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Fire and fire surrogate treatment effects on leaf litter arthropods in a western Sierra Nevada mixed-conifer forest

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Abstract

Frequent, low-intensity fires were a common feature of Sierran forest ecosystems, but suppression policies over the past century have left many forests at risk for catastrophic wildfires. Recent policies highlight the use of prescribed burning or harvesting as fire risk reduction tools, but few studies have investigated the impacts of these management practices on the leaf litter fauna of Sierran forests. This study examines how three fire and "fire surrogate" treatments, prescribed burning, overstory thinning with understory mastication, and combined thinning and burning, impact diversity and abundance of Coleoptera and other leaf litter arthropods. Pitfall trapping was used to collect litter arthropods before and immediately after treatments in replicated forest compartments. The diverse Coleoptera assemblage was dominated by only a few common species, with many rare species represented by only one or two individuals. Rank–abundance diagrams indicated that much of the change in the beetle assemblage due to the treatments was a result of changes in the numbers of rare species. Indicator species analysis showed several species closely allied with the treated compartments, but few with the untreated controls. Both NMS and CCA ordination show considerable change in overall assemblage structure on compartments treated with fire, but less change in the thinned compartments. Coleoptera species richness was slightly higher in burned compartments. Some common beetle species, families of beetles, and other common groups such as ants and spiders showed changes in abundance due to the treatments, but the changes were taxon-specific and showed no general pattern. Overall impacts of the treatments appear to be moderate, and the increased habitat heterogeneity at the compartment level may provide additional habitat for many rare species to coexist. We conclude that the use of fire and fire surrogate treatments in Sierran mixed-conifer forests is justified from the standpoint of their effects on leaf litter arthropods, but the history of management at the site and the scale of treatments must be carefully considered.

Keywords: Leaf litter arthropods; Prescribed burn; Forest restoration; Pitfall trapping

Frequent, low intensity wildfires were a common feature of Sierra Nevada forests prior to European colonization (Caprio and Swetnam, 1995; Skinner and Chang, 1996; Stephens and Collins, 2004), and use of fire as a tool by Native Americans is well documented (Anderson and Moratto, 1996). Consequently, the federal policy of fire suppression over the past century has left millions of acres throughout the western United States at risk for catastrophic wildfires (Pyne, 1982; NWCG, 2001). Despite considerable debate over the means and goals of fire reintroduction (Stephens and Ruth, 2005), there is increasing consensus that some degree of fire management will be important in restoring ecosystem processes and reducing fire risk in our conifer forests (Stephens and Moghaddas, 2005a). However, recent policies, most notably the "healthy forests initiative" (HFRA, 2003), remain controversial, as many suggest thinning in addition to fire reintroduction as a means of reducing fire risk. The effects of thinning and burning treatments on many aspects of forest ecosystems remain poorly understood.

Arthropods are critical components of forest ecosystems, and must be considered in any forestry plan that balances management with the maintenance of biodiversity (Kremen et al., 1993; Niemela et al., 1996; Perry, 1998). Leaf litter arthropods in particular act as predators and prey, contribute to nutrient cycling and decomposition (Petersen and Luxton,

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1982; Lattin, 1993), and may serve as sensitive indicators of habitat quality (Kremen et al., 1993). Leaf litter arthropods depend heavily on many structural elements in forests that may be impacted by fire management, including the amount of dead woody debris (Okland et al., 1996; Schiegg, 2000), litter abundance and composition (Koivula et al., 1999), and soil moisture (Sanderson et al., 1995). In heavily managed forests, the habitat heterogeneity brought about by practices that mimic natural disturbances such as fire and some types of thinning, may serve to increase arthropod biodiversity (Haila et al., 1994; Kaila, 1997). However, other forestry practices have been shown to have negative short- and long-term effects on diversity and abundance of some groups (Niemela et al., 1993; Bellocq et al., 2001). Alternatively, many studies that have examined the effects of burning on various arthropod groups have found these communities to be highly resilient, showing only minor short-term changes (Holliday, 1992; Niwa and Peck, 2002; Collett, 2003; Baker et al., 2004), or even increases in biodiversity (Beaudry et al., 1997; Villa-Castillo and Wagner, 2002).

There is a notable lack of information about arthropod populations in the heavily managed Sierra Nevada conifer forests (Kimsey, 1996), and little information about how communities might respond to fire and thinning treatments. In this study, we measured immediate, post-treatment responses of several arthropod groups, focusing on the Coleoptera, to fire and thinning treatments in a Sierra Nevada mixed-conifer forest. This study is part of a larger, nationwide effort, the Fire and Fire Surrogate Study (Weatherspoon and McIver, 2000), which seeks to determine the effects of fire and thinning treatments on many aspects of the forest ecosystem. Previous research at the site where this work took place has shown that fire, thinning, and thinning followed by burning can all reduce the risk of catastrophic wildfire (Stephens and Moghaddas, 2005a). Prescribed fire treatments can also significantly alter litter, duff and fuel loads and canopy density. Decayed coarse woody debris (CWD) was also significantly reduced by the fire treatments, while sound CWD was not (Stephens and Moghaddas, 2005b). The thinning treatments resulted in significant reductions in basal area, canopy cover, and an increase in some fuel and CWD loads. A pre-treatment study of arthropod biodiversity at the same sites has shown very high Coleoptera biodiversity, but that habitat factors such as volume of coarse woody debris, amount of bare mineral soil, and overstory tree basal area did not consistently or strongly predict the abundance of a variety of leaf litter groups (Apigian, 2005). Based on these results, and the results from other prescribed burn and thinning experiments, we expected relatively small effects of the treatments on abundance and diversity of our study fauna. However, the burning treatments on this site did substantially change the litter structure, so our results from pre-treatment studies (Apigian, 2005) may not adequately predict post-treatment responses. The thinning treatment had a less dramatic effect on the litter structure, but the resulting reduced canopy cover and basal area may impact some arthropod groups.

1. Methods

1.1. Study site

This study was conducted at Blodgett Forest, an experimental forest owned by the University of California on the western slope of the Sierra Nevada. Blodgett is located between approximately 1200–1500 m, near the Georgetown Divide (38°52′N, 120°40′W). Olsen and Helms (1996) provide a detailed description of the forest, its history and current management regimes. In short, the site is typical of a highly productive Sierran mixed-conifer forest (Allen, 1988). Large-scale logging was undertaken between 1900 and 1913, and most of the property was harvested with the seed–tree method at that time. Large fires in the early part of the century also burned much of the forest, and were a common feature of the landscape prior to European settlement (Stephens and Collins, 2004). Fire has been largely excluded from the property at a large scale since the middle of the 20th century. The University of California has managed Blodgett since the mid-1930s and has undertaken a range of harvesting practices on the property, including a variety of even- and uneven-aged management regimes, single tree selection, and retention of old-growth reserve stands. The site is dominated by five major overstory conifer species, Douglas-fir (*Pseudostuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*), and one major hardwood, black oak (*Quercus kellogii*). The understory is dominated by a variety of shrub and herb species.

1.2. Plot set-up and treatments

Twelve compartments within Blodgett Forest, ranging in size from 14 to 29 ha, were selected for this study (Fig. 1). A grid of 0.04 ha circular plots was established within a 10 ha core area of each compartment to reduce edge effects. All vegetation measurements and arthropod collections took place within these circular plots. Tree species, DBH, total height, height to live crown base, and crown position were recorded for all trees larger than 10 cm DBH. Coarse woody debris (CWD), litter, and duff measurements were made along two random azimuth transects from the center of each vegetation plot. Stephens and Moghaddas (2005a,b) detail vegetation and coarse woody debris protocols and results.

Four treatments were assigned at random to the 12 compartments (3 replicates of each): control, mechanical, fire, and mechanical followed by fire (“both”). Control compartments were untreated for the course of the study. Mechanical compartments underwent a thinning from below and crown thinning to increase crown spacing, followed by a mastication of approximately 85% of understory (2–25 cm DBH) conifers and hardwoods. Mastication was completed using an excavator mounted rotary masticator which shreds plant material into chips, which were then left on site. Fire compartments underwent a prescribed burn using strip head fires, while mechanical plus fire compartments were burned using backing

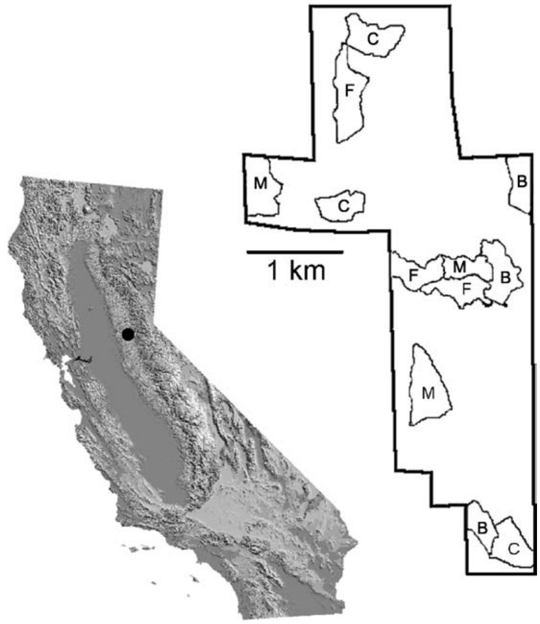

Fig. 1. Map of Blodgett Forest showing its location within California and the treatments applied to the 12 study compartments. C, control; B, mechanical followed by fire; F, fire; M, mechanical.

fires after the mechanical treatment. The burning treatments were designed to meet different management goals: the fire only treatment was designed to scorch and kill understory trees, while the fire portion of the combined treatment was intended to remove surface fuels without killing residual trees. Fire duration was longer in the mechanical plus fire compartments, while intensity was greater in the fire only compartments (Stephens and Moghaddas, 2005a). Mechanical treatments were conducted from late summer 2001 through autumn of 2002. All fire treatments were implemented in late October 2002. The prescribed burns affected soil chemical properties, with the effects of the combined treatment being most pronounced (Moghaddas, personal communication). Stephens and Moghaddas (2005a) provide more details of plot set-up and the implementation of treatments. Future papers will address in detail treatments effects on understory vegetation and soil conditions at the Blodgett Forest site.

1.3. Insect collections

Litter dwelling arthropods were collected using pitfall traps. Pitfall traps are an efficient means of collecting arthropods over long periods of time, despite their known drawbacks (Spence and Niemela, 1994). The total catch by these traps is a measure of the relative abundance of local fauna, but may be greatly influenced by the relative activity levels of different groups. Thus, results must be interpreted with some caution. Nonetheless, sufficient sampling over the length of the active period has been found to provide reasonable abundance estimates for groups such as carabid beetles (Baars, 1979; Niemela et al., 1990). Similar drawbacks exist when collecting ants and spiders with pitfall traps, but this trapping method has proved effective with these groups as well, given similar caveats (Niemela et al., 1986; Wang et al., 2001).

Our traps were constructed from 1 L polypropylene cups with a removable collection cup inside that held a small amount of 50% propylene glycol as a killing and preserving agent. Holes (2 cm diameter) around the rim of the trap provided entry for arthropods while preventing catches of small mammals and reptiles (Lemieux and Lindgren, 1999). Only the very largest beetles in the area would be restricted by the size of these holes. Five plots were selected at random in each of the 12 study compartments. A random azimuth from the plot center was chosen and five traps were arrayed along this transect at 1m intervals. We made four collections during the summer prior to treatments (2001) and four collections during the summer immediately following completion of all of the treatments (2003). Collections were made on a monthly basis from late May (soon after snowmelt) to mid September. For each collection, the traps were kept open for 5 days at a time, and then closed between collections and left in the field to prevent repeated site disturbance (Digweed et al., 1995). This trapping scheme allowed us to sample the full activity period of many arthropod groups at Blodgett Forest, as opposed taking a single point sample, with a low risk of depleting local fauna. Arthropod samples were placed in vials of 95% ethanol for storage and sorting.

1.4. Data analysis

Arthropod samples were sorted in the laboratory by Apigian and trained technicians. All arthropods were initially sorted into ‘‘morphospecies’’, and a reference collection was made. Identifications of beetles and ants were made by comparisons with museum reference collections, identification keys, and experts. If we were unable to identify all beetles to species, we assigned them a morphospecies label. It was not feasible to identify some difficult ant genera (e.g. *Formica*) to species given the volume of ants collected. Thus, for our quantitative comparisons, we grouped ants by genus. Spiders were identified as Lycosidae or ‘‘other’’, as Lycosids were by far the most abundant family captured. In several traps we collected hundreds of small, immature Lycosids that likely fell into the trap with an adult; in these cases, the juveniles were later excluded from the counts and subsequent analyses.

We used rank–abundance diagrams (Whittaker, 1965) to qualitatively compare diversity and evenness of the beetle community between the four treatments. We plotted pre-treatment data next to post-treatment data for each treatment type to compare relative change. These diagrams provide an effective means of comparing community structure and may provide greater detail than a single diversity statistic (Krebs, 1989).

We used one-way analyses of variance to test for treatment effects at the compartment level between 2001 and 2003. Means from 2003 (post-treatment) were subtracted from 2001 means (pre-treatment), and these differences were used in the ANOVA. Multiple comparisons were made using Dunnett’s test to determine effects of the three treatments individually relative to the control group. We tested for changes in abundance of several groups of arthropods: total Coleoptera, the three most common Coleoptera families (Carabidae, Tenebrionidae, and Staphylinidae), the five most common Coleoptera species (Aleocharinae sp. 2, *Dacne californica, Eleodes cordata, Metrius contractus*, and *Pactopus horni*), total ants, the four most common ant genera (*Camponotus, Formica*, *Leptothorax*, and *Liometopum*), total spiders, and the most common spider family, the Lycosidae. We also assigned a guild to each of our Coleoptera species, based upon feeding and life history, and tested these guilds for treatment effects. Guilds were assigned based upon Arnett and Thomas (2000) and Arnett et al. (2002); if no specific information was known or given about the species, we used general information about the family to assign guild membership. Means per compartments were used for analysis. In several instances traps were dislodged or destroyed by wildlife, resulting in unequal sampling effort per plot. We therefore divided our total catch per plot by the number of traps to standardize our catch. We also standardized by number of months sampled, as some compartments were inaccessible for a month during the pre-treatment period due to forestry operations. Abundance data were $\log(x + 1)$ transformed when necessary to meet assumptions of normality and homogeneity of variances.

We also used one-way ANOVAs to test for changes in beetle species richness as a result of the treatments. Unequal sample sizes, and the loss of some traps, made direct comparisons of richness impossible, since species richness is highly dependent on sample size. We used rarefaction to standardize our catches to the lowest number of beetle individuals captured in a single compartment ($N = 120$). We also used the bootstrap method (Smith and van Belle, 1984), a non-parametric estimator of species richness, to compare estimated numbers of total beetle species per treatment. The bootstrap estimator worked well with this data set in the past (Apigian, 2005) and, while potentially underestimating overall richness (Chiarucci et al., 2003), it is still an effective means of making relative comparisons between sites (Palmer, 1990; Poulin, 1998). The JMP IN statistical software (SAS institute, 2003) was used for most analyses. EstimateS (Colwell, 2005) was used for rarefaction and bootstrap estimates.

Indicator species analysis (Dufrene and Legendre, 1997) was used to determine those beetle species characteristics of certain treatment types. This analysis considers species found exclusively in a single treatment type to be perfect indicators of that habitat, and would receive an indicator value of 100. A low indicator value indicates that a species is not characteristic of the habitat in question. Monte-Carlo randomization tests are used to determine if the value is greater than expected by chance; thus, species with only one or a very few total individuals are unlikely to be considered indicators, even if they appear in only one habitat type (McCune and Grace, 2002). PC-Ord (McCune and Mefford, 1999) was used for this analysis.

We used two multivariate methods to analyze the assemblage level responses of Coleoptera to the fire and fire surrogate treatments: Canonical correspondence analysis (CCA) and non-metric multidimensional scaling (NMS). CCA is a ‘‘direct’’ gradient analysis (ordination) method that places plots in species space relative to a matrix of habitat variables (ter Braak, 1986). We ran a CCA with a matrix of our 115 most common beetle species (species found on at least 20% of our compartments) and 24 compartments (the 12 study compartments, pre- and post-treatments). Our habitat matrix initially consisted of 11 habitat variables, but we reduced the matrix to only the four most important variables (% bare mineral soil, total fuel volume, conifer basal area, and hardwood basal area) because there was very high correlation between these and other measured variables (e.g. litter depth and canopy cover). The CCA was run using the axis scores centered and standardized to compartment variance, and compartments were plotted on diagrams using linear combination scores in the PC-Ord program. NMS was used to develop an ordination based solely on species responses, unconstrained by habitat variables, as a contrast to the CCA. NMS is a non-eigenvalue based ordination technique that is appropriate for data sets that are non-normal or contain many zeros (Kruskal and Wish, 1978; Clarke, 1993; McCune and Grace, 2002). We used the ‘‘slow and thorough’’ autopilot mode in PC-Ord with a Sorenson distance matrix to seek the best NMS solution by sequentially stepping down in dimensionality. The stress at each dimensionality is compared against Monte-Carlo results from 50 randomized runs to determine the lowest number of appropriate dimensions. We plotted the first two axes of both the CCA and NMS ordinations as standard plots to compare changes as a result of the fire and mechanical treatments.

2. Results

We captured a total of 11,815 individual beetles within 49 families and 256 species during the two summers of this study. An abridged list of common species of beetles captured is provided in Appendix A, and a complete list is available in Apigian (2005) and online at http://nature.berkeley.edu/stephens-lab/research.htm. The rank–abundance curves for all treatments and years show a pattern typical of many insect communities: very few species dominate the catch with many species represented by only one or two individuals (Fig. 2A–D). The strongest pattern in the rank–abundance plots is an increase in the number of species from 2001 to 2003. The movement of the curves to the right indicates increased evenness of the community in 2003 versus 2001. The post-fire curve (Fig. 2B) shows a different response than the control curves (Fig. 2A), as there appears to be very little change from 2001 to 2003 in the lower ranked (i.e. more common) species. This pattern is less apparent for the mechanical (Fig. 2C) and mechanical plus fire treatment (Fig. 2D). This can be expressed quantitatively as the number of individuals within the 10 most common species. The numbers of individuals in the most common species declined by 19.6% from 2001 to 2003 in the fire compartment, while the control and other treatments increased (control: >50.6%, mechanical: >40.9%, both: >55.6%). Most of the community change on the burned compartments is a result of increased numbers of rare species. The ‘‘right tails’’ of the two fire treatments, representing the numbers of rare species, is longer than for the control or mechanical treatment curves. The

Table 1
Differences between pre- and post-treatment years and results of one-way ANOVAs for common beetle species

Treatment	Aleocharinae sp. 2	*D. californica*	*P. horni*	*M. contractus*	*E. cordata*
Control	6.97 ± 3.7	46.75 ± 51.96	5.15 ± 5.1	140.04 ± 152.78	−28.05 ± 106.08
Fire	−79.17 ± 126.46	37.24 ± 17.17	29.19 ± 48.55	−26.88 ± 18.1	−18.77 ± 13.51
Mechanical	−22.69 ± 53.3	48.05 ± 34.77	82.84 ± 90.11	−10.98 ± 12.06	−28.43 ± 79.91
Both	4.1 ± 9.34	17.43 ± 7.49	139.46 ± 54.73	−18.38 ± 20.83	−43.9 ± 42.08
F-value	1.586	0.469	3.466	10.469	0.959
P-value	0.267	0.712	*0.071*	**0.004**	0.458
Dunnett's test[a]	–	–	**Both (+)**	**Mech (−); both (−); fire (−)**	–

Values are means ± standard deviation. Positive values indicate that a group increased in abundance, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance. Bold text indicates $P < 0.05$ and italic text indicates $P < 0.10$.

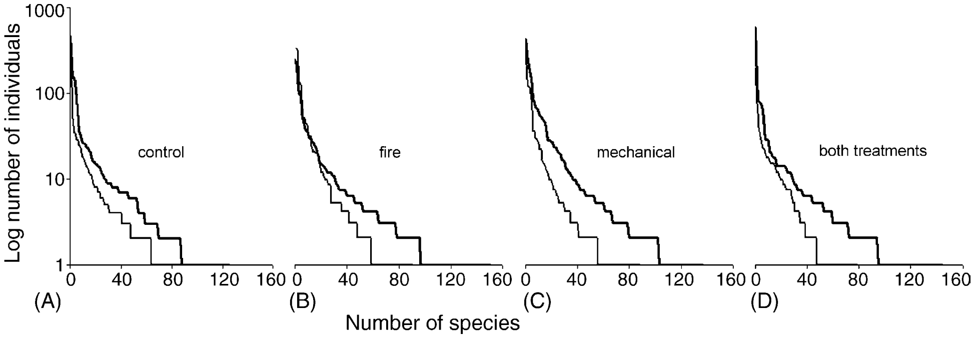

Fig. 2. (A–D) Rank–abundance diagrams showing the structure of the beetle community at Blodgett Forest for each treatment type pre- (thin lines) and post-treatments (bold lines). The shift in the line reflects changes in beetle assemblage between years.

number of rare species (species represented by only one or two individuals) in the control group increased by four species from 2001 to 2003. The mechanical treatment increased by 10, the fire by 30, and the mechanical plus fire by 32 species.

Indicator species analysis revealed several species closely associated with certain treatments (Appendix A). Most of the indicator species were found in the treated rather than the control compartments. Only two beetle species could be considered indicators of the control treatment, *Pterostichus lama*, a common Carabid beetle, and *Ichnosoma californicum*, a Staphylinid. In contrast, 9 species were indicators of the fire treatment, 18 for the mechanical treatment, and 17 for the combined treatment. Two Carabid beetles were the most common indicators of the fire and mechanical treatments, respectively: *Omus californicus* and *Pterostichus* sp. 1. A Cryptophagid was the most common species associated with the combined treatment, *Atomaria* sp. 1.

Several of the selected species and groups of species showed significant responses to the treatments. *Pactopus horni*, a common Throscid beetle, showed a positive response to the combined mechanical and fire treatment (Table 1). The catch of the most common ground beetle, *Metrius contractus*, was negatively impacted by all of the active treatments. We were unable to detect a treatment effect for the other three most common beetle species. Total abundance of Coleoptera did not change and the response of the family Carabidae mirrored that of the most common ground beetle species, showing a negative response to all active treatments (Table 2). The Staphylinidae

Table 2
Differences between pre- and post-treatment years and results of one-way ANOVAs for total Coleoptera and common beetle families

Treatment	Total Coleoptera	Carabidae	Tenebrionidae	Staphylinidae
Control	330.67 ± 76.16	132 ± 134.01	−19.67 ± 126.08	39.33 ± 17.16
Fire	36.33 ± 191.66	−49.33 ± 27.06	0.67 ± 33.01	−112.67 ± 133.1
Mechanical	285.22 ± 436.15	−48.11 ± 54.55	1.22 ± 169.8	40.67 ± 79.78
Both	254.44 ± 219.53	−38.11 ± 13.15	−32.56 ± 47.31	−1.89 ± 29.25
F-value	0.730	5.564	0.445	4.080
P-value	0.563	**0.023**	0.728	**0.050**
Dunnett's test[a]	–	**Both (−); fire (−);** *mech (−)*	–	**Fire (−)**

Values are means ± standard deviation. Positive values indicate that a group increased in abundance, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance. Bold text indicates $P < 0.05$ and italic text indicates $P < 0.10$.

Table 3
Differences between pre- and post-treatment years and results of one-way ANOVAs for Coleoptera guilds

Treatment	Coprophages	Fungivores	Herbivores	Omnivores	Predators	Scavengers	Wood-borers
Control	−1.43 ± 1.29	−59.88 ± 20.74	−27.33 ± 11.59	−1.15 ± 1.45	5.48 ± 78.27	−9.53 ± 22.38	−16.84 ± 13.64
Fire	−4.13 ± 3.47	−51.14 ± 43.02	−13.67 ± 18.58	−3.85 ± 0.82	−18.57 ± 57.77	−24.82 ± 69.8	−9.64 ± 5.22
Mechanical	−6.42 ± 8.37	−75.2 ± 23.13	−49.55 ± 12.06	−1.13 ± 3.16	22.26 ± 14.69	−8.93 ± 37.42	−37.04 ± 12.91
Both	−2.82 ± 5.42	−52.58 ± 11.35	5.44 ± 23.02	−1.3 ± 0.8	9.03 ± 18.34	15.06 ± 34.78	−14.83 ± 13.1
F-value	4.931	1.347	1.551	1.090	10.236	0.226	3.818
P-value	**0.032**	0.326	0.275	0.407	**0.004**	0.876	*0.058*
Dunnett's test[a]	–	–	–	–	**Mech (−); both (−); fire (−)**	–	**Both (+)**

Values are means ± standard deviation. Positive values indicate that a group increased in abundance, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance. Bold text indicates $P < 0.05$ and italic text indicates $P < 0.10$.

Table 4
Differences between pre- and post-treatment years and results of one-way ANOVAs for total ants and common ant genera

Treatment	Total formicidae	*Camponotus*	*Formica*	*Leptothorax*	*Liometopum*
Control	756.44 ± 1189	188.64 ± 355.16	510.9 ± 394.11	−170.26 ± 136.45	169.66 ± 64.29
Fire	531.33 ± 572.62	−54.14 ± 31.48	370.8 ± 530.46	−84.37 ± 54.48	124.32 ± 235.25
Mechanical	−866.22 ± 2147	−49.34 ± 126.71	−44.09 ± 208.05	−299.72 ± 133.08	−601.34 ± 1896
Both	742 ± 685.4	97.54 ± 234.92	224.83 ± 145.88	23.86 ± 74.22	−18.7 ± 74.54
F-value	1.118	0.849	2.873	1.680	0.412
P-value	0.397	0.505	0.103	0.248	0.749
Dunnett's test[a]	–	–	*Mech (−)*	–	–

Values are means ± standard deviation. Positive values indicate that a group increased in abundance, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance.

catch was reduced by the fire treatment. Effects on beetles at the guild level (Table 3) were limited to predators and wood-borers: predators were negatively affected by all active treatments, paralleling the responses of the two most common predaceous families (Carabids and Staphylinids), while wood-borers responded positively to the combined treatment. Ant abundance was generally unaffected by the treatments, except for a weak negative response of wood ants (*Formica*) to the mechanical treatment (Table 4). The combined treatment significantly suppressed the catch of wolf spiders (Lycosidae) and spiders as a whole (Table 5). Species richness was slightly higher in the compartments treated with fire, as measured by the rarefaction estimate, and higher in the mechanical plus fire compartments as measured by the bootstrap extrapolation (Table 6).

The CCA and NMS ordinations reveal similar patterns with regard to community level responses of Coleoptera to the treatments. The first axis of the CCA explained the most variance in the data, while axes 2 and 3 explained relatively little and failed the Monte-Carlo test (Table 7). Axis 1 is a "fire effect" gradient, represented by percent bare mineral soil (decreasing from right to left). Vectors connecting the pre- and post-treatment compartments show the relative effects of the

Table 5
Differences between pre- and post-treatment years and results of one-way ANOVAs for total spiders and Lycosidae only

Treatment	Total spiders	Lycosidae
Control	43.27 ± 64.63	−0.03 ± 18.42
Fire	−103.03 ± 21.27	−36.3 ± 41.61
Mechanical	132.09 ± 81.91	27.39 ± 8.27
Both	−122.54 ± 69.02	−69.65 ± 23.07
F-value	11.009	8.048
P-value	**0.003**	**0.008**
Dunnett's test[a]	*Fire (−)*; **both (−)**	**Both (−)**

Values are means ± standard deviation. Positive values indicate an increase, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance. Bold text indicates $P < 0.05$ and italic text indicates $P < 0.10$.

Table 6
Differences between pre- and post-treatment years and results of one-way ANOVAs for total beetles and common families

Treatment	Rarefied	Bootstrap estimate
Control	−4.65 ± 13.58	25.16 ± 14.27
Fire	14.82 ± 2.43	34.36 ± 8
Mechanical	11.02 ± 9.6	39.13 ± 7.03
Both	8.84 ± 5.79	49.49 ± 10.99
F-value	2.725	2.811
P-value	0.114	0.108
Dunnett's test[a]	*Fire* (+)	*Both* (+)

Values are means ± standard deviation. Positive values indicate an increase, negative values indicate a decline.

[a] Multiple comparisons versus control group. Sign indicates whether the treatment resulted in an increase (+) or decrease (−) in abundance.

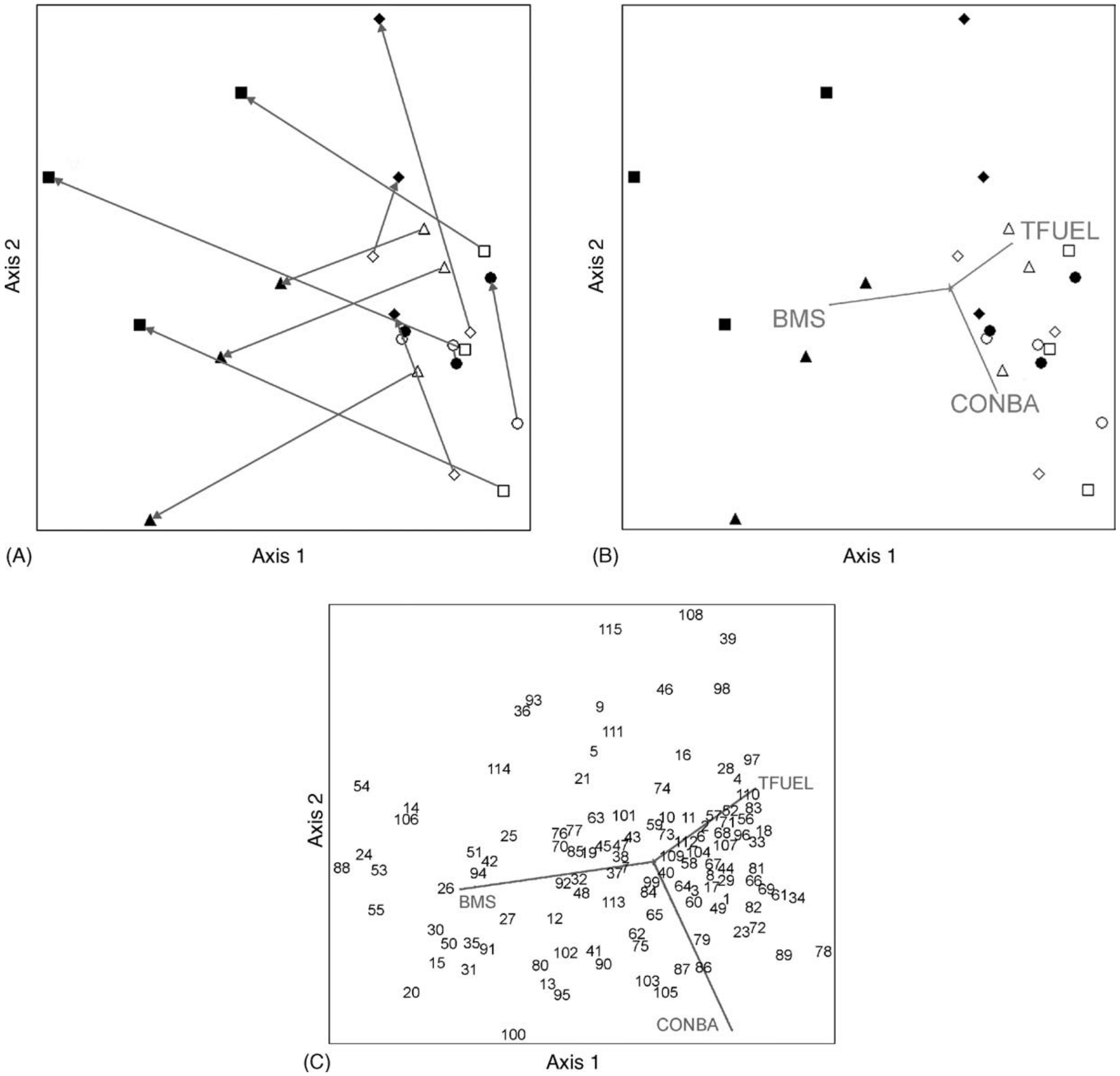

Fig. 3. (A) Canonical correspondence analysis (CCA) ordination diagram of the fire and fire surrogate compartments pre- and post-treatments. Open symbols are pre-treatment, filled symbols are post-treatment. Circles are control compartments (untreated for both years), triangles are fire only compartments, diamonds are mechanical, and squares are the combined mechanical and fire compartments. Vectors represent change from 2001 to 2003 (pre- to post-treatment). (B) Overlay of habitat variables on ordination diagram. Only variables with correlation coefficients greater than 0.200 are displayed. Direction and length of the habitat vectors show the importance of each variable. bms, % bare mineral soil; tfuel, total fuel volume; conba, conifer basal area. (C) Common beetle species displayed in ordination space. See Appendix A for species codes and note the different scales of the biplots.

treatments on the beetle community (Fig. 3A). The control plots moved relatively little, and in both directions, along the second axis. The mechanical plots tended to move up the second axis. The movement of all six of the compartments treated with fire to the left along the first axis was the most distinct change between years. Notably, all of the fire only compartments moved left and down, while the mechanical plus fire compartments moved left and slightly up, suggesting a slightly different response of the community to the two treatments. The biplot of sample units and habitat variables (Fig. 3B) reveals that percent bare mineral soil was the most important variable along axis 1, increasing to the left. Total fuel volume was an important factor for the mechanically treated compartments, while the conifer basal area vector points in the vicinity of many of the pre-treatment compartments. Fig. 3C shows the positions of the 115 most common beetle species in the CCA ordination space. The species are positioned relative to their abundances in the various compartments and their relationships with the habitat variables. The indicator species for each treatment (see above) tend to be positioned in the region of the ordination plot for which they are strongly associated, i.e. mechanical indicators in the upper right, along the total fuel vector, fire associated species in the lower left, indicators of the combined treatments in the middle to upper left and the two species associated with the control treatment in the lower right.

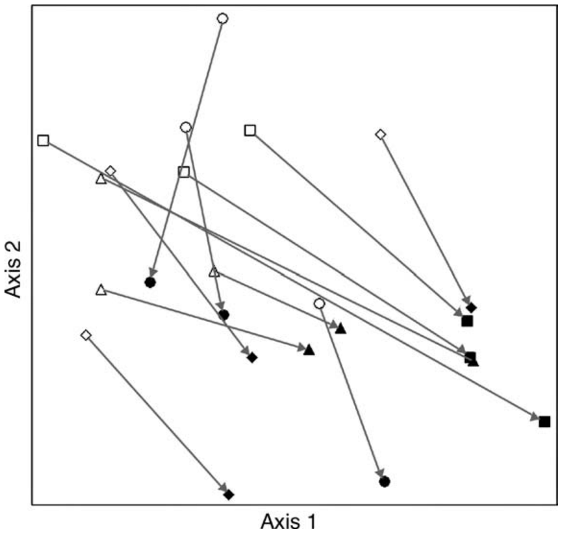

Fig. 4. Non-metric multidimensional scaling (NMS) ordination of the fire and fire surrogate compartments pre- and post-treatments. Open symbols are pre-treatment, filled symbols are post-treatment. Circles are control compartments (untreated for both years), triangles are fire only compartments, diamonds are mechanical, and squares are the combined mechanical and fire compartments. Vectors represent change from 2001 to 2003 (pre- to post-treatment). The NMS was based on a species matrix of 115 beetle species by 24 compartments (12 compartments pre- and post-treatments).

The NMS ordination reveals inherent patterns of community structure without regard to the habitat variables. Final stress for a three-dimensional NMS ordination was 9.55, which is considered ''good'' and results in an easily interpretable ordination diagram (Kruskal, 1964; Clarke, 1993). The pattern of change on our compartments relative to the treatments was similar for the NMS as for the CCA (Fig. 4). The control compartments, and, to a lesser degree, the mechanical compartments, moved down along the second axis. The first axis again represents a gradient from low to high bare mineral soil (from left to right) and fire treated compartments all moved strongly to the right along this axis. The mechanical compartments moved along axis 1 as well, but not as dramatically as the fire treatments. Axis 1 can be interpreted as an ''increasing disturbance'' axis, with fire as the primary disturbance, while axis 2 represents time.

3. Discussion

Community-level ecological studies of arthropod assemblages in California are surprisingly rare, considering the diversity of arthropods in the state in general and the importance of the Sierran mixed-conifer ecosystem. This is the first study to examine the impacts of a variety of fire management methods on the leaf litter fauna in the Sierra Nevada. Past work has shown that while the conifer forests of the Sierras hold relatively few endemic species (Kimsey, 1996), these forests harbor a high diversity of beetle and other insect fauna (Apigian, 2005). Only 8% of the mixed-conifer forest in the Sierras is formally protected for conservation, while 67% is available for timber management (Davis and Stoms, 1996). Studies such as this are keys to understanding how we can maintain biodiversity while sustainably managing our forests (Perry, 1998). The beetle community at our study site probably contains few, if any, species that could be classified as old-growth specialists, and reflects the history of management on the site. It is best described as a community of forest generalists with fairly wide tolerances for disturbance, mixed with some more open-adapted species from adjacent clear-cuts or group selection cuts. The results from this study are therefore highly applicable to other parts of the Sierra Nevada under moderate management regimes.

It is important to note that the results from this study focus on a particular group of species only: the active, litter-dwelling arthropod fauna. The clearest limitation of the pitfall trapping method is that catches are a function of activity levels of the collected fauna, as well as abundance, thus changes in activity may affect capture rates while absolute abundance remains stable. Relative abundances of the same species in different habitats may be a result of changes in activity due to a more complex litter structure or increases in bare mineral soil, for example, as much as changes in numbers of individuals. This problem has been well-documented (Spence and Niemela, 1994), however changes in ''activity–density'' of beetles, ants, and spiders may still be as ecologically important as changes to absolute abundance.

Some of our focal study groups or species were significantly impacted by the treatments. Numerical responses were, in general, negative. The two most common beetle families, Carabidae and Staphylinidae, were both negatively impacted by fire. Carabids, and the most common carabid, *Metrius contractus*, were negatively affected by both the fire and mechanical treatments. This is a response that would not have been predicted based on previous work at the same site (Apigian, 2005) which found that few environmental factors were important predictors for this group, including such factors as the amount of bare mineral soil, litter, and fuel, which were impacted by the treatments. However, the differences in litter layer habitat between treated and control compartments were much greater than any inter-plot differences before treatment (Stephens and Moghaddas, 2005a). In addition to the structural changes, the fire, and thinning treatments likely changed soil moisture and chemistry conditions, and this may be partially responsible for the differences seen in these common families. Spiders, including the most common family, the Lycosidae, were also negatively impacted by the combined thin and burn treatment. Ant captures were largely unaffected by the treatments.

Pactopus horni, a Throscid beetle, showed a positive response to the combined thinning and burning treatment. This small, litter-dwelling beetle is thought to feed largely on ectomycorrhyzal fungi, but its habits are poorly known (Arnett et al., 2002). This species may be attracted to fire, as it has been collected in burned logs (Yensen, 1975). The wood-borer guild increased as a response to the thin and burn treatment. This response is largely due to an increase in bark beetles (Scolytidae, *Hylurgops* sp., *Hylastes* sp. and *Xyleborus* sp., in particular) in these compartments. Some species of bark beetles are attracted specifically to burning (Hanula et al., 2002; Sullivan et al., 2003), and thinning treatments have been shown to be attractive to these beetles as well (Witcosky, 1986). The two measures of species richness showed positive responses to different treatments, but neither response was strong. The rarefaction corrected estimate of richness was higher in the fire treatment, while the bootstrap estimate was higher in the combined treatment. These estimates of higher richness in burned areas are consistent with other studies of areas experiencing prescribed burns (Beaudry et al., 1997; Villa-Castillo and Wagner, 2002).

Both the rank–abundance diagrams and the indicator species analysis support the conclusion that the treated compartments harbor a unique beetle community relative to the control compartments. There were as many as 32 more ‘‘rare’’ species (species represented by one or two individuals) on the treated compartments than on the control compartments. There were also several species closely associated with the treatments, as measured by indicator species analysis, while only two species were control indicators. A previous analysis of pre-treatment collection data (Apigian, 2005) found a great deal of small-scale (plot-level) spatial heterogeneity at Blodgett Forest, but much lower heterogeneity at the compartment level. These results suggest that these treatments increase habitat heterogeneity at the compartment level, and provide opportunities for slightly different beetle communities to coexist.

The CCA and NMS ordinations show similar patterns of beetle community response to treatments. The response was strongest to the fire treatments, and the increased bare mineral soil, resulting from an almost complete loss of a duff and litter layer, was the most significant habitat variable explaining the change. The change due to the mechanical only treatment was less apparent, and associated with an increase in fuel volume. The CCA also suggests that the community level response to the thin and burn treatment was slightly different than the fire alone treatment, signifying that the mastication and harvesting procedures do result in a distinct impact.

Management recommendations from this work must be made in light of the history of Blodgett Forest. This study was conducted on a site that has more than a century-long history of timber management. While fire has been largely excluded for decades (Stephens and Collins, 2004), the site has experienced a variety of harvesting regimes, including several types of even and uneven-aged management (Olsen and Helms, 1996). While the compartments chosen for this study were randomly selected from a group of stands that had experienced relatively moderate management in the form of group selection, the structure and history are very different than undisturbed stands in the Sierras, and even from the reserve stands at Blodgett Forest. Thus, while the specific treatment regimes were unique compared to what had been previously experienced on the site, it is likely that they were within the range of disturbances frequently encountered at Blodgett Forest. This is particularly true of the mechanical treatment, though perhaps less so of the fire treatment, due to fire exclusion from Blodgett Forest.

The short-term effect on the leaf-litter community at Blodgett Forest from these fire and fire surrogate treatments can be considered moderate. If recovery from these treatments is similar to that in other studies (Holliday, 1992; Abbott et al., 2003; Baker et al., 2004), it is likely that recovery can be expected within several years, and implementation of these treatments would be well-justified in terms of the impact on leaf litter arthropod communities. Considering the management history at Blodgett Forest, it is likely that the differences seen in this study are minimal relative to the differences that might be seen if an unmanaged or old-growth forest were treated similarly. As such, care should be taken when extrapolating these results to other forest types under different management regimes. The prescribed burns implemented in this study are relatively small in comparison to some managed areas, and harvesting treatments are frequently implemented at much larger scales. A smaller edge relative to the interior may reduce the ability of the local fauna to recolonize the impacted areas, or at least increase the time until full recolonization. Blodgett Forest is a forest managed with a variety of strategies, resulting in a mosaic of habitat types for a range of species. Applied to an even-aged stand, the local fauna may respond in an entirely different manner. Indeed, overall diversity may be increased by the introduction of different overstory, understory, and litter structures (Haila et al., 1994). Alternatively, applied liberally to old-growth stands, the treatments may result in the loss of some specialists (Niemela et al., 1996).

4. Conclusion

While the thinning, burning, and combination treatments did result in declines of some common arthropod groups, other groups showed the opposite response. Beetle species richness slightly increased after the fire treatments, while all of the treated compartments appear to have gained some rare species. Overall beetle community composition changed as a result of the treatments, but remained diverse and abundant. Use of fire and fire surrogate treatments, applied at similar spatial scales, appears to be justified on sites similar to Blodgett Forest in the Sierra Nevada, from the standpoint of the leaf litter arthropod community. Differences between the treatments used in this study appear to be small, and the choice of which technique to use should be based on management goals.

Table 7
Results from the Canonical correspondence analysis (CCA) of the beetle community at Blodgett Forest

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.229*	0.080	0.051
Variance in species data			
% of variance explained	16.5	5.7	3.7
Cumulative % explained	16.5	22.2	25.9
Pearson correlation Spp-Envt	0.912*	0.883*	0.792
Kendall (Rank) correlation, Spp-Envt	0.696*	0.572*	0.717

Monte-Carlo randomization test.
[*] $P < 0.05$.

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Appendix A

Abridged list of the species of Coleoptera captured during the study and total abundance of each species. This list represents two summers of trapping effort (2001 and 2003). Guild assignments are as follows: C, coprophage; F, fungivore; H, herbivore; O, omnivore; P, predator; S, scavenger; W, wood-borer. Indicator values represent the percent indication of each species for a given treatment type. Treatment indicates the habitat type for which a species was representative, based on a Monte-Carlo randomization test.

Family	Species	Total	Guild	Ordination code	Indicator value	Treatment
Anobiidae	*Ptinus* sp. 1	99	S	83	49.8	–
	Ptinus sp. 2	55	S	84	39.7	–
Bostrichidae	*Scobicia declivis*, Lec. (1857)	6	W	88	66.7	Both*
Buprestidae	*Anthaxia aeneogaster*, LaPort and Gory (1841)	21	W	15	34.4	–
Cantharidae	*Malthodes* sp.	30	O	67	48.8	–
	Podabrus sp. 1	8	P	80	35.7	–
Carabidae	*Bembidion* sp. 2	13	P	20	70.2	Fire*
	Metrius contractus, Escholtz (1829)	951	P	69	50.3	–
	Omus californicus, Escholtz (1829)	276	P	75	54.1	Fire*
	Pterostichus (*Hypherpes*) sp. 1	193	P	56	62.9	Mech***
	Pterostichus (*Hypherpes*) sp. 2	290	P	57	37.5	–
	Pterostichus (*Hypherpes*) sp. 3	80	P	58	32	–
	Pterostichus (*Hypherpes*) sp. 4	98	P	59	35.4	–
	Pterostichus (*Hypherpes*) sp. 5	49	P	60	63.6	Mech*
	Pterostichus inanis, Horn (1891)	18	P	81	26.7	–
	Pterostichus lama, Menetries (1843)	228	P	82	47	Control#
	Pterostichus morionides, Chaudoir (1868)	3	P	-	60.6	Mech#
	Tanystoma striata, Dejean (1828)	7	P	98	58	Mech*
	Trachypacus holmbergi, Mannerheim (1853)	21	P	-	81	Both*
Cerambycidae	*Centrodera spurca*, LeConte (1860)	9	W	27	67.6	Fire*
	Clytus planifrons, LeConte (1874)	24	W	30	51.7	–
	Spondylis upiformis, Mannerheim (1843)	13	W	92	60.6	Both#
	Strophiona laeta, LeConte (1857)	14	W	94	37	–
Ciidae	*Sulcacis curtulus*, Casey (1898)	8	F	95	47.6	–
Cleridae	*Cymatodera ovipennis*, LeConte (1859)	7	P	-	92.6	Both**
Cryptophagidae	*Atomaria* sp. 1	171	F	14	80.4	Both*
	Henoticus sp.	7	F	49	11.1	–
Curculionidae	*Agronus cinerarius*	21	H	2	20.5	–
	Dyslobus lecontei, Casey (1895)	58	H	42	38.6	–
	Dyslobus sp.	88	H	43	25.1	–
	Nemocestes montanus, Van Dyke (1936)	40	H	73	32.4	–
	Rhyncolus oregonensis, Horn (1873)	34	H	87	29.1	–
	Thricolepis simulator, Horn (1876)	58	H	100	74.3	Fire#
	Unknown Curculionid sp. 1	5	H	103	15.9	–
	Unknown Curculionid sp. 2	6	H	104	55.6	Fire#
	Unknown Curculionid sp. 6	30	H	105	44.9	–
Dermestidae	*Trogoderma glabrum*, Herbst (1783)	20	S	102	24.5	–
Diphyllostomatidae	*Diphyllostoma linsleyi*, Fall (1932)	8	H	-	59.5	Both*
Elateridae	*Athous imitans*, Fall (1910)	28	H	17	27.5	–
	Athous opilinus, Candeze (1860)	13	H	18	21.3	–
	Cardiophorus sp. 1	32	H	22	47.6	–

Appendix A (*Continued*)

Family	Species	Total	Guild	Ordination code	Indicator value	Treatment
Elateridae	*Cardiophorus* sp. 2	19	H	23	16.1	–
	Ctenicera imitans, Brown (1935)	36	H	35	72.4	Fire*
	Ctenicera mendax, LeConte (1853)	28	H	36	64.5	Both#
	Limonius humeralis, Candeze (1960)	8	H	66	20.8	–
	Unknown Elaterid sp. 5	24	H	106	41.7	–
Endomychidae	*Mycetina horni*, Crotch (1873)	2	F	-	75.3	Mech*
Erotylidae	*Dacne californica*, Horn (1870)	572	F	37	39.2	–
Geotrupidae	*Bolboceras obesus*, LeConte (1859)	9	U	21	30.3	–
Latridiidae	*Cartodere constrictus*	11	F	26	38.8	–
	Enicmus tenuicornis, LeConte (1878)	52	F	45	59.8	Fire#
	Metophthalmus sp.	91	F	68	54.1	Mech*
	Colon sp.	19	F	33	23.3	–
	Hydnobius sp. 2	17	F	52	75.5	Mech*
	Ptomaphagus sp.	442	S	85	53.2	–
Lucanidae	*Platyceroides latus*, Fall (1901)	41	H	79	22.3	–
Lyctidae	*Lyctus* sp. 2	2	F	-	66.7	Both*
Melandryidae	*Eustrophinus tomentosus*, Say (1827)	8	F	47	13.9	–
Melyridae	Dasytini sp. 2	26	O	38	19.6	–
	Trichochrous sp.	8	O	101	11.9	–
Monotomidae	*Hesperobaenus* sp.	27	F	50	33.1	–
Mordellidae	*Mordella* sp.	15	H	70	53.2	Both#
Mycetophagidae	*Mycetophagus californicus*, Horn (1878)	33	F	71	11.1	–
	Mycetophagus sp.	7	F	72	27.8	–
Nitidulidae	*Carpophilus* sp. 1	11	F	24	30.3	–
	Carpophilus sp. 2	6	F	25	33.3	–
	Pityophagus rufipennis, Horn (1872)	13	P	-	100	Both**
Nitidulidae	*Soronia guttulata*, LeConte (1863)	15	F	91	45.8	–
	Thalycra sp. 1	22	F	99	51.7	Fire#
Ptiliidae	Unknown Ptiliid sp. 1	304	F	107	33.1	–
	Unknown Ptiliid sp. 3	20	F	108	48.2	–
	Unknown Ptiliid sp. 4	72	F	109	55.8	Mech#
	Unknown Ptiliid sp. 5	19	F	110	87.3	Mech**
	Unknown Ptiliid sp. 6	7	F	111	37	–
Rhysodidae	*Clinidium calcaratum*, LeConte (1875)	20	F	29	41.7	–
Scarabaeidae	*Aphodius* sp.	82	C	16	67.1	Mech*
	Dichelonyx crotchi, Horn (1876)	36	H	40	37.5	–
	Dichelonyx lateralis, Fall (1901)	15	H	41	28.4	–
	Serica curvata, LeConte (1856)	31	H	90	33.3	–
Scolytidae	*Hylastes gracilis*, LeConte (1868)	23	W	53	77.7	Both*
	Hylastes macer, LeConte (1868)	71	W	54	82.6	Both*
	Hylurgops porosus, LeConte (1868)	129	W	55	53.9	–
	Xyleborinus saxeseni, Ratz. (1837)	26	W	114	43.9	–
	Xyleborus scopulorum, Hopkins (1902)	74	W	115	49.3	–
Scraptiidae	*Anaspis* sp. 1	10	H	13	19.2	–
Scydmaenidae	*Veraphis* sp. 2	11	P	113	16.1	–
Staphylinidae	*Actium* sp. 1	85	P	1	47	–
	Aleochara sp.	4	P	-	50	Both#
	Aleocharinae sp. 1	75	P	3	46.8	–
	Aleocharinae sp. 2	523	P	8	40.4	–
	Aleocharinae sp. 9	49	P	11	69.4	Mech*
	Aleocharinae sp. 12	7	P	4	22.2	–
	Aleocharinae sp. 13	14	P	-	92.9	Both**
	Aleocharinae sp. 14	6	P	5	38.5	–
	Aleocharinae sp. 15	159	P	6	50.6	Mech**
	Aleocharinae sp. 19	27	P	7	36.8	–

Appendix A (*Continued*)

Family	Species	Total	Guild	Ordination code	Indicator value	Treatment
Staphylinidae	Aleocharinae sp. 20	6	P	-	64.1	Mech*
	Aleocharinae sp. 24	13	P	9	34	–
	Aleocharinae sp. 25	36	P	10	23.3	–
	Amphichroum maculatum, Horn (1882)	6	H	12	18.5	–
	Batrisodes cicatricosis, Brendel (1890)	19	P	19	29.5	–
	Bryoporus sp.	6	P	-	90.9	Mech**
	Deinopteroloma pictum, Fauvel (1878)	39	F	39	56	Mech$^{\#}$
	Eusphalerum sp. 2	84	H	46	72.3	Mech$^{\#}$
	Gabrius sp.	4	P	-	62.5	Fire$^{\#}$
	Hesperolinus sp.	7	P	51	64.5	Both*
	Ichnosoma californicum, Bernhauer and Schubert (1912)	118	S	61	59.8	Control**
	Lathrobium sp. 1	7	P	63	37	–
	Philonthus sp. 2	10	P	78	40	–
	Quedius sp. 1	8	P	86	16.7	–
	Stenus vespertinus, Casey (1884)	3	P	-	60.6	Both$^{\#}$
	Stictolinus sp.	1	P	93	35.5	–
	Tachinus semirufus, Horn (1877)	153	P	97	51.8	Mech*
	Tachyporus californicus, Horn (1877)	76	P	96	75.3	Mech**
Tenebrionidae	*Cibdelis blaschkei*, Mannerheim (1843)	15	S	28	34.2	–
	Cnemeplatia sericea, Horn (1870)	59	S	31	38.4	–
	Coelocnemis californica, Mannerheim (1843)	174	S	32	36	–
	Coniontis sp.	113	S	34	47.9	–
	Eleodes cordata, Escholtz (1833)	1737	S	44	32.5	–
	Helops simulator, Blaisdell (1921)	92	S	48	42.7	–
	Iphthminus serratus, Mannerheim (1843)	8	P	62	20.8	–
	Nyctoporis sponsa, Casey (1907)	198	S	74	51.6	–
	Scotobaenus parallelus, LeConte (1859)	10	S	89	30	–
Throscidae	*Pactopus horni*, LeConte (1868)	1529	F	76	42.9	–
Zopheridae	*Phellopsis porcat*, LeConte (1853)	5	F	77	39.2	–
	Usechimorpha Montana, Doyen (1979)	6	F	112	60.6	Both$^{\#}$

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
$^{\#}$ $P < 0.10$.

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