Soil Arthropod Responses to Different Patch Types in a Mixed-Conifer Forest of the Sierra Nevada

James L. Marra and Robert L. Edmonds

Abstract: The Teakettle Ecosystem Experiment in the southern Sierra Nevada is using thinning and prescribed fire to recreate historical stand conditions. As part of Teakettle we assessed pretreatment diversity and density of the soil arthropod community in 1998 and 2000. We determined the density and diversity of soil microarthropods among treatment plots, the influence of patch type (closed canopy, canopy gaps, *Ceanothus* sp., and coarse woody debris [CWD]), and established baseline pretreatment data. Mites were the dominant microinvertebrates (78%). Canopy gaps had the lowest mite density and diversity, and were more sensitive to year-to-year changes in climate (1998 was an extremely wet year for the region). Soil organic matter as represented by bulk density appeared to be most closely associated with changes in species composition among different patch types. There was substantial overlap, however, in community composition among the different patch types as represented by nonmetric multidimensional scaling (NMS) ordination. No significant differences were observed for mite species richness and density among plots assigned to future treatments. The gap data suggest that in the characteristically hot, dry summers of the southern Sierra Nevada the rate of recovery of vegetation following thinning and fire treatments may have a significant influence on the recovery rate of microarthropods, not only by providing sources of energy inputs in the form of dead organic matter, but also by moderating the microclimate of the forest floor. FOR. SCI. 51(3):255–265.

Key Words: Mites, soil invertebrates, Teakettle Project, pretreatment data.

FOREST SOIL ARTHROPOD DIVERSITY and abundance are dominated by microarthropods generally in the size range of 0.1 to 2 mm. Mites and springtails are generally the most abundant groups in temperate coniferous soils. Beetles, flies, in both adult and larval stages, pseudoscorpions, spiders, and many lesser-known groups are also abundant, although not seen unless examined under magnification. Although an inconspicuous part of the ecosystem, microarthropods are nevertheless important to the functioning of soil (Seastedt 1984, Seastedt and Crossley 1987). Through their interactions with soil microbes they influence decomposition and nutrient mineralization processes, alter soil structure and porosity, and influence soil genesis (Asquith et al. 1990, Stork and Eggleton 1992).

Arthropods are sensitive bioindicators of environmental change (Moldenke and Lattin 1990) because of their rapid reproductive rates, short generation times, and the fine grain at which they occupy space in the soil. Because of their small size and enormous diversity and abundance, soil arthropods are able to partition their habitat at very fine spatial scales. The study of soil arthropod diversity and density, therefore, can provide valuable information into how ecosystems respond to different forest management practices (Moldenke et al. 2000).

The Teakettle Ecosystem Experiment, located in the mixed-conifer forest of the southern Sierra Nevada (North et al. 2002), involves the use of selective timber harvesting (thinning) and prescribed burning to create stand conditions analogous to those occurring under historical fire regimes. Before the initiation of fire and thinning treatments, a number of different studies were initiated to investigate pretreatment stand conditions (Erickson et al. 2005, Gray et al. 2005, Ma et al. 2005, Schowalter and Zhang 2005). We investigated the diversity and density of the soil arthropod community in a mixed-conifer forest as part of the Teakettle Ecosystem Experiment. The specific objectives of our pretreatment study were to (1) compare the density, diversity, and species composition of soil microarthropods among treatment plots before the initiation of thinning and burning; (2) compare differences among forest floor patch types (closed canopy, open canopy gaps, *Ceanothus* sp. patches, and coarse woody debris [CWD]); and (3) establish baseline pretreatment data for eventual comparison with posttreatment structural characteristics that contribute to the survival and recovery of soil invertebrate communities.

Materials and Methods

Study Site

The Teakettle Experimental Forest (1,300 ha) is located on the Kings River Ranger District of the Sierra National Forest approximately 80 km east of Fresno, CA. Elevations

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range from 1,880 to 2,485 m above sea level. Vegetation consists primarily of late successional mixed-conifer and California red fir (*Abies magnifica* A. Murr.) forests. In mixed-conifer forests the dominant tree species are white fir (*Abies concolor* [Gord.] Hildebrand), incense cedar (*Calocedrus decurrens* [Torr.] Florin, Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), ponderosa pine (*Pinus ponderosa* Laws), sugar pine (*Pinus lambertiana* Dougl.), and black oak (*Quercus kelloggii* Newb.). Red fir forests occupy higher elevations within the watershed compared to the mixed-conifer forests, and although California red fir dominates, white fir, Jeffrey pine, western white pine (*Pinus monticola* Dougl.), and lodgepole pine (*Pinus contorta* Dougl.) are also present. Understory species are dominated by mountain whitethorn (*Ceanothus cordulatus* Kell.). Other shrubs present are bush chinquapin (*Chrysolepis sempervirens* [Kell.] Hjelmqv.), pine-mat manzanita (*Arctostaphylos nevadensis* Gray), bitter cherry (*Prunus emarginata* Dougl.), red flowering currant (*Ribes sanguineum* Pursh), Sierra gooseberry (*Ribes roezlii* Regel), and California hazel (*Corylus cornuta* Marsh. var. *californica* [DC.] Sharp). Vegetation is patchy, with open spaces and *Ceanothus* patches.

Mean annual precipitation at the site is 125 cm, mostly falling as snow between Nov. and May. Snow packs can persist until June. Summers are hot and dry and winters are mild and moist. Spring, summer, fall, and winter air temperatures average 6.8, 15.5, 8.8, and 0.7°C, respectively. Return fire frequency for the mixed-conifer forest is 12–15 years.

The most common soils are inceptisols and entisols, and are coarse sandy loams with relatively low water-holding capacity. Soils generally develop on granitic parent materials. Soil depth varies from $<$50 cm to $>$1 m. Average forest floor depths are 5.4 cm, 3.6 cm, and 0.7 cm, respectively, for closed canopy, shrub, and gap patches (North et al. 2002).

Experimental Design

The overall Teakettle Project design consists of six stand conditions involving thinning and burning. Burn treatments have two levels: no burn and understory burn. Thinning treatments consist of no stem reduction (present forest conditions), thinning by diameter (similar to thinning from below), and thinning by density where all but a few dominant overstory trees are removed. Each of the six stand conditions is replicated three times, resulting in 18 plots. Each plot is 4 ha (200 $\times$ 200 m).

Plots were installed on each site based on cluster analysis of the spatial heterogeneity to achieve the best match of forest structure and composition of the mixed-conifer forests as outlined in North et al. (2002). Four patch types occurred over 97% of the plots: (1) closed canopy, (2) *Ceanothus* shrub, (3) open canopy gaps, and (4) exposed rock/shallow soil. The area of closed canopy patches ranged in size from approximately 6,000–15,000 m^2, with 7,500 m^2 being the most common (Malcolm North, US For. Serv. Sierra Nevada Res. Ctr., Davis, CA, personal communication). Canopy gaps ranged from 600 to 3,000 m^2, with 1,000 m^2 the most common. *Ceanothus* patches ranged from 75 to 1,000 m^2, with 300 m^2 being the most common size. A total of 402 systematic grid points were established on the 18 4-ha plots and were mapped to coordinate sampling among different studies and to follow ecosystem responses through time. K-means cluster analysis was used to classify each gridpoint into one of the four patch types and to calculate the distance of each point from the cluster center. Gridpoints falling in each of the three vegetated patch conditions were sorted by distance from cluster center and field-inspected to select 54 intensive sample points (3 patch conditions $\times$ 6 burning and thinning treatments $\times$ 3 replicates).

Soil and Coarse Woody Debris (CWD) Invertebrate Sampling

Arthropods were sampled in 1998 and 2000 with a soil corer at each of the 54 gridpoints described above and stratified by four forest floor patch types: closed canopy, open canopy gaps, *Ceanothus* sp. patches, and CWD. Samples were taken during two sample periods per year corresponding to wet and dry summer periods. Eighteen replicate cores were taken for each patch type. A total of 108 soil cores were collected in each year. The same gridpoints were used for sampling patch types for both wet and dry seasonal sampling.

Closed canopy, open canopy gaps, and CWD were sampled in 1998 and closed canopy, open canopy gaps, and *Ceanothus* patches were sampled in 2000. Each soil core was taken at a depth of 8 cm from the surface of the O horizon. The volume of each soil core was 183.2 cm^3. For CWD samples, only barkless sapwood in decay class IV logs was used (Maser et al. 1979). Because of the advanced state of decay, CWD samples were not identified to tree species. Only CWD with sapwood friable enough to sink the soil core sampler to a depth of 8 cm was used. Sample dates for 1998 were July 14–18 (wet period) and Sept. 1–4 (dry period). In 2000, samples were collected from June 19–23 (wet period) and Aug. 28–30 (dry period). The beginning of the snow-free season occurred later in 1998, resulting in later wet season sampling than in 2000. Soil cores were brought back to the laboratory at the College of Forest Resources, University of Washington, where a modified high-gradient Berlese extraction (Moldenke 1994) was used to extract arthropods from soil and CWD. Soil and CWD were placed in the extractors within 1 to 4 days of field sampling.

Oribatid mites were the most abundant arthropod group and were identified to morphospecies (Oliver and Beattie 1996). All other arthropods were identified to order or family depending on project limitations and identification expertise. Bulk specimens were sorted and identified using a dissection microscope boosted to a magnification of up to 120$\times$. A reference collection was established for each species. For abundant species like *Oppiella* sp., approximately

every tenth individual was verified with a compound microscope. Some morphospecies identified with a dissection microscope were found to contain more than one genus or species when viewed with the higher-magnification compound microscope. Since it was not possible to mount and identify all specimens with a compound microscope, some species groups listed contain more than one genus or species, as noted in Table 1.

Moisture content and bulk density were determined for each soil and CWD core from which arthropods were extracted. Bulk density values represent only the 0–8 cm core depth and not the entire soil horizon. Data for litter depth were taken from North et al. (2005).

Statistical Analyses

Data from late spring and late summer sample dates were pooled into a single value before analysis. A one-way analysis of variance (ANOVA) was used to compare differences in species number and density among different patch types in 1998 and 2000 using SPSS (1999). One-way ANOVAs were also used to compare 2-year combined data for density and diversity between closed canopy and canopy gaps and to compare moisture, bulk density, and litter depths among patch types in 1998 and 2000. A separate ANOVA was used to compare the future scheduled treatments to determine whether there were any preexisting conditions that may confound treatment effects during posttreatment sampling. No preexisting conditions were found, however.

Nonmetric multidimensional scaling (NMS) (McCune and Mefford 1997) was used to determine whether environmental gradients were associated with changes in community composition among different patch types. Separate analyses were run for 1998 and 2000 data. The NMS ordination method computes a dissimilarity matrix, which assigns ordination scores to sample units based on the species composition and abundance of individual sample units. Scores are plotted on a two-dimensional axis. Sample units with a similar community composition appear clustered in the ordination diagram. NMS was performed on Oribatid mite species composition using PC-ORD 3.0 (McCune and Mefford 1997). NMS was run using the Sorensen similarity index as a distance measure. A preliminary run of the data at six dimensions was used to determine the minimum number of dimensions needed to achieve the maximum drop in stress in the final analysis. A Monte Carlo test was used to compare the stress obtained from the real data with multiple runs of randomized versions of the same data.

Two dimensions were selected based on a low stress value and the results of the Monte Carlo test, which gave $P = 0.02$ probability that a similar stress value could be arrived at through chance for both years. The final analysis involved 100 iterations and 30 randomized runs. When stress was plotted against the number of iterations it stabilized after 18 and 30 iterations for both years.

A second matrix of environmental data was used to correlate distance in ordination space to differences in moisture content, bulk density, and litter depth. The relationship between the environmental data and ordination is represented graphically in a joint plot by a series of vectors. The length of the vector represents the strength of the correlation of the environmental factor along an environmental gradient associated with a particular direction within the ordination. A Pearson and Kendall correlation was used to determine the amount of variation in community composition associated with the ordination axes and the amount of variation along axes with environmental variables (McCune and Grace 2002).

Because the matrix of community data contained a relatively large percentage of zeros, data were transformed using the Beals smoothing function. This was done to relieve the "zero-truncation problem" common to many methods of ordination (McCune et al. 2002). Some total values for canopy gap sample units contained zero values and were therefore deleted before NMS. Corresponding sample units with positive values from closed canopy, CWD, and *Ceanothus* patches were also deleted to maintain an even number of sample units among patch types.

Indicator Species Analysis

Indicator species analysis was performed using PCORD 3.0. The Monte Carlo test was set at 1,000 randomized runs. PCORD utilizes the method of calculating species indicator values described in Dufrene and Legendre (1997). This method calculates indicator values based on the consistency of occurrence of a particular species within a group or environmental category that is expressed as a percentage of perfect indicator. An indicator value of 100 represents a perfect indication of particular patch type and a zero value represents no indication. For our analysis we looked for the consistency of occurrence of a species within the different patch types sampled: closed canopy, canopy gap, CWD, and *Ceanothus*. The Monte Carlo test examined how the calculated indicator values differed significantly from a randomized data set ($P \leq 0.05$).

Results

There was a wide representation of different microarthropod groups collected from soil and CWD samples (Table 1). Mites (Acari), however, were by far the most numerically dominant group, comprising 78% of the total number of arthropods extracted. Springtails (Collembolans) made up 13% of the total, insects 7%, and all other invertebrates only 3%.

Mite Diversity and Density

In both 1998 and 2000 species richness was significantly lower in gaps than in the two other patch types ($P < 0.05$). Gaps averaged six species per sample unit in 1998 and only one species in 2000. In comparison, closed canopy averaged nine species per sample unit in 1998 and 10 species in 2000. CWD had 10 species in 1998 while nine species were observed in *Ceanothus* sp. patches on average in 2000 (Table 2). There were no significant differences in species

Table 1. List of taxa and density of arthropod populations (No. m^{-3}) in different habitat patches (1998, closed canopy, coarse woody debris (CWD), and canopy gaps; 2000, closed canopy, *Ceanothus*, and canopy gaps)

	1998			2000		
	Closed canopy	CWD	Canopy gaps	Closed canopy	*Ceanothus*	Canopy gaps
Acari						
Astigmata	0	3,639	0	0	0	0
Mesostigmata	77,473	24,106	38,509	50,486	54,277	3,487
Prostigmata	13,493	10,613	19,255	7,126	5,155	1,061
Ixodida	0	0	0	0	0	152
Unknown	152	0	152	0	0	0
Oribatida						
Ametroproctus sp. 1	758	1,819	0	5,610	152	910
Ametroproctus sp. 2	0	0	758	0	0	0
Autogneta	0	0	303	0	0	0
Banksinoma	0	0	1,061	0	152	0
Brachychthonius	0	0	152	1,364	0	0
Caenobelba sp. 2	8,945	1,061	1,971	11,674	9,703	152
Caenobelba sp. 3	606	152	455	1,061	1,819	0
Camisia	0	152	0	303	0	0
Ceratozetes sp. 1 + *Laminizetes**	152	0	0	8,642	0	0
Ceratozetes sp. 2	0	0	3,487	1,516	152	0
Ceratozetes sp. 3	8,490	606	1,819	303	2,577	0
Ceratozetes sp. 4	455	152	303	152	455	0
Cosmochthonius	0	1,364	0	0	0	0
Cultroribula	0	0	303	0	0	0
Eporibatula + unknown species*	2,426	0	1,061	152	1,971	0
Eremaeus sp. 1	6,368	14,100	10,764	13,797	16,374	2,426
Eremaeus sp. 2	7,581	303	1,061	5,610	6,216	0
Galumna	0	0	455	0	0	0
Grypoceramerus	0	0	2,274	0	0	0
Joshuella	1,364	2,123	4,700	3,335	1,971	152
Liacarus sp. 1	910	455	152	303	152	0
Liacarus sp. 2	303	1,516	0	152	152	0
Liacarus sp. 3	0	0	0	455	0	0
Licneremaeus sp. 1	0	0	606	0	0	0
Licneremaeus sp. 2	0	0	303	0	0	0
Microtritia	10,158	303	20,316	13,342	24,106	0
Mycobates	0	0	152	0	0	0
Nanhermannia	152	0	152	0	0	0
Ommatocepheus	152	0	3,032	0	0	0
Oppia sp. 1	152	0	152	0	0	0
Oppia sp. 2	60,189	20,164	16,222	43,361	28,351	606
Oppiella sp. 1	51,093	15,161	14,858	40,328	72,773	4,700
Oppiella sp. 2	152	758	152	455	758	0
Oribatella sp. 1	3,335	0	6,368	910	0	0
Oribatella sp. 2	0	152	0	0	0	0
Oribatula	152	2,123	7,277	8,187	3,032	0
Propelops	6,822	910	455	3,184	2,577	0
Phthiracarus sp. 1	5,155	758	1,668	303	2,123	0
Phthiracarus sp. 2	455	0	0	2,274	455	0
Phthiracarus sp. 3	0	152	4,548	0	0	0
Rhynchobelba	0	0	910	0	0	0
Schelorbates sp. 1	0	0	152	910	2,426	606
Schelorbates sp. 2	1,668	2,577	152	758	1,819	0
Schelorbates sp. 3	910	0	15,161	0	910	0
Schelorbates sp. 4	152	0	0	303	3,790	0
Schelorbates sp. 5	0	0	1,061	0	0	0
Suctobelbella	152	5,458	19,255	0	0	152
Tectocepheus	0	0	12,887	0	152	0
Zygoribatula	0	4,093	0	0	0	0
unknown adult sp. 12	152	0	0	0	0	0
unknown adult sp. 14	152	0	0	0	0	0
Acari immatures						
Caenobelba immature	1,971	455	0	1,213	1,971	303
Cepheoidea immature	0	0	152	0	0	0

* More than one genus was included within this species grouping.

Table 1. (continued).

	1998			2000		
	Closed canopy	CWD	Canopy gaps	Closed canopy	*Ceanothus*	Canopy gaps
Damaeoidea immature	152	0	0	1,668	2,274	0
Eremaeus immature	12,280	3,487	11,371	16,222	7,884	606
Galumnidae immature	0	0	0	0	0	152
Gustavioidea immature	606	0	0	0	0	0
Propelops immature	0	1,364	758	3,184	0	152
unknown immatures	149,943	101,124	94,454	119,924	315,654	48,667
Collembola						
Entomobryidae	22,590	6,519	10,764	6,368	10,310	152
Hypogastruridae	3,790	606	303	2,123	1,668	0
Isotomidae	17,738	10,310	38,661	7,581	6,064	0
Onychiuridae	30,929	14,706	58,219	17,587	39,419	1,971
Sminthuridae	0	0	0	455	0	0
unknown *Collembola*	11,674	0	910	4,093	758	910
Coleoptera larvae						
Cantharidae	303	0	0	152	303	0
Elateridae	303	2,123	2,426	455	910	0
Staphylinidae	0	152	0	0	0	0
Staphylinidae or *Carabidae*	1,364	0	606	152	0	0
unknown *Coleoptera*	4,093	4,245	3,790	5,003	9,400	455
Coleoptera mature						
Leiodidae	152	0	152	0	0	0
Leptotyphlinae	303	303	0	303	152	0
Mycetophagidae	0	0	606	0	0	0
Ptilliadae	455	0	0	303	0	0
Staphylinidae	455	0	303	152	0	0
Tenebrionidae	0	0	455	0	0	0
unknown adult *Coleoptera*	0	0	152	0	0	0
Diptera larvae						
Cecidomyiidae	17,435	152	0	303	152	0
Ceratopogonidae	152	0	0	910	0	0
Chironomidae	303	0	455	606	152	303
Elateridae	0	0	0	152	910	303
Psychodidae	455	152	0	303	152	0
Sciaridae	152	152	0	152	152	152
Tipulidae	0	455	0	606	455	0
unknown *Diptera*	152	303	303	11,674	7,277	0
Diptera mature						
Cecidomyiidae	1,819	455	606	1,061	910	0
Chironomidae	1,061	910	1,516	2,274	2,123	455
Mycetophilidae	152	0	0	606	0	0
Phoridae	0	0	0	152	303	0
Psychodidae	455	910	303	606	758	303
Sciaridae	455	910	1,213	455	303	152
unknown adult *Diptera*	0	0	152	0	0	0
Other insect orders						
Homoptera	0	0	455	0	0	0
Hymenoptera formicidae	0	758	152	0	0	152
Parasitic wasps	1,213	910	606	303	303	152
Neuroptera	0	152	0	0	0	0
Psocoptera	17,587	7,581	4,245	5,306	10,006	606
Thysanoptera	1,213	455	910	1,516	3,032	1,061
Trichoptera	152	0	0	0	152	0
Other arthropods						
Araneae	1,819	152	1,213	606	910	0
Chilopoda	1,364	1,061	1,668	758	1,971	0
Diplopoda	0	152	152	0	0	0
Diplura	0	0	152	0	0	0
Oligocheata	152	0	0	0	303	0
Pauropoda	5,458	1,819	2,729	2,426	2,729	152
Protura	5,306	1,061	2,881	5,913	3,639	152
Pseudoscorpiones	4,700	1,819	1,516	3,335	5,913	0
Symphyla	2,426	1,668	455	2,123	1,364	0
Total invertebrates	593,708	460,594	282,148	455,439	685,281	71,712

Table 2. Oribatid mite density and diversity for each patch type and year

	1998			2000		
	Closed canopy	CWD	Gap	Closed canopy	*Ceanothus*	Gap
Number of species, average per sample unit*	9 (2)[a]	10 (3)[a]	6 (3)[b]	10 (2)[a]	9 (4)[a]	1 (2)[b]
Number of species, total per patch type	34	42	27	28	34	12
Number of species, total per year		56			58	
Density, average per sample unit	71 (56)[a]	62 (53)[a]	30 (31)[b]	76 (54)[a]	66 (59)[a]	4 (8)[b]
Density, total per patch type	1,283	1,116	539	1,365	1,196	72
Density total per year		2,938			2,633	

Standard deviations are in parentheses. In each year values in rows with different letters were significantly different ($P < 0.05$).
* One sample unit = 366.4 cm^3 and includes 0–8 cm depth from the litter surface and 2 sample periods pooled.

numbers in 1998 between closed canopy patches and CWD and between closed canopy and *Ceanothus* sp. patches in 2000 using pairwise post hoc tests.

Densities of mites observed in gaps were also significantly lower than in closed canopy patches for both years. Gaps averaged 30 and 4 individuals per sample in 1998 and 2000, respectively, compared to 71 and 76 individuals for closed canopy patches. No significant differences, however, were observed in post hoc tests comparing gap density with CWD and *Ceanothus* sp., although densities were higher in both patch types than in gaps. Sixty-two individuals were observed in CWD in 1998 and 66 for *Ceanothus* sp. patches in 2000.

When data were combined for both years, mite density and diversity were significantly lower in gap samples than in closed canopy samples ($P = 0.001$ and $P = 0.001$, respectively). Gaps averaged 5.8 species per sample unit compared to 12.9 for closed canopy (Table 3). Gap density averaged 38.9 individuals per sample unit compared to 159.2 for closed canopy samples. No significant differences were observed for Oribatid species richness and density among plots involving future scheduled treatments, suggesting no obvious environmental differences among plots that might confound posttreatment analysis.

In 1998, an El Niño year, soil moisture content was higher than in 2000 (Table 4). The lowest moisture content by patch type in 1998 was 0.10 g cm^{-3} in canopy gaps. This amount was higher than the highest patch moisture content of 0.06 g m^{-3} for closed canopy patches in 2000. CWD moisture content was significantly higher ($P < 0.05$) than in closed canopy and gap soils. In 1998, CWD moisture content was 0.16 g m^{-3} compared to 0.11 g m^{-3} for closed canopy and 0.10 g m^{-3} for gaps. In 1998, bulk density, usually an indicator of soil organic matter content, was significantly higher in gaps (0.76 g m^{-3}) than closed canopy (0.38 g m^{-3}) and CWD (0.16 g m^{-3}) (Table 4). Bulk density under gaps (1.03 g m^{-3}) was significantly higher ($P < 0.05$) than bulk densities under *Ceanothus* sp. patches (0.47 g m^{-3}) and closed canopy patches (0.27 g m^{-3}) in 2000.

NMS Ordination

Final stress values for 1998 and 2000 data were 14.7 and 8.7, respectively. Stress of the real data differed significantly ($P < 0.05$) from that generated by randomized data for both years as analyzed by the Monte Carlo test of sampling.

In 1998, coefficients of determination (r^2) for the correlations between ordination distances and distances in the original dimensional space were axis 1 (0.365) and axis 2 (0.547). Cumulative percentage of variance explained by the two axes was 91%. In 2000, coefficients of determination were axis 1 (0.054) and axis 2 (0.959). The cumulative percentage of variance explained by the two axes was 96%. Bulk density explained the largest amount of variation along axis 2 for both 1998 and 2000, accounting for 28% and 32% of the variation, respectively. Moisture explained surprisingly little of the variation along either axis for both years (Table 5). In 2000, litter depth explained a relatively larger percentage of the variation than moisture; however, the effect of litter depth was relatively small compared to bulk density.

The results of the NMS ordination for both years (Figures 1 and 2) show substantial overlap among different patch types. Differences in community composition among patches do not appear to align along distinct gradients of environmental change, although greater separation among patches along axis 2 is more evident in 1998 than in 2000. The most distinctive feature of the ordination is the difference in spread of individual plots among patch types. Variation among canopy gap plots is much greater than for closed canopy. In 1998, CWD had a similar spread to gaps and *Ceanothus* sp. patches fall in between gaps and closed canopy in 2000.

Table 3. Oribatid mite density and diversity for combined years

	Closed canopy	Gap
Number of species, average per sample unit*	12.9 (2.3)[a]	5.8 (3.0)[b]
Density, average per sample unit	159.2 (78.0)[a]	38.9 (31.6)[b]

Standard deviations are in parentheses. Values in rows with different letters are significantly different ($P < 0.001$).
* One sample unit = 366.4 cm^3 and includes 0–8 cm depth from the litter surface and 2 sample periods pooled.

Table 4. Environmental factors used in correlations with ordination axes in 1998 and 2000

	Moisture ($g\ cm^{-3}$)	Bulk density ($g\ cm^{-3}$)	Litter depth* (cm)
1998			
Closed canopy	0.11 (0.03)[a]	0.38 (0.15)[a]	—
Coarse woody debris (CWD)	0.16 (0.07)[b]	0.16 (0.06)[b]	—
Canopy gap	0.10 (0.02)[a]	0.76 (0.29)[c]	—
2000			
Closed canopy	0.06 (0.03)[a]	0.27 (0.11)[a]	5.15 (3.58)[a]
Ceanothus	0.05 (0.02)[a,b]	0.47 (0.23)[b]	3.57 (2.88)[a]
Canopy gap	0.04 (0.01)[a]	1.03 (0.31)[c]	0.97 (2.46)[b]

Bulk density and moisture content were determined for each sample from which arthropods were extracted. Litter depth was measured independently. Standard deviations are in parentheses. In each year values with letters in the same column are significantly different ($P < 0.05$).
* Data taken from North et al. (2005).

Indicator Species Analysis

In 1998, seven species were significantly associated with closed canopy forests compared to six for CWD and one for canopy gaps (Table 6). In 2000, nine species were associated with closed canopy forests compared to only two for *Ceanothus* and none for canopy gaps (Table 7). Five species (*Oppiella* sp. 1, *Phthiracarus* sp. 1 and sp. 2, *Caenobelba* sp. 2, and *Eremaeus* sp. 2) were common to closed canopy forests for both years, suggesting those species may be good environmental indicators of closed canopy conditions. Interestingly, of those five genera common to closed canopy forests, three (*Oppiella*, *Phthiracarus*, and *Eremaeus*) are also reportedly associated with old-growth forests at H.J. Andrews Experimental Forest in Oregon (Moldenke and Fichter 1988).

Discussion

The relative abundance of different arthropod groups represented at Teakettle was similar to that reported for soils on the Olympic Peninsula of Washington State (Marra and Edmonds 1998), where mites and collembola combined composed 92–97% of the total number of arthropods sampled.

Patch type at Teakettle influenced arthropod diversity and density. The low diversity and density in canopy gaps suggest that conditions for microarthropods in canopy gaps were much less favorable in comparison to closed canopy, CWD, and *Ceanothus* sp. patches. Soil respiration was also lowest in gaps (Ma et al. 2005). High daytime temperatures, low moisture, and low soil organic matter content likely create conditions more stressful for soil arthropods in gaps. Both soil temperature and moisture in the more exposed gaps likely exceed the level of tolerance for soil arthropods during the hot, dry summer climate of the southern Sierra Nevada. North et al. (2002) reported that summer soil surface temperatures can be as high as 60°C at Teakettle, which is well above the level of tolerance for most arthropods.

The canopy gaps selected for this study were not created as a result of the disease pockets and tree mortality that are typical features of most temperate forests. Although gaps of this type are present at Teakettle, the gaps selected for this study were characterized by a complete absence of woody vegetation, very few herbaceous plants, and little or no O soil horizon. The gaps appeared to function as patches of

Table 5. Coefficients of determination (r^2) of environmental data with ordination axes in 1998 and 2000

	1998		2000	
Factor	Axis 1	Axis 2	Axis 1	Axis 2
Moisture	0.002	0.088	0.042	0.072
Bulk density	0.001	0.279	0.088	0.323
Litter depth	—	—	0.091	0.081

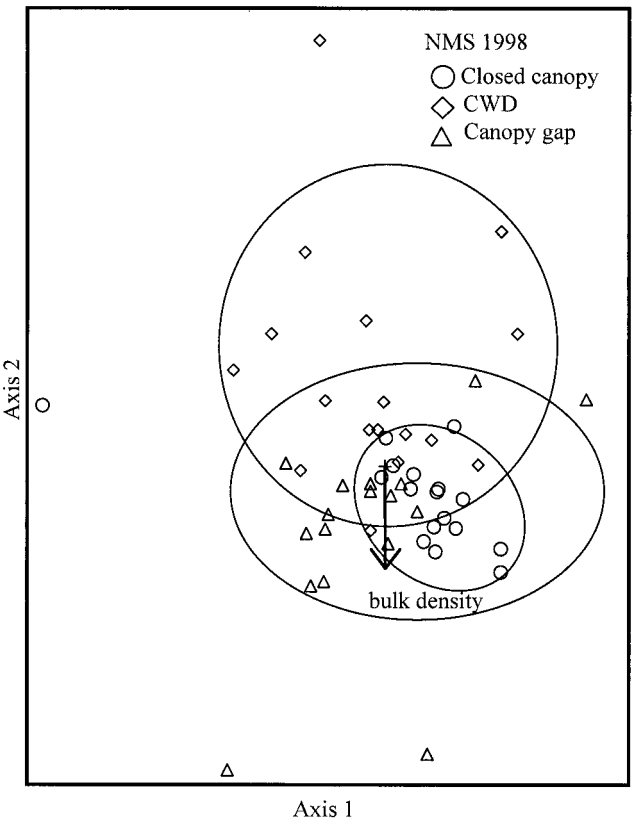

Figure 1. NMS ordination of soil arthropod communities for 1998. Scores for each plot are represented by patch type (closed canopy, coarse woody debris [CWD], and canopy gap) and were regressed on a second matrix of environmental variables that included soil moisture and bulk density.

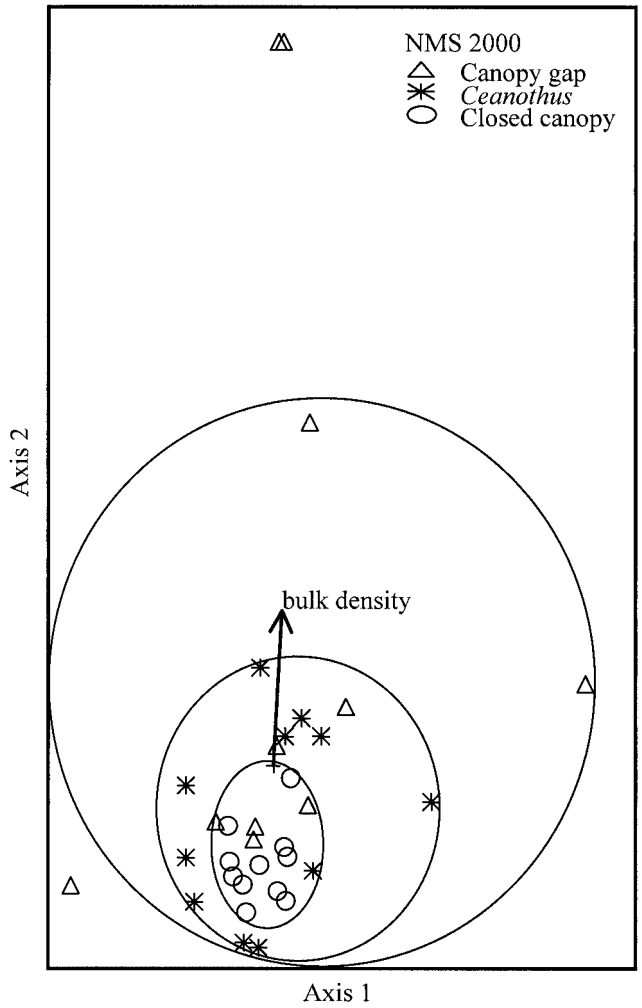

Figure 2. NMS ordination of microinvertebrate communities for 2000. Scores for each plot are represented by patch type (canopy gap, *Ceanothus*, and closed canopy) and were regressed on a second matrix of environmental variables that included soil moisture, bulk density, and forest floor depth.

shallow, coarse-textured soil, composed of recently weathered parent material with little growing vegetation. Soils within these gaps were therefore even more exposed than gaps created as a result of windthrow and tree mortality.

We thought that differences in precipitation between 1998 and 2000 would influence microarthropod communities. Precipitation in 1998, an El Niño year, was much higher than in 2000. A weather station at Grant Grove in Kings Canyon National Park, at a similar elevation 50 km south of Teakettle, recorded a maximum snow depth in 1998 of 243 cm compared to 122 cm in 2000. The average maximum snow depth for the same area from 1941 to 2001 is 133 cm, indicating 1998 was an unusually wet year for this region.

The diversity and density of microarthropods in canopy gaps were more sensitive to the change in precipitation from 1998 to 2000 than in closed canopy plots. The number of species in gaps decreased 55% from 1998 to 2000, compared to only an 18% decline observed for closed canopy

Table 6. Indicator species in 1998 in three patches (closed canopy, coarse woody debris (CWD), and canopy gap) of invertebrate habitat in Teakettle's mixed conifer determined by indicator species analysis

Closed canopy	CWD	Canopy gap
Caenobelba sp. 2 (0.001)	*Tectocepheus* (0.001)	*Liacarus* sp. 2 (0.039)
Eremaeus sp. 2 (0.001)	*Oppia* sp. 1 (0.003)	
Phthiracarus sp. 1 (0.001)	*Rhynchobelba* (0.003)	
Phthiracarus sp. 2 (0.005)	*Suctobelbella* (0.003)	
Oppiella sp. 1 (0.006)	*Banksinoma* (0.029)	
Ceratozetes sp. 1 (0.009)	*Propelops* (0.053)	
Caenobelba immature (0.029)		

P-values, in parentheses, are calculated from a Monte Carlo significance test of the observed maximum indicator value for each species.

plots. At the smaller spatial scale of the sample unit (366 cm^3) the average number of mite species per sample in closed canopy patches was very similar between 1998 and 2000, with 9 and 10 species observed, respectively. In gaps, however, there was a decline from six species per sample unit in 1998 to only one species in 2000. Total microarthropod density in canopy gaps was also seven times greater in 1998 than in 2000. In contrast, densities in closed canopy patches were very similar between the 2 years (Table 2). Higher soil moisture in 1998 appeared to account for some of the differences in density and diversity observed in canopy gaps between years. However, the NMS results indicate that very little of the variation among plots or patches was explained by moisture content for each of the years sampled. Both closed canopy and canopy gap soil moisture levels were about two times higher in 1998 than in 2000 (Table 4). For each year, moisture content was only slightly higher in closed canopy soils than in canopy gaps, with an observed increase of only 0.01 g cm^{-3} and 0.02 g cm^{-3} for years 1998 and 2000, respectively. Higher daytime peak temperatures during 2000 may also account for the differences in density and diversity observed in gaps between years; however, temperature data are lacking.

Although a significance test revealed no difference in oribatid mite density and diversity between closed canopy and *Ceanothus* patches, the total invertebrate abundance (Table 1) was 50% higher for *Ceanothus*. This difference in abundance is almost entirely a result of the higher number of unknown immature mites. Immature mites are especially patchy in their distribution, with many soil samples containing none and others having many hundreds of individuals. The high variability associated with immature mites makes assigning any biological significance to this difference suspect. Higher litter quality associated with the nitrogen-fixing *Ceanothus*, however, may account for maintaining comparable levels of diversity and density to that of closed canopy patches.

Table 7. Indicator species in 2000 in two patches (closed canopy and *Ceanothus*) of invertebrate habitat in Teakettle's mixed conifer determined by indicator species analysis

Closed canopy	*Ceanothus*
Oppiella sp. 1 (0.001)	*Propelops* (0.001)
Phthiracarus sp. 1 (0.001)	*Ametroproctus* sp. 1 (0.026)
Phthiracarus sp. 3 (0.002)	
Caenobelba sp. 2 (0.005)	
Eremaeus sp. 2 (0.005)	
Phthiracarus sp. 2 (0.005)	
Mycobates (0.006)	
Eremaeus immature (0.022)	
Caenobelba sp. 3 (0.038)	

P-values, in parentheses, are calculated from a Monte Carlo significance test of the observed maximum indicator value for each species.

NMS and Environmental Factors

Bulk density is the dry weight of soil per volume of soil. It is primarily a function of two soil characteristics, both of which can have a marked impact on soil microarthropod communities. Low bulk density is usually associated with higher soil organic matter content, and/or a more structured soil profile with a well-developed system of channels and pore spaces. Low bulk density represents conditions that are favorable to soil arthropod activity.

Differences in plant chemistry, so important for determining host choice by herbivore arthropods, are much less important for determining community composition in decomposer communities. Soil microarthropods are primarily decomposers that depend on dead organic matter for energy and nutrition. Microarthropods may circumvent differences in plant host chemistry to some degree by feeding on saprophytic microbial organisms rather than directly on decaying vegetation. This lack of plant host specificity may explain to some extent the overlap in species composition among the different patch types seen in the ordination graph.

Globally, diversity of microarthropods is primarily a function of the depth and amount of organic matter and the structural complexity of the forest floor. Higher-latitude forest floors have deeper layers of organic matter and more complex soil structure due to the slower decomposition rates compared to most tropical and temperate hardwood soils. Soil microarthropods are unique in being more diverse at higher-latitudes forests than in the lower-latitude tropical ecosystems for alpha diversity spatial scales (per m^2) (Shaw et al. 1991). This is especially true of temperate coniferous forests that tend to support a lower biomass but a higher diversity of soil arthropods than temperate hardwood forests at similar latitude. It is therefore not surprising that bulk density should emerge as one of the stronger environmental variables determining differences in community composition at Teakettle.

Temperature and moisture of interior mixed-conifer forests like Teakettle are subject to much greater fluctuations compared to coastal forests. These greater extremes in temperature and moisture will sometimes exceed the limits of tolerance for many soil arthropods. Summers at Teakettle are characteristically dry for all patch types and therefore may explain why moisture accounted for so little of the variation in the ordination.

Given low moisture levels, some soil arthropods are adapted to stress and can avoid environmental extremes by migrating vertically through the soil profile (Villani et al. 1999). Other invertebrates avoid extended periods of climatic extremes by entering into dormancy or quiescence until conditions are more favorable. Anhydrobiosis, a state of quiescence induced by dehydration, has been reported to occur in some species of Collembola, for example (Villani et al. 1999). Those organisms that are adapted to stressful conditions, as in canopy gaps, are fewer in number but can sometimes do very well because of less severe competition (Marra and Edmonds 1998).

The results of this study show that microarthropod communities within gaps are much more variable compared to closed canopy communities. The spread of points in ordination space was much greater in gaps than in closed canopy and *Ceanothus* patches. With the exception of a one species in 1998, gaps were characterized by an almost complete absence of indicator species. Changes in diversity and density from 1998 to 2000 were also much greater in gaps than in closed canopy forests. That is not to say that gaps are more species-diverse, as diversity is clearly higher in closed canopy communities. Gaps are more exposed and are therefore more sensitive to changes in environmental conditions. Communities in gaps are consequently much more difficult to characterize relative to a particular type of arthropod community represented by a particular region of ordination space or community indices. Canopy cover is important in moderating environmental extremes of both temperature and moisture, and therefore community composition is more similar from plot to plot and from year to year.

A substantial amount of the variation observed in the NMS ordination was not explained by any of the environmental factors that we measured. Given the small differences observed in moisture among patch types, temperature, particularly in gaps, likely influenced much of the variation. The amount of solar radiation reaching the soil surface will vary within and among gaps depending on aspect and slope and may contribute to the high variability we observed in gaps.

Differences among patch types may not necessarily be represented by gradients of environmental change as much as by fundamental shifts in the type and quality of environmental factors present. Differences in substrate quality, for example, that are associated with *Ceanothus*, CWD, true fir, and pine litter could obscure environmental gradients, resulting in a weaker correlation of changes in community

composition with environmental variables. Litter quality is known to influence invertebrates and litter quality is strongly influenced by plant species, especially N-fixing species. Spears et al. (2001) found that *Ceanothus* litter was three times higher in total N than Douglas-fir litter in the Oregon Cascades. At Teakettle, Erickson et al. (2005) found that soil N pools and net N mineralization rates were greater under *Ceanothus* patches than under closed canopy and canopy gaps. In contrast to N, Spears et al. (2001) found that total P concentrations were 20% greater in surface horizon soils under Douglas-fir than under *Ceanothus*.

CWD is a unique habitat for arthropods relative to the surrounding soil. Many arthropods are adapted to woody substrates and require CWD during some stage of their life cycle. It is therefore surprising that a more distinct CWD community did not emerge in the ordination analysis. CWD specialists, however, usually infest logs during very early stages of decay. The overlap in community composition between CWD and forest floor may be a function of the advanced state of decay of the logs we sampled. For this study, CWD decay was well advanced, with brown rot (and occasionally white rot) processes very evident. As CWD loses its bark it is colonized by microbes. Channels, pores, and fractures become well distributed through the sapwood and those arthropods inhabiting CWD may become less specialized and more opportunistic. Litter- and soil-inhabiting microarthropods may also be utilizing CWD as refugia during the hot, dry season because of the increased moisture-holding capacity of well-decayed wood.

Distance between sample locations and the scale at which samples are taken are known to influence the degree of similarity in soil microarthropod communities (Torgersen et al. 1995). Ordination results for soil arthropod communities on the Olympic Peninsula (Marra and Edmonds 1998) showed more clearly differentiated community types than were observed for this study. Like Teakettle, the absence of the forest canopy had a marked effect on density and diversity. However, on the Olympic Peninsula soil arthropod community composition between sites with and without a forest canopy were much more clearly separated into distinct groupings. In the Olympic Peninsula study distances between forest and clearcut locations ranged from several to tens of kilometers, whereas distances between gaps and closed canopy forests at Teakettle were only tens to a few hundred meters apart. Sites on the Olympic Peninsula were taken across watersheds, while at Teakettle samples were taken within a single watershed. Increased distance between sites with similar vegetation appeared to increase the difference in community composition on the Olympic Peninsula. Closer proximity of sample locations may also account for the similarity in community composition among patch types observed at Teakettle.

Conclusions

Significantly lower invertebrate density and diversity occurred in gaps compared to closed canopy patches, suggesting that low organic matter and high summer temperatures may be responsible for creating harsh conditions for soil arthropods in gaps in mixed-conifer forests at Teakettle. Gaps also were more sensitive to year-to-year changes in climate as suggested by the sharp decline in diversity and density from 1998 to 2000. Gaps were also characterized by almost a complete lack of indicator species compared to other patch types. Moisture may be important in affecting year-to-year changes in arthropod communities, but explained surprisingly little of the variation observed among patch types at Teakettle.

There was substantial overlap in community composition among the different patch types in both years, as represented by the ordination diagram. Bulk density explained the largest amount of variation in community composition among plots in both 1998 and 2000. Microinvertebrate community composition was most similar among plots in closed canopy patches, suggesting that the moderating influence of the canopy is an important factor in determining the forest floor arthropod community.

Gap data suggest that in the characteristically hot, dry summers of the southern Sierra Nevada the rate of recovery of vegetation following thinning and fire treatments may determine to a large extent the recovery rate of microarthropods, not only by providing sources of energy inputs in the form of dead organic matter, but also by moderating the microclimate of the forest floor.

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