Forest Ecology and Management 326 (2014) 91–100

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Canopy arthropod responses to thinning and burning treatments in old-growth mixed-conifer forest in the Sierra Nevada, California

Thomas Rambo [a,*], Timothy Schowalter [b,1], Malcolm North [c,2]

[a] Forest Biology Research Center, John Muir Institute of the Environment, University of California, Davis, CA 95616, United States
[b] Department of Entomology, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, United States
[c] USDA Forest Service, PSW Research Station, 1731 Research Park Dr., Davis, CA 95618, United States

ARTICLE INFO

Article history:
Received 18 January 2014
Received in revised form 11 April 2014
Accepted 14 April 2014

Keywords:
Arthropods
Fuels treatments
Sierra Nevada
Mixed-conifer forest
Forest thinning

ABSTRACT

We compared canopy arthropod responses to common fuels reduction treatments at Teakettle Experimental Forest in the south-central Sierra Nevada of California. We sampled arthropod communities among four dominant overstory conifer species and three dominant understory angiosperm species before and after overstory or understory thinning or no thinning treatments followed by burning or no burning treatments. Arthropods were sampled in overstory trees by climbing and bagging foliage-bearing branches and counting all arthropods by taxon in each sample. Understory plants were sampled similarly from the ground. Arthropod assemblages showed significant differences among tree species and seasons, but not among treatment combinations. Taxa showing significant differences in abundance among plant species likely reflected differences in foliage quality or other host-associated conditions among plant species. Some arthropods showed significant value as indicator species. Overall, our results indicated that the restoration treatments recommended for Sierra Nevada mixed-conifer forests have little effect on associated canopy arthropods. However, given the significant differences in arthropod assemblages among plant species, restoration treatments should ensure that the full range of plant species characterizing these forests is maintained in order to protect their associated arthropods.

1. Introduction

Forest canopy arthropods can respond dramatically to disturbances or environmental changes in ways that, in turn, alter canopy structure and function, either contributing to or undermining management goals (e.g., Mattson and Addy, 1975; Romme et al., 1986; Schowalter, 2011, 2013). For example, low intensity of feeding on foliage by insects can stimulate nutrient turnover and increase tree growth (Alfaro and Shepherd, 1991; Schowalter et al., 1991), whereas high intensity of feeding on foliage can reduce tree growth, and lead to tree mortality and opening of the canopy (Schowalter et al., 1986).

Management practices can affect arthropod populations in the same manner as natural disturbances, depending on species adaptations (Schowalter, 2011). Establishment of relatively even-aged forests dominated by commercially-valuable species has led to widespread outbreaks of defoliators and bark beetles, among others, especially when dense forests are stressed by moisture limitation (Aukema et al., 2010; Lombardero et al., 2006; Mattson and Haack, 1987; Raffa et al., 2008). Tree mortality resulting from insect outbreaks can increase the likelihood of catastrophic fire in such forests (McCullough et al., 1998), depending on the timing of ignition relative to fuel decomposition (Jenkins et al., 2008). However, silvicultural treatments designed to restore historic forest structure as a means of reducing risk of insect pest outbreaks or fire (North et al., 2007), have the potential to trigger other arthropod or pathogen responses (e.g., Witcosky et al., 1986).

This study was designed to investigate canopy arthropod responses to prescribed thinning and burning treatments (North et al., 2007; Schowalter et al., 2005). We compared arthropod communities among four dominant overstory conifer species and three dominant understory angiosperm species in mixed-conifer forest before and after the thinning and burning treatments. We expected to find significant differences in arthropod abundances and assemblage structure among treatments, specifically, reduced abundances of herbivores in treatments that reduced host plant densities.

* Corresponding author. Tel.: +1 530 754 9281.
E-mail addresses: trambo@ucdavis.edu (T. Rambo), tschowalter@agcenter.lsu.edu (T. Schowalter), mpnorth@ucdavis.edu (M. North).
[1] Tel.: +1 225 578 1634.
[2] Tel.: +1 530 754 7398.

http://dx.doi.org/10.1016/j.foreco.2014.04.014
0378-1127/

2. Methods

2.1. Study site

The Teakettle Experimental Forest (36°58′N, 119°02′W) is situated in the Sierra National Forest north of the North Fork of the Kings River, approximately 80 km east of Fresno, California (Fig. 1). The 1300 ha of Teakettle's old-growth forest spans the upper montane red fir and lower montane mixed-conifer ecotone of the southern Sierra Nevada on the west side of the crest at an approximate elevation of 2100 m. Jeffrey pine (*Pinus jeffreyi* Balf.) is dominant on more shallow upland soils, but the majority of the study area is a mix of conifer species: red fir (*Abies magnifica* A. Murray), white fir (*Abies concolor* (Gordon & Glend.) Hildebr. var. *lowiana* (Gordon) Lemmon), incense cedar (*Calocedrus decurrens* (Torr.) Florin), sugar pine (*Pinus lambertiana* Douglas) and Jeffrey pine. In a study of 526 stumps remaining from thinning prescriptions in the Teakettle Ecosystem Experiment (North et al., 2002), these respective species ranged in age up to 332, 397, 403, 354 and 407 years (North et al., 2005) with individual trees reaching heights >65 m.

Historically, this forest was co-dominated by large (>1 m diameter), widely spaced conifers with a sparse understory maintained by relatively frequent, low-intensity ground fires. Fire exclusion during the past century has promoted recruitment of more fire-intolerant species, resulting in large areas of closed canopy forest dominated by young white fir and incense cedar (<100 yrs old, <50 cm diameter). The forest now has a mean basal area of 68 m^2 ha^{-1} with 60% canopy cover characterized by discontinuous groups of trees separated by large gaps (North et al., 2004). Black oak (*Quercus kelloggi* Newb.) is found in the understory, and the canopy gaps are frequently characterized by manzanita (*Arctostaphylos patula* Greene and *A. nevadensis* Gray), bush chinquapin (*Castanopsis sempervirens* (Kellogg) Dudley ex Merriam) and whitethorn (*Ceanothus cordulatus* Kellogg).

Warm, dry summers contrast with much cooler, moist winters in this Mediterranean climate. Annual precipitation averages 125 cm and falls mainly as winter snow, which generally persists through May. Mean summer and winter temperatures in 2004 at 5 m above surface in un-thinned forest were 15.6 and 0.0 °C, respectively (Rambo and North, 2009). Soils are generally granitic Inceptisols and Entisols (North et al, 2002).

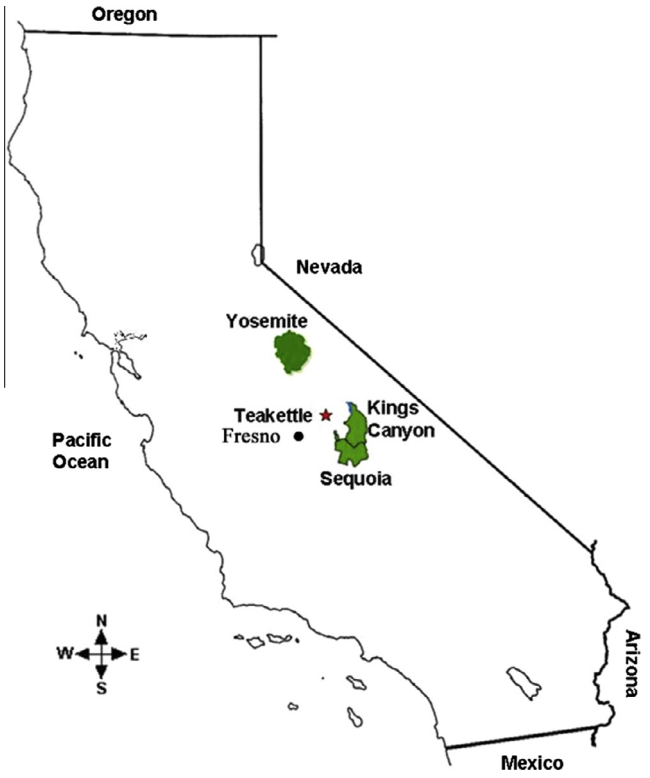

Fig. 1. Map of California showing approximate location of the Teakettle Experimental Forest in relationship to the Central Valley city of Fresno, and Yosemite, Kings Canyon and Sequoia National Parks in the Sierra Nevada.

2.2. Teakettle Ecosystem Experiment

This research was conducted within the context of the Teakettle Ecosystem Experiment, which established eighteen 200 × 200 m plots to study the ecological effects of thinning and burning on Sierra mixed-conifer forest. Analysis of the Teakettle forest structure determined that plot size needed to be approximately 4 ha to include the range of composition and stand variability that characterizes the discontinuous canopy cover of southern Sierra mixed-conifer forest (North et al., 2002). Treatments included two different forest thinning strategies. Six plots were thinned primarily from the understory following California Spotted Owl Report (CASPO) guidelines (Verner et al., 1992), which retained 40% of live BA while removing trees 25–76 cm diameter at breast height (dbh). This treatment left an average of 44 trees ha^{-1} with a mean dbh of 91 cm (see Rambo and North, 2009 for stand visualizations and metrics). Originally designed to minimize impact on Spotted Owl habitat, CASPO guidelines became a widely used thinning practice in the Sierra Nevada during the 1990s, and continues as a ladder fuels reduction treatment (SNFPA, 2004). Another six plots were thinned primarily from the overstory, which harvested all trees ⩾ 25 cm (dbh) except for 22 large trees ha^{-1} left regularly dispersed 20–25 m apart (Rambo and North, 2009). This prescription was widely practiced in Sierra Nevada forests prior to CASPO and approximates fuels reduction thinning currently used in defensible space zones where tree crowns are spaced widely to reduce potential for crown fire spread. Six plots were left unthinned. Half of the plots in each thinning treatment were subsequently treated with broadcast slash and surface fuel prescribed burning. Thinning treatments were performed in the fall of 2000 and spring of 2001, and the prescribed burning in the fall of 2001.

2.3. Sampling

In the pre-treatment year of 2000, sampling was conducted in late spring (June) and again in summer (August) to represent seasonal variation in arthropod assemblages. In the post-treatment year of 2002, sampling was done once in late spring. The overstory in each of five plots was sampled by climbing one tree each of incense cedar, white fir, Jeffrey pine and sugar pine. Three crown strata were distinguished for collecting three samples in each tree: one from within 5 m above the lowest live branches, one from mid-crown, and one from within 5 m of the tree top.

Each sample was collected by slipping a 40 l plastic bag quickly and stealthily over a randomly selected live branch (ca. 0.5 m length, 30–50 g dry wt.), clipping the branch, and sealing the bag for lowering to the ground. This sampling technique emphasizes the sedentary fauna present on foliage and twig surfaces at any given sampling time (e.g., aphids, caterpillars, spiders, mites) while potentially underrepresenting more mobile species that could be alarmed and escape capture (Schowalter, 1995; Schowalter and Ganio, 1999). Other sampling techniques have different biases. For example, interception trapping emphasizes flying adult insects that may or may not be associated with a particular plant or even a particular treatment unit, and canopy fogging emphasizes unattached arthropods that can reach ground collectors when many

Table 1
Results from analysis of variance of more common arthropod taxa among treatments for both years, showing mean abundances standardized by g of dry foliar weight (st dev). Values within a row with different superscripts are significantly different ($P < 0.05$). BC = understory thin and burn, BS = overstory thin and burn, BN = burn only, UC = understory thin only, UN = no treatment, US = overstory thin only.

Pre-treatment	BC	BN	BS	UC	UN	US
	$n = 19$	$n = 26$		$n = 24$	$n = 26$	$n = 25$
Coleoptera	0.026	0.002		0.001	0.002	0.002
	(0.079)	(0.006)		(0.004)	(0.010)	(0.006)
Crab spiders	0.000	0.011		0.001	0.002	0.004
(Philodromidae)	(0.000)	(0.037)		(0.006)	(0.006)	(0.013)
Geometrid caterpillars	0.003	0.003		0.004	0.004	0.004
	(0.011)	(0.011)		(0.011)	(0.017)	(0.014)
Leafhoppers	0.002	0.002		0.002	0.000	0.001
(Cicadellidae)	(0.007)	(0.008)		(0.009)	(0.002)	(0.006)
Microlepidoptera	0.009	0.000		0.001	0.001	0.000
(Tortricidae)	(0.035)	(0.000)		(0.004)	(0.004)	(0.002)
Mirid plant bugs	0.010^{ab}	0.006^{a}		0.015^{b}	0.005^{a}	0.003^{ab}
	(0.027)	(0.029)		(0.036)	(0.022)	(0.010)
Sheet-weaving spiders	0.001	0.003		0.004	0.000	0.004
(Linyphidae)	(0.002)	(0.016)		(0.009)	(0.002)	(0.017)
Thrips, black	0.002^{ab}	0.012^{a}		0.001^{b}	0.002^{ab}	0.007^{ab}
	(0.005)	(0.030)		(0.003)	(0.006)	(0.016)
Thrips, red	0.006	0.004		0.001	0.002	0.002
	(0.015)	(0.010)		(0.003)	(0.005)	(0.005)
Thrips, yellow	0.041^{a}	0.023^{ab}		0.000^{b}	0.014^{ab}	0.007^{ab}
(*Frankliniella occidentalis*)	(0.100)	(0.081)		(0.000)	(0.050)	(0.015)
Treehoppers	0.000^{a}	0.005^{ab}		0.002^{ab}	0.015^{b}	0.000^{a}
(Membracidae)	(0.000)	(0.025)		(0.008)	(0.039)	(0.000)
Post-treatment	$n = 36$	$n = 32$	$n = 33$	$n = 31$	$n = 37$	$n = 36$
Aphid sp. 2	0.012^{ab}	0.113^{ab}	0.028^{ab}	0.005^{ab}	0.000^{a}	0.016^{b}
	(0.065)	(0.617)	(0.150)	(0.025)	(0.000)	(0.060)
Aphid sp. 3	3.082	6.28	1.096	0.771	4.296	3.083
	(12.815)	(27.269)	(5.670)	(4.293)	(16.980)	(13.231)
Bdellid mites	0.003^{abc}	0.003^{abc}	0.001^{ac}	0.010^{b}	0.015^{abc}	0.001^{c}
	(0.007)	(0.008)	(0.004)	(0.028)	(0.076)	(0.008)
Comb-footed spiders	0.003	0.005	0.001	0.004	0.006	0.000
(Theridae)	(0.013)	(0.015)	(0.005)	(0.015)	(0.021)	(0.002)
Crab spiders	0.031	0.018	0.014	0.012	0.013	0.016
(*Xysticus* sp.)	(0.104)	(0.058)	(0.042)	(0.051)	(0.042)	(0.062)
False spider mites	0.005	0.006	0.004	0.004	0.030	0.018
(*Pentamerismus erythreus*)	(0.028)	(0.023)	(0.013)	(0.014)	(0.163)	(0.075)
Leafhoppers	0.024^{ab}	0.010^{ab}	0.003^{ab}	0.016^{a}	0.001^{b}	0.012^{ab}
(Cicadellidae)	(0.075)	(0.043)	(0.009)	(0.037)	(0.005)	(0.035)
Minute brown scavenger beetles	0.003	0.026	0.011	0.003	0.014	0.006
(Lathridiidae)	(0.014)	(0.128)	(0.043)	(0.012)	(0.043)	(0.016)
Minute pirate bugs	0.001	0.002	0.005	0.003	0.005	0.015
(Anthocoridae)	(0.003)	(0.008)	(0.016)	(0.009)	(0.023)	(0.058)
Mirid plant bugs	0.023^{a}	0.008^{bc}	0.005^{ac}	0.005^{ac}	0.004^{bc}	0.009^{ac}
	(0.071)	(0.042)	(0.016)	(0.010)	(0.015)	(0.031)
Oribatid mites	0.000^{ab}	0.001^{ab}	0.000^{a}	0.003^{b}	0.001^{ab}	0.001^{ab}
(*Scapheremaeus nr. marginalis*)	(0.002)	(0.002)	(0.000)	(0.009)	(0.002)	(0.004)
Platygastrid wasps	0.003	0.001	0.005	0.005	0.014	0.001
	(0.013)	(0.003)	(0.026)	(0.015)	(0.071)	(0.003)
Thrips, black	0.013	0.016	0.017	0.022	0.007	0.020
	(0.033)	(0.045)	(0.058)	(0.066)	(0.015)	(0.074)
Thrips, red	0.004^{ac}	0.004^{a}	0.006^{abc}	0.000^{bc}	0.000^{b}	0.002^{abc}
	(0.016)	(0.012)	(0.003)	(0.000)	(0.000)	(0.007)
Thrips, yellow	0.103^{abc}	0.098^{abc}	0.047^{ac}	0.079^{b}	0.291^{b}	0.003^{c}
(*Frankliniella occidentalis*)	(0.309)	(0.300)	(0.254)	(0.157)	(1.186)	(0.008)

small arthropods might be excluded by interception before reaching the ground (e.g., Majer and Recher, 1988; Blanton, 1990).

The understory was sampled from the ground in each of the same plots by similarly bagging foliated branches from three manzanita (*A. patula*) and three *Ceanothus* shrubs. Black oaks were likewise sampled in the four study plots in which they occurred. In the post-treatment year, all plants were resampled and the same protocol was used to additionally sample one each of the above four conifer species and three each of manzanita and *Ceanothus* shrubs in the other 13 experimental plots. Black oaks were additionally sampled in the other 10 plots in which they occurred.

Conifer subsamples and shrub and black oak samples were identified by plot, shrub and tree, and tree stratum, and kept chilled until transported and processed in the lab. There, each bag was first inspected for large or mobile arthropods, which were identified and quickly transferred to alcohol to prevent escape. Each branch and any debris in or adhering to the bag was then carefully scanned under a 10× dissecting microscope, and all arthropods found were also tabulated and transferred to alcohol. Arthropods were identified to the lowest possible rank. Voucher specimens are preserved in the Louisiana State Arthropod Museum (LSAM) at Louisiana State University, and in the Oregon State Arthropod Collection (OSAC) at Oregon State University. Plant

Table 2
Results from analysis of variance of more common arthropod taxa among plant species for both years showing mean abundances standardized by g of dry foliar weight (st dev). Values within a row with different superscripts are significantly different ($P < 0.05$). Cade = incense cedar, Pije = Jeffrey pine, Pila = sugar pine, Abco = white fir, Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*.

Pre-treatment	Cade $n = 10$	Pije $n = 10$	Pila $n = 10$	Abco $n = 10$	Quke $n = 21$	Arpa $n = 30$	Ceco $n = 29$
Coleoptera	0.000^{a}	0.000^{a}	0.001^{ab}	0.001^{ab}	0.000^{a}	0.021^{b}	0.000^{a}
	(0.000)	(0.000)	(0.003)	(0.003)	(0.000)	(0.063)	(0.000)
Crab spiders	0.000	0.002	0.000	0.000	0.002	0.001	0.012
(Philodromidae)	(0.000)	(0.004)	(0.000)	(0.000)	(0.009)	(0.006)	(0.036)
Geometrid caterpillars	0.000^{a}	0.000^{ab}	0.000^{b}	0.000^{b}	0.000^{b}	0.003^{b}	0.012^{a}
	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.010)	(0.022)
Leafhoppers	0.000	0.001	0.000	0.000	0.000	0.003	0.003
(Cicadellidae)	(0.000)	(0.003)	(0.000)	(0.000)	(0.000)	(0.010)	(0.008)
Microlepidoptera	0.000^{a}	0.000^{a}	0.002^{b}	0.000^{a}	0.000^{a}	0.002^{ab}	0.006^{ab}
(Tortricidae)	(0.000)	(0.000)	(0.004)	(0.000)	(0.000)	(0.006)	(0.028)
Mirid plant bugs	0.000^{ac}	0.004^{acd}	0.014^{bd}	0.001^{abc}	0.016^{abc}	0.000^{a}	0.013^{bc}
	(0.000)	(0.010)	(0.034)	(0.003)	(0.045)	(0.000)	(0.029)
Sheet-weaving spiders	0.000^{ac}	0.000^{ac}	0.001^{abc}	0.003^{b}	0.000^{c}	0.001^{c}	0.008^{ab}
(Linyphidae)	(0.000)	(0.000)	(0.003)	(0.005)	(0.000)	(0.005)	(0.022)
Thrips, black	0.001^{ade}	0.002^{ade}	0.010^{bc}	0.008^{cd}	0.015^{ad}	0.003^{ae}	0.000^{e}
	(0.003)	(0.004)	(0.011)	(0.015)	(0.033)	(0.011)	(0.000)
Thrips, red	0.005^{a}	0.009^{a}	0.014^{b}	0.006^{a}	0.000^{c}	0.000^{c}	0.000^{c}
	(0.007)	(0.019)	(0.013)	(0.008)	(0.000)	(0.000)	(0.000)
Thrips, yellow	0.000^{ab}	0.003^{abc}	0.006^{ac}	0.001^{abc}	0.019^{abc}	0.000^{b}	0.049^{c}
	(0.000)	(0.009)	(0.013)	(0.003)	(0.059)	(0.000)	(0.106)
Treehoppers	0.000^{a}	0.000^{a}	0.000^{a}	0.000^{a}	0.021^{b}	0.001^{a}	0.002^{a}
(Membracidae)	(0.000)	(0.000)	(0.000)	(0.000)	(0.048)	(0.007)	(0.013)
Post-treatment	$n = 18$	$n = 18$	$n = 18$	$n = 18$	$n = 25$	$n = 54$	$n = 54$
Aphid sp. 2	0.000^{a}	0.000^{a}	0.000^{a}	0.000^{a}	0.000^{a}	0.098^{b}	0.007^{a}
	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.487)	(0.053)
Aphid sp. 3	0.000^{a}	0.000^{a}	0.000^{a}	0.000^{a}	25.676^{b}	0.000^{a}	0.000^{a}
	(0.000)	(0.000)	(0.000)	(0.000)	(37.134)	(0.000)	(0.000)
Bdellid mites	0.001^{ad}	0.003^{bc}	0.000^{ad}	0.007^{c}	0.000^{d}	0.009^{ad}	0.008^{ab}
	(0.002)	(0.005)	(0.000)	(0.008)	(0.000)	(0.063)	(0.024)
Comb-footed spiders	0.001	0.002	0.000	0.002	0.001	0.004	0.008
(Theridae)	(0.002)	(0.004)	(0.000)	(0.004)	(0.004)	(0.152)	(0.021)
Crab spiders	0.000^{a}	0.003^{ac}	0.001^{a}	0.003^{bc}	0.068^{bc}	0.001^{a}	0.032^{bc}
(*Xysticus* sp.)	(0.000)	(0.006)	(0.002)	(0.005)	(0.139)	(0.007)	(0.068)
Leafhoppers	0.001^{abd}	0.001^{ad}	0.003^{bc}	0.001^{ad}	0.000^{d}	0.009^{ac}	0.031^{bc}
(Cicadellidae)	(0.003)	(0.002)	(0.005)	(0.002)	(0.000)	(0.025)	(0.074)
Minute brown scavenger beetles	0.002^{a}	0.000^{a}	0.000^{a}	0.000^{a}	0.061^{b}	0.001^{a}	0.009^{a}
(Lathridiidae)	(0.007)	(0.000)	(0.000)	(0.000)	(0.151)	(0.008)	(0.028)
Minute pirate bugs	0.000^{a}	0.008^{b}	0.001^{a}	0.002^{a}	0.013^{a}	0.004^{a}	0.006^{a}
(Anthocoridae)	(0.000)	(0.007)	(0.002)	(0.004)	(0.064)	(0.021)	(0.022)
Mirid plant bugs	0.001^{ae}	0.003^{bc}	0.001^{ae}	0.005^{cde}	0.032^{bdf}	0.001^{a}	0.016^{cef}
	(0.002)	(0.005)	(0.005)	(0.009)	(0.073)	(0.003)	(0.052)
False spider mites	0.131^{a}	0.000^{b}	0.000^{b}	0.000^{b}	0.000^{b}	0.000^{b}	0.000^{b}
(*Pentamerismus erythreus*)	(0.236)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)
Platygastrid wasps	0.004^{a}	0.001^{b}	0.000^{b}	0.001^{b}	0.020^{b}	0.001^{b}	0.006^{b}
	(0.005)	(0.002)	(0.000)	(0.002)	(0.087)	(0.005)	(0.024)
Scapheremaeus nr. marginalis mites	0.002^{ab}	0.002^{a}	0.002^{a}	0.004^{a}	0.000^{b}	0.000^{b}	0.000^{b}
	(0.005)	(0.004)	(0.004)	(0.012)	(0.000)	(0.000)	(0.000)
Thrips, black	0.007^{a}	0.082^{c}	0.006^{a}	0.009^{ad}	0.014^{b}	0.008^{bd}	0.010^{b}
	(0.006)	(0.122)	(0.006)	(0.018)	(0.062)	(0.022)	(0.038)
Thrips, red	0.002^{abc}	0.003^{b}	0.000^{ac}	0.007^{b}	0.000^{ac}	0.002^{abc}	0.001^{ac}
	(0.007)	(0.008)	(0.000)	(0.021)	(0.000)	(0.009)	(0.004)
Thrips, yellow	0.006^{acg}	0.038^{abg}	0.004^{abd}	0.000^{bef}	0.334^{cdf}	0.021^{cde}	0.212^{g}
(*Frankliniella occidentalis*)	(0.009)	(0.082)	(0.005)	(0.000)	(1.439)	(0.060)	(0.398)

foliage was oven-dried at 50 °C for one week to reach constant weight and then weighed.

2.4. Analyses

Arthropod abundances were first standardized by dividing numbers per taxon by the weight in grams of dried foliage in each sample. Foliage samples taken from within a single tree are not independent samples. Therefore, we treated each branch of foliage taken from within any single tree as a subsample, with the tree as the sample unit. Standardized subsample values were averaged for each tree in analyses.

The relationship between foliar arthropod communities and plot treatments, plant species and seasonality were then examined using non-metric multidimensional scaling ordination (Kruskal, 1964; PC-ORD, McCune and Mefford, 2011). The quantitative version of Sørensen's similarity index was used as the distance measure (Sørensen, 1948). Primary matrices were restricted to include only those arthropod taxa with at least 5% frequency of occurrence across plant samples. The secondary matrices contained the categorical variables of plot treatment and plant species, with the addition of season (June vs. August) for the pre-treatment year 2000. To optimize clarity of the arthropod patterns among these variables, ordinations were performed with the overstory

Table 3
Results from analysis of variance of more common arthropod taxa showing mean abundances standardized by g of dry foliar weight (st dev) between (a) pre-treatment June and August seasons and (b) pre- and post-treatment years. Values within a row with different superscripts are significantly different ($P < 0.05$).

Pre-treatment	June ($n = 59$)	August ($n = 61$)
Panel (a)		
Coleoptera	0.001 (0.004)	0.010 (0.045)
Crab spiders (Philodromidae)	0.007 (0.026)	0.000 (0.004)
Geometrid caterpillars	0.006^{a} (0.016)	0.001^{b} (0.009)
Leafhoppers (Cicadellidae)	0.003 (0.009)	0.000 (0.001)
Microlepidoptera (Tortricidae)	0.003 (0.020)	0.001 (0.004)
Mirid plant bugs	0.013^{a} (0.034)	0.002^{b} (0.014)
Sheet-weaving spiders (Linyphidae)	0.005^{a} (0.016)	0.000^{b} (0.000)
Thrips, black	0.005 (0.019)	0.005 (0.014)
Thrips, red	0.004^{a} (0.010)	0.001^{b} (0.006)
Thrips, yellow (*Frankliniella occidentalis*)	0.030^{a} (0.083)	0.002^{b} (0.009)
Treehoppers (Membracidae)	0.009^{a} (0.031)	0.000^{b} (0.000)
Pre- vs. post-treatment	Pre ($n = 120$)	Post ($n = 205$)
Panel (b)		
Aphid sp. 2	0.000^{a} (0.000)	0.028^{b} (0.253)
Aphid sp. 3	0.000^{a} (0.000)	3.131^{b} (15.270)
Bdellid mites	0.001^{a} (0.007)	0.006^{b} (0.035)
Coleoptera	0.006^{a} (0.033)	0.000^{b} (0.001)
Comb-footed spiders (Theridae)	0.001^{a} (0.008)	0.003^{b} (0.014)
Crab spiders (Philodromidae)	0.004^{a} (0.019)	0.000^{b} (0.001)
Crab spiders (*Xysticus* sp.)	0.000^{a} (0.001)	0.018^{b} (0.063)
False spider mites (*Pentamerismus erythreus*)	0.028^{a} (0.259)	0.012^{b} (0.078)
Geometrid caterpillars	0.004^{a} (0.013)	0.001^{b} (0.008)
Leafhoppers (Cicadellidae)	0.001^{a} (0.007)	0.011^{b} (0.042)
Microlepidoptera (Tortricidae)	0.002 (0.014)	0.001 (0.009)
Minute brown scavenger beetles (Lathridiidae)	0.002^{a} (0.012)	0.010^{b} (0.057)
Minute pirate bugs (Anthocoridae)	0.001^{a} (0.006)	0.005^{b} (0.027)
Mirid plant bugs	0.008 (0.026)	0.009 (0.038)
Orabatid mites (*Scapheremaeus nr. marginalis*)	0.000 (0.002)	0.001 (0.004)
Platygastrid wasps	0.001^{a} (0.009)	0.005^{b} (0.033)
Sheet-weaving spiders (Linyphidae)	0.003^{a} (0.011)	0.000^{b} (0.000)
Thrips, black	0.005^{a} (0.017)	0.016^{b} (0.052)
Thrips, red	0.003^{a} (0.008)	0.002^{b} (0.009)
Thrips, yellow (*Frankliniella occidentalis*)	0.016^{a} (0.060)	0.106^{b} (0.548)
Treehoppers (Membracidae)	0.005 (0.022)	0.001 (0.010)

conifers and separately for the understory shrubs with black oak. This resulted in primary matrices for pre-treatment of 35 plant samples and 22 arthropod taxa for the overstory, and 48 plant samples and 12 arthropod taxa for the understory. The overstory and understory primary matrices for post-treatment contained 66 plant samples and 19 arthropod taxa, and 112 plant samples and 21 arthropod taxa, respectively. Beals smoothing (Beals, 1984) improved the interpretability of ordination results by mitigating the problem of an excessive number of zero-value matrix cells. This transformation replaces each cell's value with a probable value based on a species' actual occurrence with the other species in a sample.

Cluster analysis of plant species in arthropod space was used with Euclidean distance and Ward's method of linkage (Wishart, 1969) to see if particular plant species could be defined by the more common arthropod taxa (PC-ORD, McCune and Mefford, 2011). Multi-response permutation procedures (MRPP, Mielke, 1984) were used with Euclidean distance to test if groups derived from clustering were more different from each other than would be expected from random partitioning of the data, and to quantify the degree of chance-corrected homogeneity within groups (effect size).

The indicator species analysis method of Dufrêne and Legendre (1997) provides a modified importance value based on relative abundance and frequency. This analysis was restricted to those arthropod taxa with at least 5% frequency of occurrence across plant samples to determine if any had significant indicator importance with respect to the plant species (PC-ORD, McCune and Mefford, 2011).

Analysis of variance (ANOVA) was used to test for differences among the more common individual arthropod taxa between years, within years among treatment plots and plant species, and between the June and August seasons in 2000 (SAS, 2010). The extreme non-parametric nature of the data required the use of non-parametric rank F test analyses. Means were separated via orthogonal contrasts ($P < 0.05$). Additionally, the standardized abundances of the invertebrate communities were regressed between years by plant species to determine if there might be a lack of independence in those communities between years.

3. Results

Analysis of variance of the abundances of the more common arthropod taxa provided poor evidence for rejecting the null hypothesis of no differences among treatments for both the pre- and post-treatment years (Table 1). However, there was strong evidence for rejecting the hypothesis of no compositional differences among plant species for both pre- and post-treatment years (Table 2), between June and August pre-treatment seasons (Table 3a), and between pre- and post-treatment years (Table 3b). Multiple regression analyses of the arthropod communities of the conifer species showed significant correlations between years ($P < 0.05$). Regressions for the understory plants were not significant.

In the pre-treatment year ordination of all plant species, there was a grouping pattern of *Ceanothus* samples towards the positive end of the primary axis, which explained 59% of the original

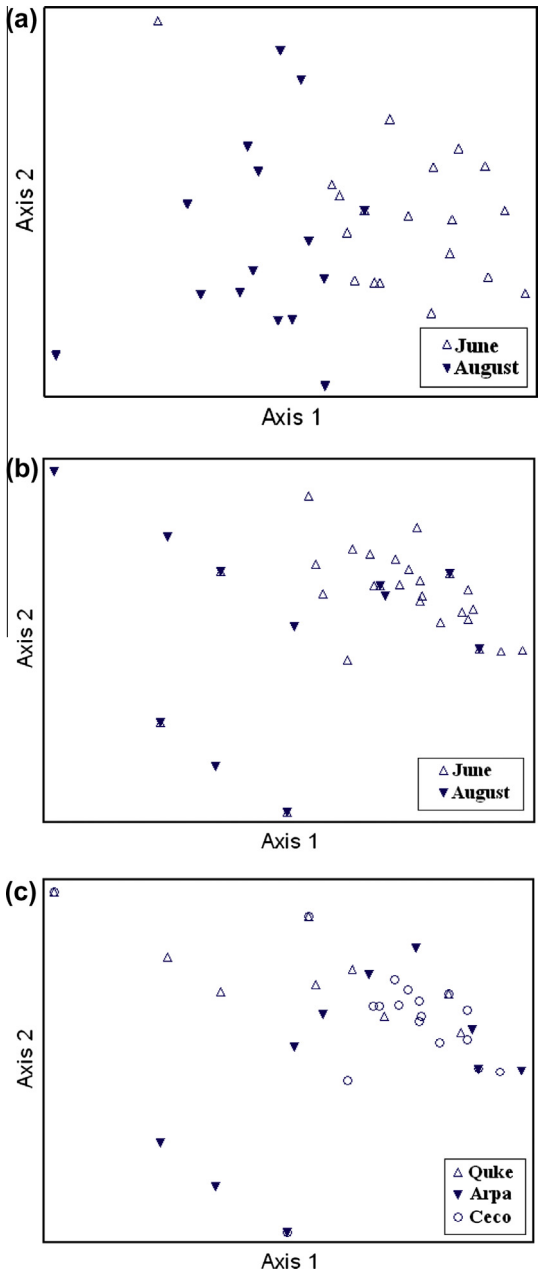

Fig. 2. Pre-treatment non-metric multidimensional scaling ordination graphs of plant species in arthropod space illustrating community compositional differences between seasons for (a) the overstory conifers and (b) the understory shrubs and black oak, and (c) the distribution of understory samples in arthropod space. Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*. See Table 4.

distance matrix. Any other potential patterns were masked by the confusion of the 74 plant samples in arthropod space. The separate overstory ordination provided no meaningful insight towards any differences in arthropod community composition among conifer species. However, there was a clear compositional difference between the June and August samplings (Fig. 2a). The primary axis of this ordination explained 49% of the matrix information. The understory ordination demonstrated a seasonal difference in invertebrate community composition similar to that found in the overstory (Fig. 2b), and also the same grouping of *Ceanothus* apparent in the ordination with all plant species (Fig. 2c). The primary axis explained 68% of the original matrix information, while the secondary axis, which only explained 21% of the matrix information, was nevertheless important in shaping the arthropod space. Arthropod taxa most positively associated with the above described axes of pre-treatment ordinations are listed in Table 4.

Table 4
Pre-treatment Pearson and Kendall correlation values (r) of arthropod taxa with axes from non-metric multidimensional scaling ordinations of plant species in arthropod taxa space, including the amount of information explained by axes.

All plant species	
Axis 1 (R^2 = 0.59)	
Linyphid spiders	r = 0.58
Mirid plant bugs	r = 0.57
Philodromid spiders	r = 0.54
Yellow thrips (*Frankliniella occidentalis*)	r = 0.50
Leafhoppers (Cicadellidae)	r = 0.40
Overstory (Fig. 2a)	
Axis 1 (R^2 = 0.49)	
Mirid plant bugs	r = 0.76
Seed bugs (Lygaeidae)	r = 0.67
Erythraeid mites	r = 0.64
Eremaeus sp. mites	r = 0.57
Brown lacewings	r = 0.48
Snake flies	r = 0.46
Bdellid mites	r = 0.43
Jumping spiders (Salticidae)	r = −0.44
Crab spiders (*Xysticus* sp.)	r = −0.53
Pentamerismus erythreus	r = −0.57
Black thrips	r = −0.68
Understory (Fig. 2b and c)	
Axis 1 (R^2 = 0.68)	
Linyphid spiders	r = 0.74
Mirid plant bugs	r = 0.72
Philodromid spiders	r = 0.68
Yellow thrips (*Frankliniella occidentalis*)	r = 0.60
Weevils (Curculionidae)	r = 0.58
Geometrid caterpillars	r = 0.42
Axis 2 (R^2 = 0.21)	
Philodromid spiders	r = 0.81
Weevils (Curculionidae)	r = 0.80
Linyphid spiders	r = 0.76
Mirid plant bugs	r = 0.67

In post-treatment ordinations, no pattern of samples of all plant species in arthropod space indicated any difference in invertebrate community composition among treatments. However, distinct compositional differences were apparent among plant species. Likewise, neither the overstory nor understory ordinations distinguished any meaningful differences among treatments, but both ordinations clarified the compositional distinctions among plant species (Fig. 3a and b). The primary axis of the overstory ordination accounted for 65% of the original matrix information. While the secondary axis only accounted for 20% of the matrix information, it had an influence on the positioning of conifer samples in arthropod space. The understory ordination was mainly shaped by the strength of its primary axis, which explained 61% of the original distance matrix. Again, the distribution of samples in arthropod space was also influenced by the secondary axis although it only accounted for 21% of matrix information. Arthropod taxa most strongly correlated with these relevant axes of post-treatment ordinations are listed in Table 5.

The ordination across years for all plant species exhibited a weak but distinct separation of arthropod composition by year along the secondary axis, which only accounted for 11% of the matrix information. Separate ordinations for the overstory and understory showed clearly that this between-years compositional difference was driven by the overstory (Fig. 4), while the understory ordination showed no distinction between years. Arthropods most strongly correlated with the informative overstory secondary axis are listed in Table 6.

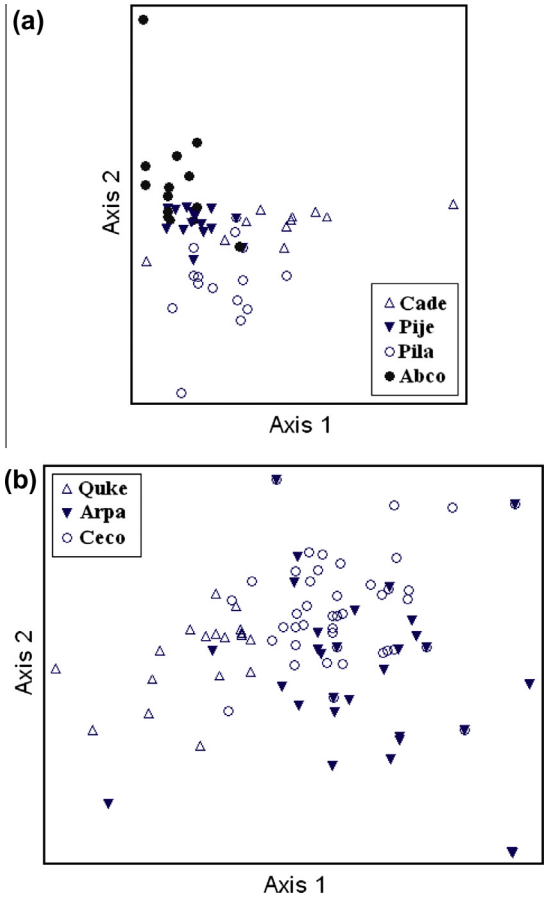

Fig. 3. Post-treatment non-metric multidimensional scaling ordination graphs of plant species in arthropod space illustrating community compositional differences among plant species for (a) the overstory conifers and (b) the understory shrubs and black oak. Cade = incense cedar, Pije = Jeffrey pine, Pila = sugar pine, Abco = white fir, Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*. See Table 5.

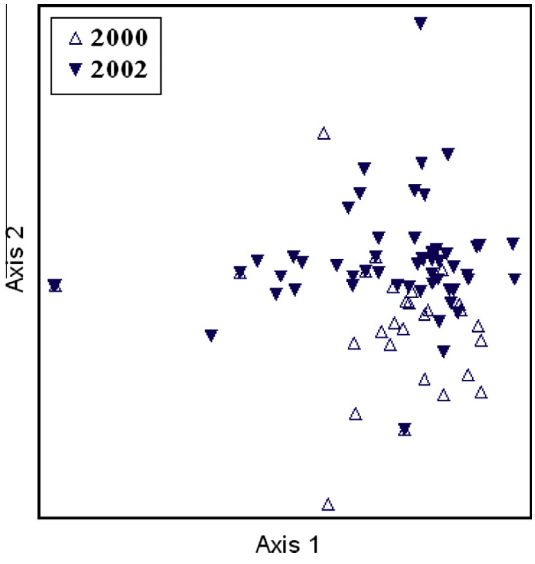

Fig. 4. Non-metric multidimensional scaling ordination graph of overstory conifers in arthropod space illustrating community compositional differences between years. See Table 6.

Table 6
Pearson and Kendall correlation values (r) of arthropod taxa with axes from non-metric multidimensional scaling ordinations of plant species in arthropod taxa space across pre- and post-treatment years, including the amount of information explained by axes.

Overstory (Fig. 4)	
Axis 2 (R^2 = 0.23)	
Pineus coloradensis	r = 0.70
Leafhoppers (Cicadellidae)	r = 0.60
Yellow thrips (*Frankliniella occidentalis*)	r = 0.52
Black thrips	r = 0.42
Seed bugs (Lygaeidae)	r = −0.48
Erythraeid mites	r = −0.58
Red thrips	r = −0.75

Table 5
Post-treatment Pearson and Kendall correlation values (r) of arthropod taxa with axes from non-metric multidimensional scaling ordinations of plant species in arthropod taxa space, including the amount of information explained by axes.

Overstory (Fig. 3a)			
Axis 1 (R^2 = 0.65)		Axis 2 (R^2 = 0.20)	
False spider mites (*Pentamerismus erythreus*)	r = 0.96	Spruce aphids (*Elatobium abietinum*)	r = 0.72
Platygastrid wasps	r = 0.62	Bdellid mites	r = 0.60
Comb-footed spiders (Theridae)	r = −0.55	Crab spiders (*Xysticus* sp.)	r = 0.43
Scapheremaeus nr. marginalis mites	r = −0.58	Seed bugs (Lygaeidae)	r = 0.40
Minute pirate bugs (Anthocoridae)	r = −0.60	Pine needle scale (*Chionaspis pinifoliae*)	r = −0.46
Bdellid mites	r = −0.66	Leafhoppers (Cicadellidae)	r = −0.66
Mirid plant bugs	r = −0.67	*Pineus coloradensis*	r = −0.72
Seed bugs (Lygaeidae)	r = −0.75		
Crab spiders (*Xysticus* sp.)	r = −0.76		
Understory (Fig. 3b)			
Axis 1 (R^2 = 0.61)		Axis 2 (R^2 = 0.21)	
Leafhoppers (Cicadellidae)	r = 0.61	Comb-footed spiders (Theridae)	r = 0.64
Aphid sp. 2	r = 0.56	Aphid sp. 4	r = 0.59
Bdellid mites	r = 0.55	Weevils (Curculionidae)	r = 0.55
Psyllid plant lice	r = 0.51	Geometrid caterpillars	r = 0.40
False darkling beetles (Melandryidae)	r = 0.46	Black thrips	r = −0.56
Ladybird beetles (Coccinellidae)	r = −0.40	Aphid sp. 2	r = −0.61
Lathridiid scavenger beetles	r = −0.46		
Crab spiders (*Xysticus* sp.)	r = −0.51		
Soldier beetles (Cantharidae)	r = −0.55		
Aphid sp. 3	r = −0.92		

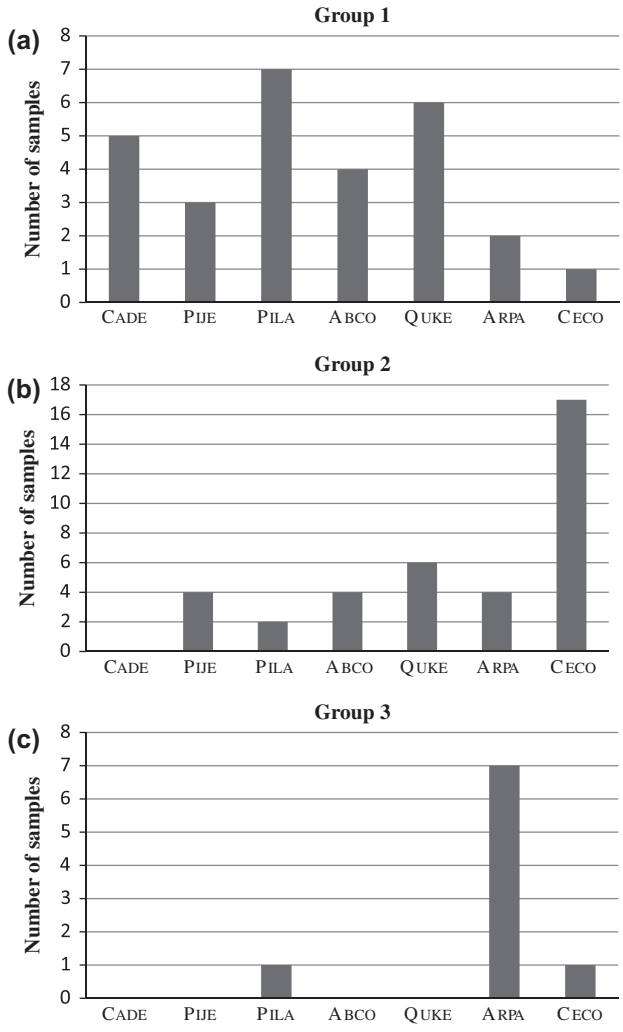

Fig. 5. Pre-treatment cluster analysis results of plant species by arthropod composition showing the three groups dominated by (a) overstory conifers, (b) *Ceanothus*, and (c) manzanita. Cade = incense cedar, Pije = Jeffrey pine, Pila = sugar pine, Abco = white fir, Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*.

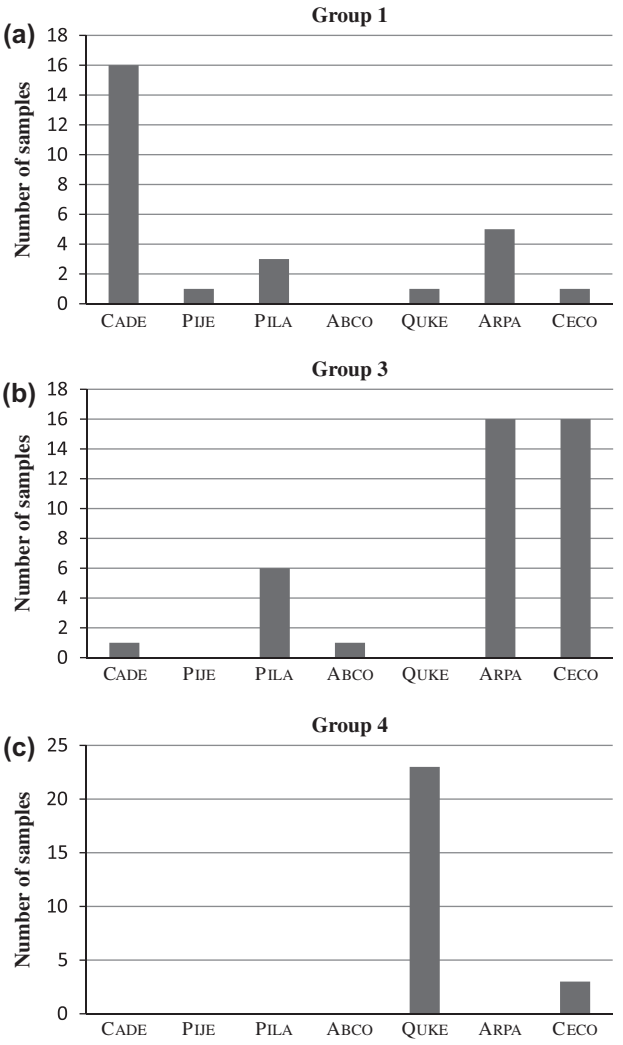

Fig. 6. Post-treatment cluster analysis results of plant species by arthropod composition showing the three interpretable groups that were dominated by (a) incense cedar; (b) understory shrubs; and (c) black oak. Cade = incense cedar, Pije = Jeffrey pine, Pila = sugar pine, Abco = white fir, Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*.

Pre-treatment cluster analysis of plant species by arthropod composition produced three coherent groupings with 28% of the matrix information remaining (% chaining = 2.42). One group was dominated by the overstory conifers, one by *Ceanothus*, and one by manzanita shrubs (Fig. 5). MRPP confirmed that these groups were more different from one another than would be expected by random partitioning of the data ($P = 0.0000$, Euclidean distance, chance-corrected within-group agreement $A = 0.2651$). Indicator species analysis revealed that geometrid caterpillars and yellow thrips (*Frankliniella occidentalis*) were significant indicators of *Ceanothus*, miscellaneous Coleoptera were indicators of manzanita, and treehoppers (Membracidae) were indicators of black oak (Table 7).

Table 7
Indicator species values of arthropod taxa for sampled plant species before and after treatments. Cade = incense cedar, Pije = Jeffrey pine, Pila = sugar pine, Abco = white fir, Quke = black oak, Arpa = manzanita, and Ceco = *Ceanothus*. Values in bold are statistically significant ($P < 0.05$).

	Cade	Pije	Pila	Abco	Quke	Arpa	Ceco
Pre-treatment							
Coleoptera	0	0	0	0	0	**51**	0
Geometrid caterpillars	0	0	0	0	0	6	**31**
Treehoppers (Membracidae)	0	0	0	0	**28**	1	0
Frankliniella occidentalis	0	1	2	0	**7**	0	**30**
Post-treatment							
Aphid sp. 2	0	0	0	0	0	**27**	0
Black thrips	3	**52**	2	4	1	2	1
Leafhoppers (Cicadellidae)	0	0	2	0	0	6	**23**
Minute brown scavenger beetles	0	0	0	0	**27**	0	2
Pentamerismus erythreus	**94**	0	0	0	0	0	0
(*Xysticus* sp.)	0	1	0	2	**19**	0	11

Post-treatment cluster analysis of plants produced four groupings that left 35% of the matrix information remaining (% chaining = 2.43). The first group was predominantly incense cedar; the second group was not interpretable as being biologically meaningful, as it was co-dominated by Jeffrey pine, white fir, *Ceanothus* and manzanita; the third group was co-dominated by the understory shrubs; and the fourth group was predominantly black oak (Fig. 6). Indicator species analysis showed that false spider mites (*Pentamerismus erythreus*) were significant indicators of incense cedar, black thrips were indicators of Jeffrey pine, aphid sp. 2 indicated manzanita, leafhoppers (Cicadellidae) were indicators of *Ceanothus*, and minute brown scavenger beetles (Lathridiidae) and crab spiders (*Xysticus* sp.) were indicators of black oak (Table 7).

4. Discussion

In our study, arthropod communities appeared to be structured more strongly by tree and shrub species than by different forest management practices. We found no significant differences in community composition or the abundance and richness of arthropods between different types of fuels treatments widely used in the Sierra Nevada. Similar results were reported for arthropod responses to alternative harvest practices in Douglas-fir forests in Oregon and Washington (Schowalter et al., 2005). These results suggest that arthropod populations and communities are relatively robust within the range of environmental variation created by these treatments.

Composition of canopy arthropod communities also differed significantly among these same plant species in earlier work in the Teakettle Forest (Schowalter and Zhang, 2005). Again, differences were most dramatic between conifers and angiosperms, but assemblages could also be distinguished among individual plant species, which were attributed to biochemical differences among plants and their foliage. Such biochemical differences likely influence the respective compositions of herbivorous arthropod communities among plant species, which would in turn influence the composition of their respective predator communities.

After host species, differences in arthropod assemblages were most apparent between sample seasons and years, suggesting that communities respond to macroenvironmental conditions influenced by weather and drying that occur over the Mediterranean summer (see Schowalter and Zhang, 2005; Rambo and North, 2009). To a large extent, seasonal variation in arthropod communities reflects changes in foliage quality or other host conditions during the growing season, as reported in previous studies (Schowalter, 1995; Schowalter and Ganio, 1998). Across all four of the conifer species sampled in this study, K^+, Ca^{2+}, Mg^{2+}, Cl^-, NO_3^-, PO_4^{3-}, and SO_4^{2-} were found in significantly greater concentrations ($P < 0.05$) in fall season foliar leachate than in spring samples and fall leachate acidity increased significantly over spring values for Jeffrey pine, incense cedar and white fir (Rambo, 2012).

The significant correlations of the conifer invertebrate communities between years provided strong evidence that the post-treatment compositions may not be independent from those that were present pre-treatment. For that reason, the combined sample sets for the two years were not used to assess differences in composition among plant species since resampled plants could have been weighted towards their pre-treatment samples in such a way as to bias results across years. However, any such weighting would only have served to diminish differences between years, so the compositional differences exhibited in the ordination results (Fig. 4) were, if anything, conservative.

The Teakettle Experiment was an ambitious replicated experiment to assess treatment effects on multiple organisms and processes. The treatments are widely used fuels reduction methods in many fire-suppressed western forests. There has been concern that these treatments might negatively impact biodiversity, including that of arthropods. Overall, our results indicated that the restoration treatments recommended for Sierra Nevada mixed-conifer forests (North et al., 2007) have little effect on associated canopy arthropods. The absence of significant effects on canopy arthropods suggests that this group is relatively robust to these treatments. Nevertheless, stem density reduction should be beneficial in reducing the susceptibility to and spread of cyclical outbreaks of arthropod pests such as the Douglas-fir tussock moth (*Orgyia pseudotsugata*), bark beetles and other insect species. Plant species diversity was important in representing the full range of arthropod diversity. Maintaining the full variety of plant species characterizing these forests is important to maintain their associated arthropod communities.

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