

Canopy Arthropod Assemblages in Four Overstory and Three Understory Plant Species in a Mixed-Conifer Old-Growth Forest in California

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Abstract: We compared canopy arthropod assemblages among overstory conifer and understory angiosperm species at Teakettle Experimental Forest in the Sierra Nevada in California during 1998–2000. Arthropods were sampled from upper, middle, and lower crown levels of one overstory tree of each of the four dominant conifer species (Jeffrey pine, sugar pine, white fir, and incense cedar), and from three understory plants of each of the major understory species (California black oak, manzanita, and white-thorn ceanothus) in each of five replicate plots during June and Aug. in each of the 3 years to represent seasonal and annual variation in abundances. Many taxa differed significantly in abundance among plant species, with one to five taxa being significant indicators for each plant species. Five to eight taxa on each plant species showed significant differences in abundance among years. Aphids and scale insects, predaceous mirids, and some detritivores showed peak abundances in 1999, a particularly dry year, whereas most other taxa showed lowest abundances during 1999 or declining abundances during this period, suggesting association with wetter conditions. Nonmetric multidimensional scaling (NMS), supported by multi-response permutation procedure (MRPP), showed that arthropod assemblages differed significantly among the seven plant species, especially between overstory conifers and understory angiosperms, and among the 3 years. These data indicate that the diversity and structure of arthropod communities depend on vegetation structure and/or condition, perhaps as modified by annual variation in weather conditions. *FOR. SCI.* 51(3):233–242.

Key Words: Insect, spider, mite, disturbance.

FOREST CANOPIES REPRESENT major ecological functions (e.g., photosynthesis, evapotranspiration, and interception of light, water, wind, and nutrients) that control biomass accumulation and environmental conditions (Ruangpanit 1985, Chen et al. 1995, Lewis 1998). Arthropods can dramatically alter canopy structure and function in ways that can stabilize primary production or interfere with management goals (e.g., Mattson and Addy 1975, Romme et al. 1986, Schowalter 2000). For example, low intensity of feeding on foliage by insects can stimulate nutrient turnover and increase tree growth (Alfaro and Shepherd 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).

Factors affecting arthropod abundances and assemblage structure are not well understood (Barker and Pinard 2001, Foggo et al. 2001). Individual plant species typically have relatively distinct arthropod assemblages, due to characteristic biochemical interactions between host and associated species. Arthropod species can respond positively, negatively, or not at all to particular environmental changes, depending on their adaptations to temperature, relative humidity, changes in plant growth, chemistry, or abundance, etc. (Shure and Phillips 1991, Schowalter 1985, Schowalter

and Turchin 1993, Dudt and Shure 1994, Schowalter 1995, Ozanne et al. 1997, Roland and Taylor 1997, Schowalter and Ganio 1999). Because insects are small, have short generation times, and rapid reproductive rates, their population sizes can change rapidly in response to changes in environmental conditions such as those resulting from changes in weather or in host abundance or biochemical condition (Schowalter 1985).

This study was designed to compare canopy arthropod abundances among four dominant overstory conifer species and three dominant understory angiosperm species in a mixed-conifer forest before thinning and burning treatment. We expected significant differences in arthropod abundances and assemblage structure among plant species that would be selected for posttreatment study.

Methods

We studied canopy arthropod assemblages on five replicate plots at the Teakettle Experimental Forest, 80 km east of Fresno, in Sierra County, CA, during 1998–2000. This site is located at 2,000–2,500 m elevation and is dominated by old-growth (>300 years old), mixed-conifer forest. Annual precipitation averages 110 cm at 2,100 m and falls

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mostly as snow between Nov. and Apr. Mean, maximum, and minimum July temperatures are 17, 30, and 3°C, respectively (Berg 1990). Soils are generally Xerumbrepts and Xeropsamments typical of the southwestern slopes of the Sierra Nevada (USDA Forest Service 1993).

El Niño conditions prevailed during 1998, bringing above-average precipitation (186 cm), especially winter snow, restricting access until mid July; La Niña conditions prevailed during 1999, with less than average precipitation (101 cm); intermediate conditions prevailed during 2000 (136 cm). Temperatures varied somewhat among years. An outbreak of Douglas-fir tussock moth (*Orgyia pseudotsugata* [McDunnogh]) began in 1997 and collapsed during 1999; extensive fir mortality occurred in areas of severe defoliation east of Teakettle, but was negligible at Teakettle (M. North, USDA Forest Service Sierra Nevada Research Ctr., Davis, CA., personal communication, Aug. 2000).

Historically, this forest was co-dominated by large (>1 m diameter), widely spaced Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.), sugar pine (*Pinus lambertiana* Douglas), white fir (*Abies concolor* Gord. and Glend.), and incense cedar (*Calocedrus decurrens* [Torrey]) in approximately equal proportions. However, fire exclusion during the past century has promoted recruitment of white fir, resulting in large areas of closed canopy forest dominated by young white fir (<100 years old, <70 cm diameter). Understory vegetation is primarily composed of patches of manzanita (*Arctostaphylos patula* Greene), and white-thorn ceanothus (*Ceanothus cordulatus* Kellogg) under canopy openings. California black oak (*Quercus kelloggii* Newb.) also is abundant, primarily along outcrops (Barbour et al. 1988, McKelvey and Busse 1996).

During 1997, 18 200-m² plots in a 1,300 ha area were established for the purpose of studying effects of thinning and burning on these forests. Work described here characterizes the pretreatment condition of the forest. Following treatment, additional data will be collected from all plots to evaluate canopy arthropod responses to the treatments.

For this study, we sampled one overstory tree of each of the four dominant conifer species and three individuals of each of three understory species in each of five plots distributed among the 18 scheduled for treatment. Samples from overstory trees were collected by climbing each tree, using the single-rope technique, quickly slipping a plastic bag over a randomly selected, foliated branch (0.5 m, 30–50 g dry wt), clipping the branch, and sealing the bag. Each tree was sampled at upper (within 5 m of top), middle, and lower (within 5 m of lowest foliated branches) crown levels, without regard to aspect, in June and Aug. each year to represent the seasonal variation in arthropod abundances observed in previous studies (Schowalter 1995, Schowalter and Ganio 1998) that reflect responses to seasonal pattern of climate and foliage development. In addition, three understory manzanita and ceanothus were sampled in each plot; California black oaks were sampled in four plots where they occurred. Samples from understory plants were collected at the same time from the ground by quickly slipping a plastic bag over a randomly selected, foliated branch (as above).

This sampling technique emphasizes the sedentary fauna that is present on foliage and twig surfaces at any given sampling time (e.g., aphids, caterpillars, spiders, mites) and tends to underrepresent highly mobile species that could be alarmed and escape (Schowalter 1995, Schowalter and Ganio 1999). Other sampling techniques have different biases, e.g., interception trapping emphasizes flying adult insects that may or may not be associated with a particular plant or even a particular treatment unit; canopy fogging emphasizes unattached arthropods that would reach collectors on the ground and would exclude many small arthropods that would be intercepted before reaching the ground (e.g., Majer and Recher 1988, Blanton 1990).

Samples were sorted in the laboratory by inspecting bags for mobile arthropods, then scanning samples under a dissecting microscope (10×) and collecting, identifying, and tabulating all arthropods. Plant material was dried at 50°C and weighed. Arthropod abundances were standardized as number per kilogram of plant sample.

Data Analyses

Arthropod taxa often are categorized into functional groups to reflect compartmentalization of natural communities and to focus on similar resource utilization strategies (Romoser and Stoffolano 1998). We followed previous functional group designations, i.e., folivores (all foliage-chewing caterpillars, sawflies, beetles, etc.), sap-suckers (aphids, scale insects, leafhoppers, etc.), gall-formers (primarily gall midges), predators (especially spiders, mites, beetles, snakeflies, etc.) and detritivores (primarily bark lice, springtails, and oribatid mites), for comparative purposes (see Schowalter et al. 1981, Schowalter 1995, Schowalter and Ganio 1999). However, species within functional groups may respond to environmental changes in different ways (Schowalter et al. 1999). Therefore, we analyzed data for sufficiently abundant species as well as for functional groups. We also calculated total arthropods and Simpson index (Magurran 1988) for each sample.

Sample data for three canopy levels (upper, middle, and lower) were pooled for each treatment and plant species to represent the arthropod community and to ensure sufficient abundance data for analyses. Residuals from the untransformed data for the 20 most abundant taxa (for the combined 3-year data set) and for functional groups were assessed for equal variance and normality. Results indicated a failure to satisfy both assumptions. Therefore, data were transformed to their natural logarithms ($y + 1$), stabilizing variance and normality for most taxa and groups (Christensen 1996). However, pooling and transformation did not normalize data for several taxa due to insufficient abundance in some treatment units, but were an improvement over untransformed data. All analyses were conducted separately for each of the seven plant species.

We tested the null hypothesis that arthropod abundances did not differ among plant species or year using analysis of variance (ANOVA) on transformed data for a completely randomized block design. All ANOVAs were conducted

Table 1. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on incense cedar from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	1.13 (0.76)	1.34 (0.94)	0.57 (0.36)	1.01 (0.39)	0.48	0.13	0.88
Gallformer	0.89 (0.89)	0.00 (0.00)	0.35 (0.35)	0.41 (0.31)	0.26	0.56	0.58
Sap-suckers	298 (104)	2.61 (1.34)	359 (278)	220 (100)	4.95	4.81	0.029*
<i>Pentamerismus</i>	288 (107)	0.00 (0.00)	358 (278)	215 (100)	4.84	7.09	0.009*
Predators	50.2 (17.9)	9.01 (1.55)	8.63 (1.18)	22.6 (7.61)	0.31	11.08	0.002*
Eulophidae	2.75 (0.79)	0.00 (0.00)	0.00 (0.00)	0.92 (0.42)	0.16	14.46	0.001*
Gamasida	20.4 (14.3)	0.00 (0.00)	0.00 (0.00)	6.79 (5.11)	1.02	6.28	0.014*
Detritivores	6.05 (2.04)	7.23 (1.45)	6.73 (4.56)	6.67 (1.61)	1.03	0.63	0.55
Miscellaneous	264 (188)	10.3 (2.82)	21.0 (7.94)	98.3 (65.9)	0.88	10.07	0.003*
Thrips sp. 1	48.0 (25.7)	3.76 (1.63)	1.02 (0.45)	17.6 (9.81)	1.02	9.83	0.003*
Thrips sp. 2	28.5 (8.19)	4.53 (1.78)	1.83 (1.13)	11.7 (4.16)	0.75	10.22	0.003*
Thrips sp. 3	185 (168)	1.77 (0.88)	4.80 (1.43)	63.9 (56.7)	2.61	2.56	0.12
Simpson index	0.48 (0.08)	0.84 (0.01)	0.47 (0.15)	0.59 (0.07)	0.024	3.87	0.05*
Total count	620 (176)	30.5 (3.61)	396 (275)	349 (120)	1.23	8.14	0.006*

Data represent pretreatment abundances for pooled June and August for 1998–2000, respectively.
n = 5; * significant effect (*P* < 0.05).

Table 2. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on Jeffrey pine from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	3.53 (1.48)	0.00 (0.00)	0.59 (0.37)	1.37 (0.63)	0.34	5.92	0.016*
Lepidoptera larvae	2.95 (1.14)	0.00 (0.00)	0.00 (0.00)	0.98 (0.51)	0.21	10.78	0.002*
Sap-suckers	3.92 (1.83)	24.3 (19.7)	1.97 (1.97)	10.0 (6.69)	1.82	1.41	0.28
<i>Chionaspis</i>	0.44 (0.44)	16.1 (14.6)	0.00 (0.00)	5.52 (4.93)	1.15	2.48	0.13
<i>Cinara</i> sp.	0.00 (0.00)	7.07 (4.52)	0.00 (0.00)	2.36 (1.65)	0.69	4.21	0.041*
Predators	42.5 (7.49)	12.3 (2.89)	20.1 (2.86)	25.0 (4.31)	0.21	8.39	0.005*
Miridae	11.8 (4.03)	3.95 (1.48)	3.82 (2.57)	6.53 (1.84)	1.02	2.06	0.17
Rhaphidiidae	7.59 (2.36)	2.07 (0.42)	1.52 (1.17)	3.73 (1.10)	0.44	5.73	0.018*
Eulophidae	1.80 (0.51)	0.00 (0.00)	0.00 (0.00)	0.60 (0.28)	0.1	14.41	0.001*
<i>Xysticus</i>	3.51 (1.19)	0.58 (0.35)	1.74 (0.80)	1.94 (0.56)	0.29	4.71	0.031*
Detritivores	6.96 (2.43)	6.94 (2.61)	2.58 (1.16)	5.49 (1.28)	0.98	0.84	0.46
Thysanura	0.00 (0.00)	2.01 (1.33)	0.00 (0.00)	0.67 (0.48)	0.25	4.04	0.046*
<i>Scapheremaeus</i>	5.13 (2.31)	0.84 (0.35)	1.22 (0.75)	2.39 (0.92)	0.63	2.17	0.16
Miscellaneous	132 (74.9)	20.3 (11.2)	15.4 (6.79)	56.0 (27.5)	1.8	3.21	0.076
Thrips sp. 1	23.3 (13.5)	6.06 (3.69)	2.92 (1.97)	10.8 (4.98)	1.52	2.39	0.13
Thrips sp. 2	90.0 (52.7)	6.92 (3.11)	1.99 (1.10)	32.3 (19.5)	1.53	7.57	0.007*
Thrips sp. 3	12.9 (7.03)	6.39 (5.59)	8.75 (5.49)	9.36 (3.33)	1.81	0.77	0.49
Simpson index	0.79 (0.05)	0.81 (0.02)	0.83 (0.03)	0.81 (0.02)	0.002	0.18	0.83
Total count	189 (80.0)	63.5 (27.2)	44.3 (4.85)	97.6 (31.4)	0.86	2.63	0.11

Data represent pretreatment abundances for pooled June and August for 1998–2000, respectively.
n = 5; * significant effect (*P* < 0.05).

using the PROC GLM procedure in SAS version 8.2 (SAS Inst., Inc. 2001).

The large number of taxa and analyses may suggest a high probability of type I errors. However, we expect the same error rate if these species were studied and reported individually, i.e., we expect 5% of significant differences (1 taxon per 20 analyzed on each plant species) to occur by chance alone, as demonstrated by Progar et al. (1999). Evaluation of multiple taxa in an integrated study has the advantage of indicating the degree of consistency of responses to treatments among taxa, even at the risk of some type I errors (Moran 2003). Furthermore, analyzing multiple taxa should reduce the probability of type II error, i.e., some taxa should show nonsignificant responses erroneously, but

if treatments have general effects on arthropods, then we would expect substantially more than 5% of our taxa or groups to show significant responses.

We analyzed data separately by year because of the distinct weather conditions prevailing during each of the 3 years. Canopy insects are small and short-lived, making abundances highly responsive to changes in temperature and moisture. Although the number of eggs laid one year influence the next year's potential population, the dramatic changes in weather during our study minimized any auto-correlation that might affect our results between years.

We used the indicator species method of Dufrene and Legendre (1997) to analyze indicator values for individual arthropod taxa for each plant species in each of the 3 years

Table 3. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on sugar pine from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance Means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	1.49 (0.63)	0.38 (0.38)	1.42 (0.59)	1.10 (0.32)	0.38	1.19	0.34
Gallformers	0.00 (0.00)	0.00 (0.00)	5.54 (2.47)	1.85 (1.03)	0.16	28.77	<0.0001*
Sap-suckers	7.42 (1.99)	28.7 (21.0)	2.64 (1.19)	12.9 (7.20)	1.43	1.28	0.31
Aphid sp. 5	0.00 (0.00)	18.2 (17.5)	0.00 (0.00)	6.05 (5.87)	1.26	1.76	0.21
<i>Chionaspis</i>	0.52 (0.52)	8.49 (4.03)	0.00 (0.00)	3.00 (1.63)	0.65	6.59	0.011*
Predators	26.4 (6.06)	23.5 (17.1)	30.7 (11.9)	26.9 (6.74)	0.91	1.46	0.27
Miridae	7.09 (3.22)	2.71 (0.82)	12.4 (8.34)	7.41 (2.97)	1.11	0.53	0.6
Reduviidae	1.94 (0.94)	0.00 (0.00)	3.75 (1.16)	1.89 (0.62)	0.44	5.31	0.022*
<i>Camponotus</i>	0.00 (0.00)	0.00 (0.00)	1.89 (0.85)	0.63 (0.36)	0.21	5.68	0.018*
Gamasida	4.08 (1.73)	0.00 (0.00)	0.00 (0.00)	1.36 (0.74)	0.42	5.91	0.016*
Detritivores	2.72 (1.25)	2.71 (1.32)	0.00 (0.00)	1.81 (0.66)	0.6	2.75	0.1
Miscellaneous	236 (31.2)	11.4 (4.74)	30.8 (8.93)	92.7 (29.0)	0.39	33.37	<0.0001*
Thrips sp. 1	9.15 (3.30)	3.03 (0.88)	6.70 (5.23)	6.29 (2.04)	0.99	1.36	0.29
Thrips sp. 2	46.8 (17.4)	6.77 (3.98)	9.42 (3.04)	21.0 (7.43)	0.82	7.54	0.007*
Thrips sp. 3	178 (46.4)	0.89 (0.37)	13.0 (5.77)	64.0 (26.0)	1.33	16.91	0.001*
Simpson index	0.45 (0.03)	0.73 (0.09)	0.81 (0.03)	0.67 (0.05)	0.006	10.18	0.003*
Total count	274 (36.2)	66.8 (41.8)	65.6 (19.5)	135 (31.8)	0.71	7.89	0.006*

Data represent pretreatment abundances for pooled June and August 1998–2000, respectively. $n = 5$; * significant effect ($P < 0.05$).

Table 4. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on white fir from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	6.57 (2.94)	2.26 (0.96)	0.72 (0.46)	3.19 (1.17)	0.53	4.54	0.034*
<i>Orgyia</i>	6.57 (2.94)	0.00 (0.00)	0.00 (0.00)	2.19 (1.23)	0.18	29.8	<0.0001*
Gallformer	0.00 (0.00)	0.46 (0.46)	0.00 (0.00)	0.15 (0.15)	0.09	1	0.39
Sap-suckers	12.1 (2.59)	64.1 (23.1)	3.52 (2.11)	26.6 (10.2)	0.67	15.53	0.001*
<i>Chionaspis</i>	0.89 (0.56)	4.35 (2.03)	0.00 (0.00)	1.75 (0.82)	0.42	5.84	0.017*
<i>Elatobium</i>	0.00 (0.00)	53.3 (19.8)	0.00 (0.00)	17.8 (9.09)	0.41	53.59	<0.0001*
Other Homoptera	3.86 (1.96)	0.00 (0.00)	0.00 (0.00)	1.29 (0.78)	0.27	10.19	0.003*
Predators	54.2 (16.7)	40.1 (9.82)	12.2 (2.93)	35.5 (7.63)	0.49	5.33	0.022*
Miridae	28.7 (15.7)	26.8 (9.55)	1.05 (0.65)	18.8 (6.59)	1.56	5.6	0.019*
Reduviidae	2.86 (1.37)	0.00 (0.00)	0.00 (0.00)	0.95 (0.55)	0.31	5.54	0.019*
Parasitic Hymenoptera	0.00 (0.00)	3.02 (1.06)	0.00 (0.00)	1.00 (0.50)	0.09	28.3	<0.0001*
Erythraeidae	7.62 (4.68)	0.00 (0.00)	4.07 (3.11)	3.89 (1.92)	1.46	1.33	0.3
Detritivores	17.7 (10.0)	4.83 (1.42)	5.81 (1.74)	9.46 (3.53)	1.22	0.43	0.66
Psocoptera	12.2 (7.37)	2.71 (1.11)	2.89 (1.89)	5.95 (2.65)	1.39	1.17	0.34
Miscellaneous	39.4 (7.40)	90.5 (46.9)	19.7 (7.66)	49.8 (16.8)	0.69	2.62	0.11
Lygaeidae	0.00 (0.00)	0.00 (0.00)	3.62 (1.11)	1.21 (0.57)	0.22	13.69	0.001*
Thrips sp. 1	2.13 (0.94)	58.6 (48.3)	1.19 (0.78)	20.6 (16.6)	1.92	2.94	0.091
Thrips sp. 2	26.3 (4.82)	24.1 (16.9)	7.98 (4.78)	19.4 (6.02)	0.89	3.1	0.082
Thrips sp. 3	6.33 (1.92)	5.45 (5.45)	4.59 (1.83)	5.45 (1.88)	1.37	1.08	0.37
Simpson index	0.82 (0.04)	0.64 (0.07)	0.81 (0.04)	0.76 (0.04)	0.005	3.49	0.07
Total count	130 (25.5)	202 (35.5)	41.9 (5.67)	125 (22.2)	0.15	21	0.0001*

Data represent pretreatment abundances for pooled June and August 1998–2000, respectively. $n = 5$; * significant effect ($P < 0.05$).

as well as the 3 years combined. This method combined a species' relative abundance with its relative frequency of occurrence in the various groups of sites. The resulting value, expressed as a percentage of perfect indication, describes a taxon's reliability for indicating a grouping parameter such as thinning and legacy retention. The index is maximum (100) when all individuals of a species are found in a single group of sites and when the species occurs in all sites of that group; the indicator index for a given species is independent of other species' relative abundance. The sta-

tistical significance of the species indicator values is evaluated based on the proportion of 1,000 randomized regrouping trials that equaled or exceeded the maximum indicator value observed (Monte Carlo test). Results were considered significant at $P < 0.05$.

We further investigated the arthropod community structure using nonmetric multidimensional scaling (NMS), with rare species down-weighted. NMS has the advantage over other multivariate analyses in not relying on a particular distribution of the data. However, NMS ordination is not

Table 5. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on manzanita from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance Means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	5.93 (2.16)	9.09 (3.90)	8.32 (2.28)	7.78 (1.58)	0.91	0.3	0.75
Other Lepidoptera larvae	3.75 (2.64)	7.65 (2.88)	1.46 (1.46)	4.29 (1.46)	1.25	1.93	0.19
Sap-suckers	130 (46.7)	548 (224)	2.01 (1.25)	227 (94.3)	2.61	12.66	0.001*
<i>Chionaspis</i>	0.00 (0.00)	5.23 (3.59)	0.00 (0.00)	1.74 (1.29)	0.68	2.57	0.12
Psyllidae	1.15 (1.15)	9.02 (9.02)	0.00 (0.00)	3.39 (3.01)	1.22	0.6	0.56
Aphid sp. 1	0.00 (0.00)	529 (218)	0.00 (0.00)	176 (94.8)	0.6	90.7	<0.0001*
Aphid sp. 2	99.6 (48.3)	0.00 (0.00)	0.00 (0.00)	33.2 (19.5)	1.66	12.44	0.001*
Cicadellidae	17.7 (7.35)	3.91 (2.84)	2.01 (1.24)	7.88 (3.09)	1.59	2.52	0.12
<i>Pentamerismus</i>	9.12 (9.12)	0.00 (0.00)	0.00 (0.00)	3.04 (3.04)	0.98	1	0.39
Predators	61.6 (12.1)	23.3 (6.97)	12.0 (5.73)	32.3 (7.34)	1.14	5.66	0.02*
Miridae	0.00 (0.00)	7.35 (4.00)	0.00 (0.00)	2.45 (1.54)	0.66	5.49	0.02*
Neuroptera	4.66 (3.53)	0.60 (0.60)	0.00 (0.00)	1.76 (1.24)	0.75	1.6	0.24
Gamasida	14.9 (12.3)	0.00 (0.00)	0.00 (0.00)	4.98 (4.23)	1.23	2.43	0.13
Linyphiidae	6.30 (3.34)	0.00 (0.00)	1.13 (1.13)	2.48 (1.31)	0.84	3.14	0.08
<i>Xysticus</i>	5.03 (1.46)	0.72 (0.72)	0.00 (0.00)	1.92 (0.78)	0.43	8.14	0.006*
Detritivores	0.00 (0.00)	2.05 (1.42)	2.20 (2.20)	1.42 (0.85)	0.74	0.88	0.44
Miscellaneous	178 (84.8)	23.3 (6.99)	38.6 (17.9)	80.1 (32.7)	1.53	3.81	0.05*
Thrips sp. 1	162 (74.5)	5.79 (2.95)	0.00 (0.00)	55.9 (30.5)	0.94	30.94	<0.0001*
Thrips sp. 2	2.83 (1.78)	10.5 (5.92)	2.42 (1.58)	5.24 (2.20)	1.65	0.75	0.49
Thrips sp. 3	12.9 (10.2)	0.91 (0.91)	0.00 (0.00)	4.59 (3.53)	1.11	2.97	0.09
Misc. Coleoptera	0.00 (0.00)	0.00 (0.00)	24.1 (17.8)	8.02 (6.28)	0.48	21.04	0.0001*
Diptera	0.00 (0.00)	5.13 (2.78)	10.1 (10.1)	5.08 (3.42)	1.55	1.34	0.29
Simpson index	0.72 (0.04)	0.34 (0.07)	0.68 (0.09)	0.58 (0.06)	0.03	6.31	0.013*
Total count	375 (130)	606 (234)	63.1 (20.7)	348 (102)	0.88	7.05	0.009*

Data represent pretreatment abundances by pooled June and August 1998–2000, respectively.
n = 5; * significant effect (*P* < 0.05).

Table 6. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on ceanothus from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance Means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	423 (328)	32.1 (8.38)	31.6 (7.51)	162 (113)	1.09	3.67	0.057
Geometridae	28.6 (8.45)	18.9 (6.67)	14.3 (2.35)	20.6 (3.76)	1.64	0.1	0.9
Other Lepidoptera larvae	372 (325)	8.97 (0.57)	1.12 (1.12)	127 (110)	3.74	2.96	0.09
Curculionidae	10.8 (6.35)	0.00 (0.00)	8.40 (7.00)	6.41 (3.17)	1.74	2.06	0.17
Gallformers	156 (126)	0.00 (0.00)	0.00 (0.00)	52.0 (44.0)	3.32	2.58	0.12
Sap-suckers	359 (138)	366 (200)	349 (335)	358 (128)	3.33	2.56	0.12
Misc. Coccoidea	151 (137)	0.00 (0.00)	335 (335)	162 (118)	6.19	1.41	0.28
Psyllidae	18.6 (8.29)	25.7 (13.6)	2.54 (1.56)	15.6 (5.58)	2.51	1.53	0.26
Aphid sp. 1	22.8 (12.3)	0.00 (0.00)	0.00 (0.00)	7.59 (4.75)	1.32	5.42	0.021*
Aphid sp. 4	0.00 (0.00)	315 (200)	0.00 (0.00)	105 (73.5)	3.67	5.52	0.02*
Cicadellidae	58.4 (16.9)	24.2 (9.21)	4.09 (1.73)	28.9 (8.46)	1.34	6.88	0.01*
<i>Pentamerismus</i>	90.0 (90.0)	0.00 (0.00)	0.00 (0.00)	30.0 (30.0)	2.49	1	0.39
Predators	240 (86.4)	63.6 (22.2)	39.4 (7.28)	114 (36.5)	0.48	6.92	0.01*
Miridae	58.0 (24.7)	35.7 (13.9)	9.50 (3.42)	34.4 (10.3)	1.09	3.63	0.058
Chalcidae	98.4 (73.3)	0.00 (0.00)	1.12 (1.12)	33.2 (25.8)	1.86	8.16	0.006*
Gamasida	15.7 (9.77)	0.00 (0.00)	0.00 (0.00)	5.23 (3.61)	1.05	5.38	0.021*
Philodromidae	8.69 (4.42)	5.30 (3.46)	11.0 (6.66)	8.33 (2.76)	2.31	0.23	0.79
Linyphiidae	9.74 (4.56)	0.00 (0.00)	10.8 (4.79)	6.85 (2.42)	1.67	2.93	0.09
Detritivores	18.1 (11.8)	36.5 (13.7)	3.57 (1.47)	19.4 (6.65)	2.06	3.37	0.069
Psocoptera	2.62 (2.62)	27.1 (6.17)	0.00 (0.00)	9.90 (3.86)	0.59	24.82	<0.0001*
Miscellaneous	1220 (518)	502 (258)	52.2 (19.3)	590 (220)	1.48	8.02	0.006*
Thrips sp. 1	923 (362)	372 (268)	49.5 (19.8)	448 (169)	2.36	5.51	0.02*
Thrips sp. 2	74.7 (28.4)	121 (114)	0.00 (0.00)	65.3 (38.8)	3.72	4.22	0.041*
Diptera	33.9 (31.3)	5.07 (3.56)	0.00 (0.00)	13.0 (10.5)	2.37	1.24	0.32
Misc. insects	161 (161)	0.00 (0.00)	0.00 (0.00)	53.7 (5.37)	2.98	1	0.39
Simpson index	0.64 (0.05)	0.62 (0.07)	0.68 (0.14)	0.64 (0.05)	0.02	0.02	0.98
Total count	2410 (663)	1000 (470)	476 (335)	1300 (349)	0.99	6.05	0.015*

Data represent pretreatment abundances for pooled June and August 1998–2000, respectively.
n = 5; * significant effect (*P* < 0.05).

Table 7. Mean (standard error) abundances (no./kg plant material) of the most abundant arthropod taxa on black oak from 1998 to 2000 at Teakettle Experimental Forest, California

Taxon	Abundance means (SE)				MSE	F-value	P-value
	1998	1999	2000	1998–2000			
Folivores	0.00 (0.00)	5.88 (5.88)	0.00 (0.00)	1.60 (1.60)	0.71	1.45	0.29
Sap-suckers	36.1 (13.0)	307 (74.4)	0.00 (0.00)	96.9 (44.8)	1.46	19.07	0.001*
<i>Chionaspis</i>	0.00 (0.00)	13.8 (8.25)	0.00 (0.00)	3.76 (2.74)	0.79	5.55	0.031*
Psyllidae	0.00 (0.00)	28.6 (28.6)	0.00 (0.00)	7.79 (7.79)	1.66	1.45	0.29
Aphid sp. 3	0.00 (0.00)	142 (64.4)	0.00 (0.00)	38.8 (25.1)	0.26	90.93	<0.0001*
Other Aphidae	8.59 (8.59)	0.00 (0.00)	0.00 (0.00)	3.13 (3.13)	1.19	0.85	0.46
Cicadellidae	25.5 (13.4)	123 (56.1)	0.00 (0.00)	42.7 (21.0)	1.88	8.59	0.01*
Membracidae	63.9 (52.2)	0.00 (0.00)	17.6 (12.3)	29.6 (19.6)	4.31	1.07	0.39
Predators	361 (114)	119 (28.0)	32.6 (13.6)	176 (60.0)	0.63	8.51	0.011*
Miridae	252 (98.6)	71.6 (21.1)	24.6 (16.6)	120 (46.3)	4.34	1.08	0.39
Reduviidae	11.5 (11.5)	0.00 (0.00)	0.00 (0.00)	4.18 (4.18)	1.39	0.85	0.46
Cantharidae	9.11 (9.11)	8.14 (4.09)	0.00 (0.00)	5.53 (3.43)	1.79	1.44	0.29
Coccinellidae	4.69 (4.69)	7.06 (3.53)	0.00 (0.00)	3.63 (1.98)	1.34	1.71	0.24
Formicidae	6.58 (6.58)	3.55 (3.55)	0.00 (0.00)	3.36 (2.49)	1.53	0.56	0.59
Eulophidae	21.2 (13.9)	0.00 (0.00)	0.00 (0.00)	7.71 (5.61)	1.75	2.49	0.14
Ichneumonidae	6.58 (6.58)	0.00 (0.00)	0.00 (0.00)	2.39 (2.39)	1.03	0.85	0.46
Anyphaenidae	11.5 (11.5)	0.00 (0.00)	0.00 (0.00)	4.18 (4.18)	1.39	0.85	0.46
Linyphiidae	8.83 (8.83)	0.00 (0.00)	0.00 (0.00)	3.21 (3.21)	1.21	0.85	0.46
<i>Xysticus</i>	0.00 (0.00)	10.5 (10.5)	0.00 (0.00)	2.87 (2.87)	1.01	1.45	0.29
Detritivores	0.00 (0.00)	9.68 (1.29)	3.39 (3.39)	3.87 (1.68)	0.68	7.15	0.016*
Miscellaneous	3770 (997)	390 (148)	56.6 (26.6)	1500 (637)	2.08	12.08	0.004*
Thrips sp. 1	3670 (988)	343 (169)	13.5 (7.89)	1430 (629)	1.49	24.68	0.0004*
Thrips sp. 2	19.4 (13.8)	39.4 (24.4)	14.5 (8.03)	23.1 (8.42)	3.96	0.18	0.84
Thrips sp. 3	6.44 (4.20)	0.00 (0.00)	0.00 (0.00)	2.34 (1.69)	0.86	2.45	0.15
Elateridae	6.58 (6.58)	0.00 (0.00)	0.00 (0.00)	2.39 (2.39)	1.03	0.85	0.46
Simpson index	0.22 (0.06)	0.74 (0.06)	0.57 (0.19)	0.49 (0.09)	0.1	2.87	0.11
Total count	4140 (1080)	832 (228)	92.7 (20.3)	1770 (679)	0.26	55.98	<0.0001*

Data represent pretreatment abundances for pooled June and August 1998–2000, respectively.
n = 4; * significant effect (*P* < 0.05).

Table 8. Mean squares table for canopy arthropod functional group abundances and Simpson's diversity index among four overstorey conifer and three understorey angiosperm species from 1998 to 2000 at Teakettle Experimental Forest, California

Functional group	MSE	F-value	P-value		
			Year	Plant species	Year × plant species
Folivores	0.63	13.09	0.03*	<0.0001*	0.04*
Gallformers	0.55	2.22	0.1	0.07	0.02*
Sap-suckers	2.36	6.99	<0.0001*	<0.0001*	<0.0001*
Predators	0.59	7.47	<0.0001*	<0.0001*	0.017*
Detritivores	1.06	3.13	0.0023*	0.0001*	0.12
Miscellaneous	1.22	9.41	<0.0001*	<0.0001*	0.0008*
Simpson index	0.013	4.54	0.08	0.0002*	<0.0001*

See Tables 1–7 for functional group abundances.

reproducible. Rare taxa, defined as occurring in <5% of the sampling units, were excluded from the NMS. We conducted NMS for abundances among treatments and among years. Multiple response permutation procedure (MRPP) was used to verify treatment groups. MRPP is a nonparametric procedure for testing the hypothesis that two or more groups of entities are not significantly different. MRPP has the advantage of not being based on assumptions of distribution (such as normality and homogeneity of variances) that are seldom met in ecological community data (Mielke 1979, Biondini et al. 1985, Mielke and Berry 2001). Where the overall MRPP indicated significant differences among groups, we tested pairs of groups to see which differed from each other. We used PC-ORD (ver. 4) for NMS, MRPP,

and indicator species analysis (McCune and Mefford 1999).

Results

The most abundant taxa on each plant species are shown in Tables 1–7. The arthropod assemblage on incense cedar was dominated by large numbers of a false spider mite (*Pentamerismus erythreus* [Ewing]), and thrips species 3; other tree species had relatively more even distribution of abundances among taxa. Large numbers of the Douglas-fir tussock moth were found on white fir, reflecting the outbreak of this species in the area around Teakettle. All three understorey species were dominated by aphids and thrips, but

Table 9. Indicator values (percentage of perfect indication, based on relative abundance and relative frequency) for canopy arthropods with significant ($P < 0.05$) values by tree species at Teakettle Experimental Forest, California for combined 1998–2000 samples

Taxon	Incense cedar	Jeffrey pine	Sugar pine	White fir	Manzanita	Ceanothus	Black oak
Sap-suckers							
<i>Nuculaspis</i>	0	0	60	0	0	0	0
Misc. scales	1	0	1	0	0	48	2
Psyllidae	3	0	2	11	6	32	2
<i>Cinara</i>	0	60	0	0	0	0	0
<i>Elatobium</i>	0	0	1	93	0	0	0
Aphid sp. 1	0	0	0	0	73	16	0
Aphid sp. 2	0	0	0	0	80	0	0
Aphid sp. 3	0	0	0	0	0	0	60
Aphid sp. 4	0	0	0	0	0	60	0
Cicadellidae	11	10	9	5	20	27	10
Membracidae	0	0	0	0	2	3	46
Other Homoptera	0	0	0	38	4	13	0
<i>Pentamerismus</i>	74	0	0	0	2	3	0
Folivores							
<i>Orgyia pseudotsugata</i>	0	1	1	54	0	13	0
Geometridae	1	0	0	0	13	67	2
Other Lepidoptera larvae	4	9	1	2	25	43	1
Diprionidae	0	0	0	3	0	52	0
Curculionidae	1	4	0	0	9	50	0
Gallformers							
Gall midge larvae	15	0	67	2	0	0	0
Predators							
Miridae	9	12	12	16	4	20	24
Berytidae	0	1	7	48	0	30	0
Rhaphidiidae	1	49	4	2	1	8	0
Chalcidae	0	0	0	0	0	80	0
Erythraeidae	8	8	0	36	0	0	0
Linyphiidae	6	3	5	8	10	34	2
Pseudoscorpionida	0	43	6	0	0	0	0
Detritivores							
Psocoptera	16	2	7	21	0	38	0
Sciaridae	2	5	0	0	0	34	4
<i>Scapheremaeus</i>	20	37	1	14	0	0	2
Miscellaneous							
Lygaeidae	0	7	3	44	3	0	0
Thrips sp. 1	11	10	9	10	15	23	17
Thrips sp. 3	20	17	27	14	8	2	2
Misc. Coleoptera	0	1	2	7	69	0	0

ceanothus also had large numbers of lepidopteran larvae and scale insects, and black oak had abundant cicadellids, membracids, and predaceous mirids. Black oak and ceanothus had the largest mean total abundances (1,770 and 1,300/kg plant material, respectively), but Jeffrey pine and white fir had the highest Simpson diversity, reflecting relatively even distribution of a small number of individuals among functional groups (98 and 125/kg plant material, respectively). More than 60% of the total arthropods on black oak and incense cedar belonged to a single functional group, sap-sucking herbivores. Most taxa declined in abundance from 1998 to 2000 or had minimal abundances in 1999, but aphids, pine needle scales (*Chionaspis pinifoliae* [Fitch]), predaceous mirids, and detritivores generally had peak abundances in 1999.

Functional group organization differed significantly among plant species and years (Table 8). Folivores were most abundant on ceanothus; sap-suckers on incense cedar, manzanita, and ceanothus; predators on ceanothus and black

oak; and detritivores on ceanothus. Sap-suckers apparently disappeared on incense cedar, but peaked on other plant species, during 1999. Other functional groups showed varying patterns of abundance among plant species during the 3 years.

Indicator values, representing taxa that were distinct among plant species, are shown in Table 9. *Pentamerismus* characterized incense cedar; aphids (*Cinara* sp.), raphidiids, and pseudoscorpions characterized Jeffrey pine; black pineleaf scales (*Nuculaspis californica* [Coleman]) and gall midge larvae characterized sugar pine; Douglas-fir tussock moth, spruce aphids (*Elatobium abietinum* [Walker]), berytidae, and lygaeids characterized white fir; aphid species 1 and 2 and an unidentified beetle characterized manzanita; geometrids, diprionids, curculionids, aphid sp. 4, an unidentified coccoid, and chalcid wasps characterized ceanothus; aphid sp. 3 and membracids characterized black oak.

NMS distinguished arthropod assemblages on all seven plant species in 1998 and for the 3 years' combined data, but arthropod assemblages were less distinct during 1999 and

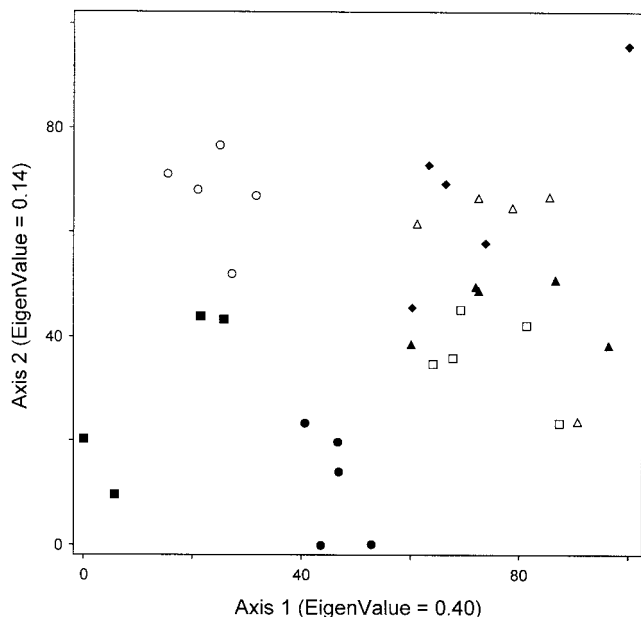


Figure 1. Nonmetric multidimensional scaling (NMS) of arthropod assemblages (for taxa present in >5% of samples) on four overstory conifer and three understory angiosperm species at Teakettle Experimental Forest in the southern Sierras during 1998. \blacktriangle , incense cedar; \triangle , Jeffrey pine; \square , sugar pine; \blacklozenge , white fir; \bullet , manzanita; \circ , Ceanothus; \blacksquare , black oak.

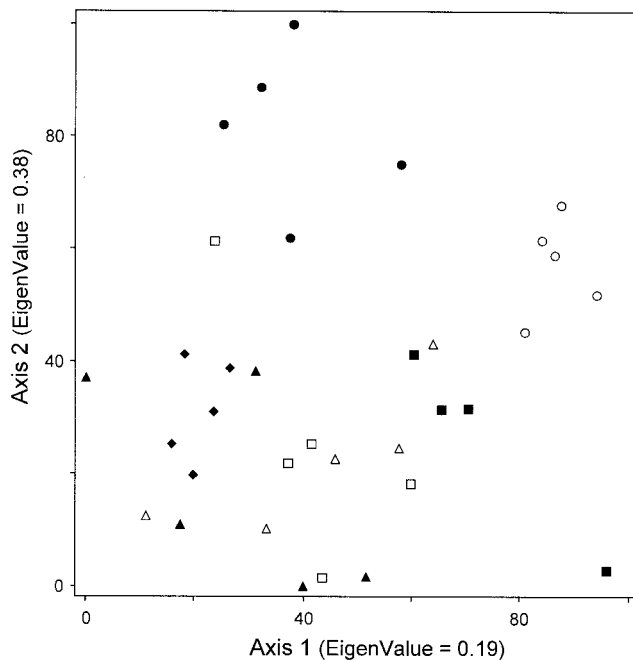


Figure 3. Nonmetric multidimensional scaling (NMS) of arthropod assemblages on four overstory conifer and three understory angiosperm species at Teakettle Experimental Forest in the southern Sierras during 2000. Symbols as in Figure 1.

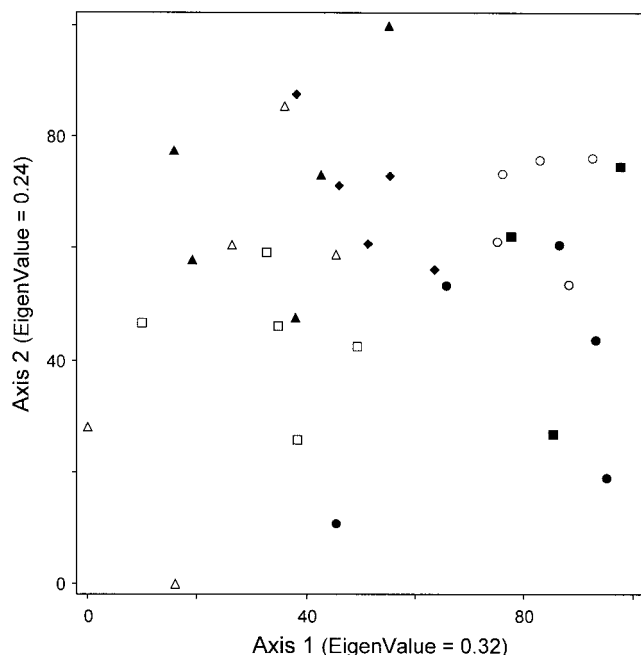


Figure 2. Nonmetric multidimensional scaling (NMS) of arthropod assemblages on four overstory conifer and three understory angiosperm species at Teakettle Experimental Forest in the southern Sierras during 1999. Symbols as in Figure 1.

2000 (Figures 1–4). Nevertheless, MRPP confirmed that arthropod assemblages differed significantly among plant species. Only sugar pine versus Jeffrey pine and sugar pine versus incense cedar ($P > 0.1$) and Jeffrey pine versus incense cedar in 1999 ($P = 0.087$), and Jeffrey pine versus white fir ($P = 0.066$) and Jeffrey pine versus incense cedar

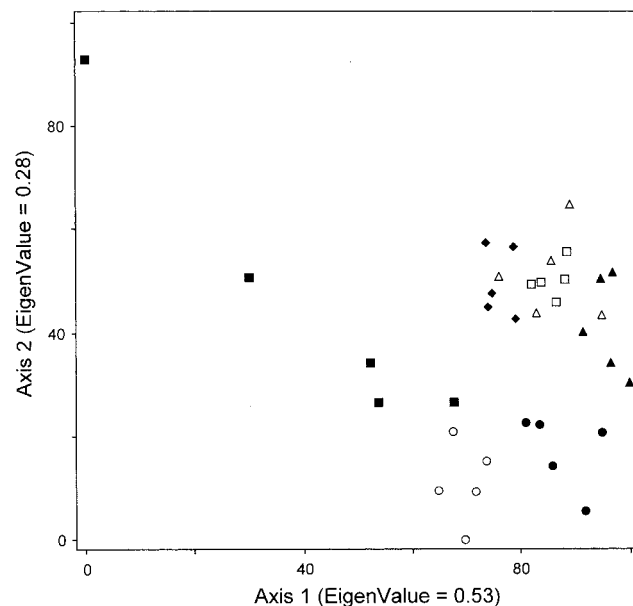


Figure 4. Nonmetric multidimensional scaling (NMS) of arthropod assemblages on four overstory conifer and three understory angiosperm species at Teakettle Experimental Forest in the southern Sierras for the 3-year period 1998–2000. Symbols as in Figure 1.

($P = 0.074$) in 2000 were not significantly different. These data, supported by the results from ANOVA and indicator species analysis, indicated that each plant species supports a unique arthropod assemblage.

Discussion

This study was designed to provide pretreatment data on arthropod assemblages among plant species and on annual

variation. We demonstrated that canopy arthropod assemblages differed significantly among plant species and years. Assemblages differed most dramatically between conifers and angiosperms, but assemblages also could be distinguished among individual plant species, likely reflecting biochemical differences. Although arthropod abundances could not be directly compared among plant species because of distinct species associations, we did observe significant differences in functional group assemblage structure among plant species. Trends in arthropod abundances among years suggest responses to the dramatic variation in weather during this study. We note the possibility that one significant response per 20 taxa tested could be erroneous ($P = 0.05$), but 30–50% of taxa on each plant species showed significant differences in abundance between years, with consistent patterns among taxa in functional groups indicating general responses to changes in environmental conditions. Given the sensitivity of small, poikilothermic organisms to changes in weather and the long time intervals between sampling, results for each year should be relatively independent. These data will facilitate posttreatment sampling and data analysis.

We expected arthropod presence and abundance to differ among plant species. Arthropod abundances and assemblage structure among species in this study are similar to results from Schowalter and Ganio (1998) for an old-growth conifer forest in southwestern Washington. In particular, both incense cedar and western red cedar (*Thuja plicata* Donn.) were dominated by false spider mites. This arthropod assemblage structure was distinct from assemblages on species of Pinaceae (pines, firs, and hemlock) in both studies. For herbivorous species, biochemical interactions with plant defenses and nutritional factors determine host preferences (Harborne 1988). Predator abundances typically reflect prey abundance, but some predators also may be affected by differences in chemistry or architecture among plant species or the abundance of other predators (Halaj et al. 1997). Abundances also can be affected in unknown ways by indirect effects of associated species. The distinct arthropod assemblages suggest that sampling most, or all, of the seven plant species may be necessary to evaluate effects of thinning and burning treatments.

Furthermore, arthropod abundances differed significantly among years, indicating effects of environmental variation. Weather, especially drought conditions, can affect arthropod survival directly, via lethal temperatures or desiccation; or indirectly, via changes in host biochemistry or predator abundances (Mattson and Haack 1987, Price 1991, Waring and Cobb 1992, White 1969). Plant architecture or vegetation structure can modify weather conditions (Chen et al. 1995, Parker 1995). Most taxa were more abundant during 1998 and/or 2000, compared to 1999, suggesting that their populations are favored by wetter conditions prevailing during these 2 years, whereas several aphid and scale insect species, predaceous mirids, and some detritivores showed peak abundances in 1999, a particularly dry year, suggesting that their populations are favored by drier conditions. Similar variation among species in response to

weather variables has been reported by Majer et al. (2001) and Progar and Schowalter (2002). These data are consistent with responses of various arthropod groups to canopy-opening disturbances (e.g., Schowalter 1995, Schowalter and Ganio 1999), which create warmer, drier conditions (Chen et al. 1995, Lewis 1998). Analysis of posttreatment responses will need to address factors affecting annual variation in arthropod abundances among these plant species.

Literature Cited

- ALFARO, R.I., AND R.F. SHEPHERD. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by the Douglas-fir tussock moth. *For. Sci.* 37:959–964.
- BARBOUR, M.G., B.M. PAVLIK, AND J.A. ANTOS. 1988. Seedling growth and survival of red and white fir in a Sierra Nevada ecotone. *Am. J. Bot.* 77:927–938.
- BARKER, M.G., AND M.A. PINARD. 2001. Forest canopy research: Sampling problems and some solutions. *Plant Ecol.* 153:23–38.
- BERG, N.H. (ED.) 1990. Experimental forests and ranges. Field research facilities of the Pacific Southwest Research Station. USDA Forest Service PSW-GTR-119, USDA Forest Service Pacific Southwest Res. Stn., Berkeley, CA.
- BIONDINI, M.E., C.D. BONHAM, AND E.F. REDENTE. 1985. Secondary successional patterns in a sagebrush community as they relate to soil disturbance and soil biological activity. *Vegetio* 60:25–36.
- BLANTON, C.M. 1990. Canopy arthropod sampling: A comparison of collapsible bag and fogging methods. *J. Agric. Entomol.* 7:41–50.
- CHEN, J., J.J. FRANKLIN, AND T.A. SPIES. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Applic.* 5:74–86.
- CHRISTENSEN, R. 1996. Analysis of variance, design and regression. Chapman and Hall, London, UK.
- DUDT, J.F., AND D.J. SHURE. 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology* 75:86–98.
- DUFRENE, M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67:345–366.
- FOGGO, A., C.M.P. OZANNE, M.R. SPEIGHT, AND C. HAMBLER. 2001. Edge effects and tropical forest canopy invertebrates. *Plant Ecol.* 153:347–359.
- HALAJ, J., D.W. ROSS, AND A.R. MOLDENKE. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* 109:313–322.
- HARBORNE, J.B. 1988. Introduction to ecological biochemistry, 3rd ed. Academic Press, London.
- LEWIS, T. 1998. The effect of deforestation on ground surface temperatures. *Glob. Planet. Change* 18:1–13.
- MAGURRAN, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.
- MAJER, J.D., AND H.F. RECHER. 1988. Invertebrate communities on Western Australian eucalypts—A comparison of branch

- clipping and chemical knockdown procedures. *Austr. J. Ecol.* 13:269–278.
- MAJER, J.D., R.L. KITCHING, B.E. HETERICK, K. HURLEY, AND K.E.C. BRENNAN. 2001. North-south patterns within arboreal ant assemblages from rain forests in eastern Australia. *Biotropica* 33:643–661.
- MATTSON, W.J., AND N.D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515–522.
- MATTSON, W.J., AND R.A. HAACK. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37:110–118.
- MCCUNE, B., AND M.J. MEFFORD. 1995. PC-Ord. multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, OR.
- MCKELVEY, K.S., AND M. BUSSE. 1996. Twentieth-century fire patterns on forest service lands. P. 1119–1138 in *Sierra Nevada Ecosystem Project, Vol. II., Wildland Resources Center Rep. 37*, University of California, Davis, CA.
- MIELKE, P.W. JR. 1979. On the asymptotic non-normality of null distributions of MRPP statistics. *Commun. Statistics* A5:1409–1424.
- MIELKE, P.W. JR., AND K.J. BERRY. 2001. Permutation methods: A distance function approach. Springer, New York.
- MORAN, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- OZANNE, C.M.P., C. HAMBLER, A. FOGGO, AND M.R. SPEIGHT. 1997. The significance of edge effects in the management of forests for invertebrate diversity. P. 534–550 in *Canopy arthropods*, Stork, N.E., J. Adis, and R.K. Didham (eds.). Chapman and Hall, London, UK.
- PARKER, G.G. 1995. Structure and microclimate of forest canopies. P. 73–106 in *Forest canopies*, Lowman, M.D., and N.M. Nadkarni (eds.). Academic Press, San Diego, CA.
- PRICE, P.W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62:244–251.
- PROGAR, R.A., AND T.D. SCHOWALTER. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas-fir *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. *Ecography* 25:129–138.
- PROGAR, R.A., T.D. SCHOWALTER, AND T. WORK. 1999. Aboreal invertebrate responses to varying levels and patterns of green-tree retention in northwestern forests. *Northwest Sci.* 73: 77–86.
- ROLAND, J., AND P.D. TAYLOR. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386:710–713.
- ROMME, W.H., D.H. KNIGHT, AND J.B. YAVITT. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *Am. Natur.* 127:484–494.
- ROMOSER, W.S., AND J.G. STOFFOLANO JR. 1998. The science of entomology (4th ed.). McGraw-Hill, Boston, MA.
- RUANGPANIT, N. 1985. Percent crown cover related to water and soil losses in mountainous forest in Thailand. P. 462–471 in *Soil erosion and conservation*, El-Swaify, S.A., W.C. Moldenhauer, and A. Lo (eds.). Soil Conservation Society of America, Ankeny, IA.
- SAS INSTITUTE, INC. 2001. SAS user's guide. SAS Institute Inc., Cary, NC.
- SCHOWALTER, T.D. 1985. Adaptations of insects to disturbance. P. 235–252 in *The ecology of natural disturbance and patch dynamics*. Pickett, S.T.A., and P.S. White (eds.). Academic Press, Orlando, FL.
- SCHOWALTER, T.D. 1995. Canopy arthropod community responses to forest age and alternative harvest practices in western Oregon. *For. Ecol. Manage.* 78:115–125.
- SCHOWALTER, T.D. 2000. *Insect ecology: An ecosystem approach*. Academic Press, San Diego, CA.
- SCHOWALTER, T.D., AND L.M. GANIO. 1998. Vertical and seasonal variation in canopy arthropod abundances in an old-growth conifer forest in southwestern Washington. *Bull. Entomol. Res.* 88:633–640.
- SCHOWALTER, T.D., AND L.M. GANIO. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecol. Entomol.* 24:191–201.
- SCHOWALTER, T.D., AND P. TURCHIN. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *For. Sci.* 39:201–210.
- SCHOWALTER, T.D., W.W. HARGROVE, AND D.A. CROSSLEY JR. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31:177–196.
- SCHOWALTER, T.D., D.C. LIGHTFOOT, AND W.G. WHITFORD. 1999. Diversity of arthropod responses to host plant water stress in southern New Mexico. *Am. Midl. Natur.* 142:281–290.
- SCHOWALTER, T.D., J.W. WEBB, AND D.A. CROSSLEY JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62: 1010–1019.
- SHURE, D.J., AND D.L. PHILLIPS. 1991. Patch size of forest openings and arthropod populations. *Oecologia* 86:325–334.
- USDA FOREST SERVICE. 1993. *Soil survey of Sierra National Forest Area, California*. 313 p.
- WARING, G.L., AND N.S. COBB. 1992. The impact of plant stress on herbivore population dynamics. P. 167–226 in *Plant-Insect interactions*, vol. 4. Bernays, E.A. (ed.). CRC Press, Boca Raton, FL.
- WHITE, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50:905–909.