the mobility of the large hunting spiders, ants, and Carabid beetles that dominate this guild. Unburned patches may have provided refuges and source populations. Hunting spiders and carabids have been known to recolonize disturbed sites quickly and from distances of up to 90 m (Aitchison-Benell 1994). Omnivores, which also showed few proportional difference among treatments, are also likely to benefit from unburned patches, and, given their diverse feeding habits, are possibly less sensitive to changes following fires than are more specialized arthropods.

There is a concern that that early season prescribed burns, which are often conducted before the main historic fire season and coincide with the active period for many plant and animal species, may more negatively (or less

positively) affect arthropod communities than late season prescribed burns. However, in our study, we found few significant differences between burning season treatments. In fact early season burn treatment had effects that were generally intermediate between that of the unburned control and the late season burn treatment. The likely explanation for this result is that early season burns were of lower intensity and patchier than late season burns and that these intensity-related effects were more important than direct effects of the timing of burning in relation to arthropod phenology. This result is consistent with observed effects of early and late season burning on vegetation (Schwilk et al. 2006, Knapp et al. in press).

It is possible that results of comparisons between burn season treatments could have been partially confounded by differences in the time between the burns and the arthropod evaluation. Because late season burns were conducted in the fall of 2001, with early season burns conducted the following spring, arthropod populations in the fall burn treatment had an extra seven months to recover prior to the summer of 2003 survey. However, the study area was under snow from 13 November 2001 until the first week of May 2002, (Sequoia National Park, unpublished data), which presumably slowed arthropod re-colonization of fall burn units and minimized the potential confounding effect of time since treatment. Furthermore, the time between fires and the arthropod evaluation should have been sufficient for most arthropod species in both burn treatment areas to colonize the area and establish reproducing populations. In summary, while some results of this study, such as the trend toward greater abundance and significantly higher species richness in the late season burn treatment may in part be explained by more time for recovery, the significant correlation of vegetation heterogeneity with arthropod heterogeneity, along with the tendency for the early season burning treatment to be intermediate between the control and the late season burn treatment for many other community measures, suggests that the effect of burn treatments on environmental variables likely played a larger role.

Many of the environmental variables significantly associated with the ordination axes (Table 3) are either directly or indirectly related to fire intensity and severity. Proportion of the ground surface burned, litter depth, and duff depth were directly affected by patterns of fuel consumption and the resulting fire intensity. Prior to the burns, over half of the total fuel load in all units consisted of the litter and duff layers. A greater proportion of the ground surface was burned in the late season than in the early season treatment, with no surface burned in controls; of the initial litter and duff loads, 33 percent remained following early season burns, while only 12 percent remained following late season burns (Knapp et al. 2005). This greater heterogeneity (more unburned patches) and reduced fuel consumption of the early season burns was attributed to higher fuel moisture levels (Knapp and Keeley, 2006).

Slope is directly related to fire behavior, with steeper slopes more likely to have experienced higher fire intensity (Knapp and Keeley 2006). Elevation and aspect of the trapping site both can indirectly influence fire behavior. A higher proportion of the forest was

composed of firs at the higher elevations of the study area. Fir needles burned with lower flame lengths than pine needles, while fires also tended to be patchier in areas dominated by fir, particularly with early season burns (Knapp and Keeley 2006). This is due to the slow drying of the compact, shorter-needle litter following snow melt (see Fonda et al. 1998, Stephens et al. 2004). Drying of fuels is also often slower on northerly aspects.

This study detected few significant differences in the arthropod community between early and late season prescribed fire treatments. Arthropod community composition and guild structure, however, were strongly influenced by environmental factors altered by fire. If differences in vegetation and fuel components resulting from prescribed burns in either season persist though time, it is possible that differences in the arthropod community may become more apparent with a longer-term evaluation. Still, differences between early and late season prescribed burns are likely to remain relatively minor in comparison to the overall effect of fire on the arthropod community.

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