

Longer-Term Effects of Selective Thinning on Microarthropod Communities in a Late-Successional Coniferous Forest

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ABSTRACT Microarthropod densities within late-successional coniferous forests thinned 16–41 yr before sampling were compared with adjacent unthinned stands to identify longer term effects of thinning on this community. Soil and forest floor layers were sampled separately on eight paired sites. Within the forest floor oribatid, mesostigmatid, and to a marginal extent, prostigmatid mites, were reduced in thinned stands compared with unthinned stands. No differences were found for Collembola in the forest floor or for any mite suborder within the soil. Family level examination of mesostigmatid and prostigmatid mites revealed significant differences between stand types for both horizons. At the species level, thinning influenced numerous oribatid mites and Collembola. For oribatid mites, significant or marginally significant differences were found for seven of 15 common species in the forest floor and five of 16 common species in soil. Collembola were affected less, with differences found for one of 11 common species in the forest floor and three of 13 common species in soil. Multivariate analysis of variance and ordination indicated that forest thinning had little influence on the composition of oribatid mite and collembolan communities within either the forest floor or soil. Differences in microclimate or in the accumulation of organic matter on the forest floor were likely most responsible for the observed patterns of abundance. Considering the role that microarthropods play in nutrient cycling, determining the functional response of a wide range of taxa to thinning may be important to effective ecosystem management.

KEY WORDS microarthropods, Acari, Oribatida, Collembola, forest thinning

MICROARTHROPODS DOMINATE FOREST FLOOR faunas in both diversity and abundance (Wallwork 1976). They are functionally diverse, with many contributing significantly to both short- and long-term productivity of forest ecosystems by facilitating processes involved in nutrient cycling (Seastedt 1984, Moore et al. 1988, Shaw et al. 1991). Primary contributions to nutrient cycling include reducing the particle size of organic material through comminution (Berthet 1967), regulating microbe numbers through grazing (Hanlon and Anderson 1980), releasing nutrients immobilized by bacteria and fungi (Ineson et al. 1982, Seastedt and Crossley 1983), and disseminating microbes via movement throughout forest floor and soil (Behan and Hill 1978, Kitchell et al. 1979). Field studies that manipulated microarthropod abundances suggest that changes in population sizes can influence rates of

forest floor decomposition and mineralization (Santos et al. 1981, Kajak 1997, Lawrence and Wise 2000).

Despite the importance of microarthropods in forest ecosystems, relatively little attention has been given to the impact of forest management practices on their abundance and community structure. Most work has investigated shorter-term effects of clearcutting (Huhta et al. 1967, Vlug and Borden 1973, Huhta 1976, Abbott et al. 1980, Seastedt and Crossley 1981, Marra and Edmonds 1998). Although results from these studies vary, they generally show that populations of many taxa characteristic of the mature forest decrease after timber harvest. Such reduced abundances are largely attributed to microclimatic stresses that occur on the forest floor after canopy removal, such as higher temperatures and lower moisture levels. To some degree, microclimatic impacts are influenced by regional climatic differences. For example, within forests of the southeastern United States, declines in oribatid mite abundance was attributed to prolonged exposure to temperatures exceeding tolerance thresholds (Seastedt and Crossley 1981). Conversely, within the more moderate climate experienced on the Olympic peninsula, Washington, temperature and moisture stress did not limit microarthropod densities in clearcut stands (Marra and Edmonds 1998). Changes in the standing crop of organic material also may contribute to postharvest differences in microarthropod abun-

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dances (Mitchell 1978, Seastedt and Crossley 1981). However, Huhta (1976) suggested short-term increases in soil invertebrate abundances were associated with an input of logging debris, whereas longer term decreases in abundance were driven by the accelerated decomposition of organic matter. McIver et al. (1992) illustrated the pattern of forest floor spider community succession with increasing time after clearcutting. It is possible that microarthropod communities show similar successional patterns.

In the Pacific Northwest, a shift in emphasis from timber production to ecosystem management has resulted in selective thinning largely replacing clearcutting as the principal method of timber extraction (McComb et al. 1993). Although thinning can be an effective tool for maintaining wildlife populations, it is not known how forest floor and soil microarthropod communities are affected. Short-term effects are likely to be less extreme than those caused by clearcutting because microclimatic changes on the forest floor are theoretically less severe. However, longer term effects are poorly understood. Studying the response of soil arthropods 14 yr after selective harvest of California coastal redwoods, Hoekstra et al. (1995) found predator abundance to be lower in thinned stands compared with old-growth and 75+ year-old second growth stands and phytophagous taxa were no less abundant in thinned stands. It is unknown what role climate played within the relatively moderate conditions found in the coastal redwood zone of central California.

The objective of this study was to determine the longer term effects of selective thinning of late-successional forests on forest floor and soil microarthropod communities in the Cascade Mountains of southern Oregon. We compared arthropod abundance and community composition of stands thinned 16–41 yr ago to adjacent unthinned stands.

Materials and Methods

Study Sites. The study area was located within the Medford Resource Area, Bureau of Land Management, of the Cascade Mountains of southern Oregon. Study sites were located within a 10-km radius of 42° 07', 122° 26'. Elevation ranged from 1,092 to 1,556 m. Sites were dominated by white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, but some also included sugar pine, *Pinus lambertiana* Dougl.; ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws.; and incense-cedar, *Libocedrus decurrens* Torr. Geological features consisted of tertiary volcanic rocks of the Western Cascade Range, tertiary and quaternary volcanic rocks of the High Cascade Range, and quaternary surficial deposits and intrusive rocks (USDI 2000). Soils were loam in nature, ranging from very cobbly to gravelly (Johnson 1993). Climate is characterized by warm, dry summers and cold, moist winters. Mean monthly temperatures range from -2.0°C (January) to 16.4°C (July). Annual precipitation is ≈ 87 cm,

with 70% of that amount falling as snow in November–March.

Eight pairs of late-successional stands (USDA et al. 1993) were chosen for study. Each pair consisted of a thinned stand and an adjacent, or nearby, unthinned stand. Paired stands were contiguous (separated by a road) in all stands but two; both of these exceptions were separated by <1.5 km. All paired stands were similar in elevation, aspect, and slope. Thinned stands were generally selectively harvested for overstory reduction, mortality salvage, or commercial thinning. Thinning occurred between 16 and 41 yr before this study; two stands were thinned on two occasions. Although some large-diameter trees were harvested from most stands, all stands contained large trees as well as numerous snags and much downed coarse woody material. Overstory canopy cover, forest floor (litter and duff) depth, and tree basal area were significantly higher in unthinned stands ($81.7 \pm 2.1\%$ [mean \pm SEM], 4.4 ± 0.9 cm, and 7.4 ± 0.3 m²/ha, respectively) compared with thinned stands ($53.7 \pm 4.0\%$, 3.2 ± 0.6 cm, and 4.6 ± 0.2 m²/ha, respectively) (Table 1). Thinned stands were still classified as late-successional forest under current ecosystem management guidelines (USDI 2000).

Microarthropod Sampling. Within each stand, 16 forest floor and soil samples were taken at 12.5-m intervals along transects. Transects originated >50 m from a stand boundary and generally ran along terrain contours. No sample point was closer than 0.5 m to a tree or log with a diameter >10 cm. Forest floor samples were collected using a putty knife guided by a 10 by 10-cm plastic panel. Forest floor included freshly fallen needles and leaves as well as the packed, dark-colored fermentation and humus layers that extended down to the mineral soil. After forest floor collection, the top 5 cm of soil was collected using a stainless steel corer (7.8 cm in diameter) lined with a 5-cm-long thin-walled polyvinyl chloride plastic sheath (≈ 240 cm³). Forest floor and soil samples were sealed in zip-lock plastic bags, immediately placed into chilled coolers, and transported to the laboratory where they were maintained at 5°C until microarthropod extraction took place. Extraction of forest floor samples began immediately upon return to the laboratory, and soil samples were processed 2–3 d later. From each transect, sets of four consecutive samples from each depth were composited in the laboratory for extraction (thus, four collections of extracted microarthropods were obtained from each site). Microarthropods were extracted from both forest floor and soil samples by using 40-W incandescent light bulbs atop 20-cm-diameter Berlese-type funnels (Moldenke 1994). Lights were alternated on and off at 2-h intervals during the first 24 h and then were left on continuously until the samples became desiccated (dry to touch). Forest floor and soil samples were taken on two occasions: 21–23 June and 4–6 October 1999. October samples were taken adjacent to those collected in June.

Due to the large number of microarthropods within many samples, it was often necessary to reduce sample

Table 1. Year of thinning and measurements of forest structure and microarthropod densities (no./400 cm² of forest floor) for thinned and unthinned sites

Site name ^a	Treatment	Yr thinned	Canopy cover (%) ^b	Forest floor depth (cm) ^b	Basal area (m ² /ha) ^b	Microarthropod group				
						Oribatida	Mesostigmata	Prostigmata	Astigmata	Collembola
BC	Thinned	1983	54.7 ± 9.2	4.1 ± 1.0	4.0 ± 0.3	322.9 ± 107.9	73.6 ± 35.9	485.3 ± 180.3	68.3 ± 38.4	156.9 ± 74.6
	Unthinned		89.1 ± 2.0	6.2 ± 0.7	9.0 ± 0.4	1,370.0 ± 338.6	119.3 ± 42.9	2,928.3 ± 1,148.6	151.8 ± 70.6	106.8 ± 15.3
EC	Thinned	1983	53.8 ± 9.3	2.7 ± 0.5	3.7 ± 0.6	327.5 ± 100.6	51.5 ± 24.3	980.5 ± 504.9	25.0 ± 16.0	73.5 ± 37.2
	Unthinned		88.5 ± 6.9	4.3 ± 0.4	9.5 ± 0.8	745.5 ± 181.3	113.5 ± 53.2	1,380.0 ± 235.2	45.5 ± 16.1	210.6 ± 80.6
HO	Thinned	Late 1960s	43.4 ± 9.5	3.3 ± 0.5	4.7 ± 0.8	270.9 ± 106.6	26.3 ± 19.1	260.9 ± 104.7	3.0 ± 2.4	53.3 ± 18.3
	Unthinned		80.0 ± 5.3	4.7 ± 0.6	8.5 ± 0.6	996.5 ± 135.7	132.5 ± 28.1	1,595.0 ± 208.8	16.0 ± 6.9	253.1 ± 95.8
SC	Thinned	1978 and 1991	53.2 ± 9.3	2.3 ± 0.7	4.8 ± 0.8	357.5 ± 116.4	56.3 ± 32.1	706.5 ± 226.8	4.0 ± 2.9	94.9 ± 62.5
	Unthinned		71.7 ± 3.0	4.1 ± 0.7	5.4 ± 0.5	571 ± 116.4	162.0 ± 41.1	1,902.0 ± 410.4	53.0 ± 25.3	173.9 ± 43.9
JC	Thinned	1963	46.2 ± 6.6	3.3 ± 0.6	3.7 ± 0.5	140.0 ± 51.3	19.5 ± 15.0	624.3 ± 234.7	5.0 ± 5.0	26.6 ± 22.3
	Unthinned		76.1 ± 4.9	3.6 ± 0.4	7.4 ± 0.7	727.0 ± 260.8	109.0 ± 42.4	1,243.0 ± 133.7	24.0 ± 11.1	45.6 ± 25.2
YS	Thinned	1964 and 1990	77.7 ± 6.0	3.7 ± 0.4	6.4 ± 0.6	659.0 ± 146.4	74.0 ± 31.5	1,147.0 ± 213.6	49.0 ± 15.1	93.9 ± 51.7
	Unthinned		84.5 ± 5.3	3.3 ± 0.4	7.0 ± 0.7	850.0 ± 118.9	107.0 ± 25.9	1,139.0 ± 232.4	48.0 ± 33.1	205.8 ± 52.6
RO	Thinned	1958	62.2 ± 7.0	3.2 ± 0.9	4.1 ± 0.5	313.8 ± 76.1	39.5 ± 20.1	662.3 ± 227.0	6.0 ± 4.8	23.1 ± 12.4
	Unthinned		84.4 ± 5.1	4.5 ± 0.8	4.8 ± 0.3	211.5 ± 20.3	10.5 ± 7.6	838.0 ± 210.7	12.0 ± 7.1	3.3 ± 2.5
MC	Thinned	1979	66.8 ± 7.7	2.6 ± 0.5	5.7 ± 0.6	569.0 ± 105.3	65.0 ± 28.4	1,438.0 ± 198.9	53.0 ± 26.2	63.9 ± 25.2
	Unthinned		79.4 ± 4.4	4.2 ± 0.9	8.6 ± 0.7	563.0 ± 139.7	78.0 ± 41.8	1,111.0 ± 216.7	44.0 ± 12.9	43.3 ± 16.5

Measurement values presented are means ± SEM. Methodology for measurement of forest structure is described in Peck and Niwa (2005). Microarthropod densities are average values between June and October sample dates ($n = 4$ samples per site per date).

^a BLM site names: BC, South Fork Beaver Creek; EC, East Chinquipin; HO, Hobart; SC, Soda Camp; JC, Jenny Creek; YS, Yew Springs; RO, Rosebud; MC, Mill Creek.

^b Differences between thinned and unthinned stands were statistically significant (Wilcoxon's signed ranks test for paired comparisons; $P < 0.05$).

sizes by systematically dividing samples into smaller fractions for identification. Generally, one-half to one-eighth of each sample was sorted and enumerated. This procedure likely led to the underrepresentation of rare species. All microarthropods were identified to at least the suborder level by using a dissecting microscope. Whenever possible, mesostigmatid and prostigmatid mites were identified to the family level, and adult oribatid mites and Collembola were identified to species or morphospecies level. Oribatid mites were cleared with lactic acid, temporarily mounted on cavity slides and identified using a compound microscope. Their classification follows Marshall et al. (1987). Collembola were cleared in 10% KOH for 5–10 min, mounted in polyvinyl alcohol on glass slides, and identified using a phase contrast compound microscope following Christiansen and Bellinger (1998). Voucher material was deposited in the USDA–Forest Service, Western Forest Insect Collection (Oregon State University, Corvallis, OR).

Data Analysis. Before analysis, average values for microarthropod counts from the four collections within each site, depth and date were calculated, yielding a value representing the density of microarthropods within the forest floor (400-cm² surface area) and soil (960 cm³). Counts from soil samples were later standardized to represent 400-cm² surface area for presentation. The density values presented can be converted to number of individuals per square meter by multiplying by 25. For each taxon analyzed, residuals (estimates of model errors) were examined to determine whether transformation of the counts was necessary to meet the assumptions of the parametric test (Sabin and Stafford 1990). Response data

that failed to meet the assumptions of the test were ln-transformed ($Y + 0.5$) and residuals reexamined. Taxa with too few samples containing counts were not analyzed, regardless of their overall abundance (39 oribatid mites and 46 Collembola were not analyzed). For each depth, a split-plot analysis of variance (ANOVA) was used to analyze microarthropod abundances. Within blocks (paired stands), stand type (thinned or unthinned) was the whole-plot factor, and date of collection (June and October) was the subplot factor. Interactions between date and treatment were examined to determine if responses to thinning differed with season. Only statistically significant interactions are reported. The relationship between time since thinning and microarthropod abundance was investigated for each mite suborder and Collembola by using regression models by comparing the age of the thin with the difference in abundance of each taxon between paired thinned and unthinned stands. This analysis was only performed on forest floor samples because no significant differences were found between thinned and unthinned sites in soil for these groups. General linear models within SAS statistical software (PROC GLM; SAS Institute 1991) were used for ANOVA and regression analyses. Strong evidence of statistical differences was accepted when $P < 0.05$, and evidence was considered marginal, but suggestive, when $0.05 < P < 0.10$.

Multivariate techniques were used to further evaluate the influence of thinning on oribatid mite and Collembola communities within the forest floor and soil layers. Principle Coordinate Analysis (ORD), followed by Nonmetric Multidimensional Scaling (NMDS), were used to ordinate each stand into spe-

Table 2. Comparison of mean \pm SEM densities (no./400 cm² of surface area) of forest floor and soil microarthropods between thinned and unthinned stands

Taxon	Layer	June		Oct.		P value ^a	
		Thinned	Unthinned	Thinned	Unthinned	Date	Treatment
Oribatid mites ^b	Forest floor	392.0 \pm 56.8	876.8 \pm 127.4	344.4 \pm 77.4	631.9 \pm 130.2	**	**
	Soil	823.5 \pm 121.5	658.1 \pm 51.8	570.4 \pm 50.3	494.2 \pm 56.8	**	NS
Mesostigmatid mites	Forest floor	68.1 \pm 13.7	137.0 \pm 23.2	40.6 \pm 8.6	80.3 \pm 14.8	**	**
	Soil	119.4 \pm 25.7	117.7 \pm 10.7	113.2 \pm 10.0	115.9 \pm 24.3	NS	NS
Ologamasidae	Forest floor	10.5 \pm 2.8	21.3 \pm 5.1	14.9 \pm 3.0	37.3 \pm 8.5	*	**
	Soil	37.6 \pm 10.9	43.3 \pm 5.0	49.7 \pm 7.8	49.5 \pm 15.2	NS	NS
Zerconidae	Forest floor	20.3 \pm 5.7	35.5 \pm 7.8	5.4 \pm 2.8	19.3 \pm 5.9	**	*
	Soil	27.2 \pm 5.5	37.0 \pm 5.8	18.1 \pm 1.6	27.0 \pm 6.5	*	NS
Other families (3) ^c	Forest floor	0.8 \pm 0.5	4.0 \pm 2.1	2.0 \pm 1.5	2.5 \pm 1.2	— ^d	—
	Soil	5.2 \pm 1.9	0.5 \pm 0.5	6.2 \pm 1.0	3.5 \pm 1.4	—	—
Prostigmatid mites	Forest floor	708.3 \pm 102.4	1,235.8 \pm 139.2	952.8 \pm 199.9	1,884.8 \pm 410.1	*	*
	Soil	1,195.2 \pm 142.1	610.5 \pm 83.0	2,308.4 \pm 291.6	2,610.4 \pm 565.8	**	NS
Alicorhagiidae	Forest floor	7.6 \pm 2.8	14.0 \pm 4.4	3.1 \pm 1.7	11.0 \pm 5.8	NS	**
	Soil	25.6 \pm 10.8	28.5 \pm 9.4	26.0 \pm 8.9	35.2 \pm 10.7	NS	NS
Eupodidae	Forest floor	31.9 \pm 9.9	60.3 \pm 18.4	0.2 \pm 0.2	0.0 \pm 0.0	**	NS
	Soil	179.5 \pm 31.6	28.5 \pm 20.3	0.0 \pm 0.0	0.0 \pm 0.0	**	*
Nanorchestidae	Forest floor	1.6 \pm 1.0	3.0 \pm 1.9	12.3 \pm 3.4	17.3 \pm 3.8	**	NS
	Soil	0.6 \pm 0.5	0.0 \pm 0.0	183.5 \pm 73.6	80.5 \pm 24.5	**	**
Rhagidiidae	Forest floor	36.8 \pm 11.7	25.8 \pm 4.9	1.1 \pm 0.8	1.4 \pm 0.8	**	NS
	Soil	19.8 \pm 6.1	6.0 \pm 4.2	6.9 \pm 1.2	8.1 \pm 2.8	NS	NS
Tydeidae	Forest floor	0.0 \pm 0.0	0.0 \pm 0.0	85.6 \pm 17.4	67.5 \pm 13.4	**	NS
	Soil	0.0 \pm 0.0	0.0 \pm 0.0	14.1 \pm 6.6	0.8 \pm 0.5	—	—
Other families (9) ^c	Forest floor	18.8 \pm 5.7	32.3 \pm 5.1	13.4 \pm 1.8	38.4 \pm 9.3	NS	**
	Soil	23.9 \pm 6.3	14.1 \pm 6.1	51.6 \pm 23.3	25.6 \pm 11.0	NS	**
Astigmatid mites	Forest floor	36.4 \pm 15.5	59.5 \pm 14.5	19.3 \pm 9.0	47.4 \pm 24.6	NS	**
	Soil	34.3 \pm 12.2	18.9 \pm 6.3	88.2 \pm 28.7	89.0 \pm 32.0	**	NS
Collembola ^b	Forest floor	119.4 \pm 29.4	182.8 \pm 51.3	27.1 \pm 9.5	75.8 \pm 30.5	**	NS
	Soil	338.6 \pm 70.6	478.2 \pm 69.0	169.7 \pm 37.1	215.5 \pm 48.6	**	NS

^a NS, not significant; *, 0.05 < P < 0.10; **, < 0.05.

^b See Tables 3 and 4 for densities of the most common species of oribatid mites and Collembola, respectively.

^c Digamasellidae, Polyaspididae, and Uropodidae.

^d Too few individuals were collected to test for statistical differences.

^e Bdellidae, Bimichaeliidae, Cunaxidae, Paratydeidae, Pediculidae, Penthalodidae, Pygmephoridae, Scutacaridae, and Trombididae.

cies-space and to graph for visual comparison. Multivariate analysis of variance (MANOVA) was then used to determine whether these communities differed significantly between thinned and unthinned stands. Only those species whose relative abundance was $\geq 0.1\%$ of the total were included in the analyses. Thus, the number included were 39 and 33 oribatid mites in litter and soil, respectively, and 30 and 28 Collembola in litter and soil, respectively. PC-ORD was used for ORD and NMDS analyses (McCune and Mefford 1997). BioStat (SigmaSoft 1993) was used for MANOVA.

Results

Microarthropod densities within both the forest floor and soil were dominated by prostigmatid mites (1,152.6 \pm 160.0 and 1,681.1 \pm 162.5/400 cm² surface area, respectively), followed by oribatid mites (562.2 \pm 81.6 and 631.1 \pm 38.7), Collembola (101.8 \pm 19.0 and 300.7 \pm 35.0), mesostigmatid mites (77.3 \pm 10.6 and 115.9 \pm 8.2), and astigmatid mites (38.0 \pm 9.3 and 57.6 \pm 12.1) (Table 2). Overall, microarthropod density was slightly greater in soil than in the forest floor, with 2,786.4 \pm 185.5 individuals/400 cm² in soil and 1,929.7 \pm 258.2 in the forest floor. The difference between horizons was greatest for Collembola, with

nearly three times more extracted from soil than the forest floor.

Based largely on identifications of adults, 15 families of prostigmatid mites and five families of mesostigmatid mites were identified (Table 2). Prostigmatid mites were dominated by Eupodidae and Nanorchestidae, each comprising $\approx 24\%$ of the total, followed by Tydeidae (13.5%), Alicorhagiidae (12.3%), and Rhagidiidae (8.5%). Within mesostigmatid mites, Ologamasidae comprised 55.2% of the individuals identified to family followed by Zerconidae, comprising 39.7%.

Seasonal differences in abundance were found for most taxa (Table 2). For mesostigmatid mites, no seasonal difference was found within soil, but significantly more individuals were collected from the forest floor in June than in October. The pattern within the forest floor was reversed for the dominant families, because Zerconidae was more abundant in June and Ologamasidae was marginally more numerous in October. Juvenile mesostigmatid mites, not identified to the family level, were more numerous in June, representing 54.6% of the total, compared with 35.7% in October. This difference in juvenile abundance led to the greater numbers of mesostigmatid mites in the forest floor in June. In contrast, prostigmatid mites were more abundant in both horizons in October. Between-family differences also existed for adult

Table 3. Comparison of mean \pm SEM densities (no./400 cm² surface area) of the most abundant oribatid mite species in forest floor and soil between thinned and unthinned stands

Species ^a	Forest floor				Soil			
	Thinned	Unthinned	P value		Thinned	Unthinned	P value	
			Date	Treatment			Date	Treatment
<i>Brachychthonius</i> sp.	8.0 \pm 2.1	11.4 \pm 3.9	June**	NS	48.7 \pm 13.1	45.5 \pm 10.6	June**	NS
<i>Epidamaeus arcticolus</i> (Hammer)	8.8 \pm 1.6	20.8 \pm 3.7	June*	**	14.4 \pm 3.0	18.0 \pm 3.3	NS	NS
<i>Eremaeus occidentalis</i> Behan-Pelletier	16.3 \pm 3.5	35.4 \pm 5.5	NS	**	11.9 \pm 2.6	9.5 \pm 2.7	NS	NS
<i>Eueremaes stiktos</i> (Higgins)	3.6 \pm 1.6	13.0 \pm 3.8	Oct.**	**	0.5 \pm 0.4	0.1 \pm 0.1	— ^b	—
<i>Gustavia</i> sp.	16.6 \pm 16.6	25.2 \pm 6.9	June**	NS	33.1 \pm 8.1	25.8 \pm 11.2	NS	NS
<i>Joshuella striata</i> Wallwork	12.5 \pm 2.0	15.0 \pm 2.0	NS	NS	12.0 \pm 3.1	9.4 \pm 4.1	NS	NS
<i>Liacarus bidentatus</i> Ewing	2.9 \pm 0.8	3.1 \pm 1.0	NS	NS	8.0 \pm 2.7	3.6 \pm 1.4	Oct.**	NS
<i>Metrioppia oregonensis</i> Woolley & Hig.	6.5 \pm 2.1	16.5 \pm 4.0	June**	*	19.1 \pm 7.0	9.8 \pm 3.3	NS	NS
<i>Mycobates incurvatus</i> Hammer	1.9 \pm 1.0	9.1 \pm 3.6	NS	NS	3.2 \pm 1.0	1.5 \pm 0.8	NS	**
<i>Neorizetes rugosula</i> (Ewing)	10.6 \pm 3.2	21.2 \pm 4.5	Oct.**	*	2.3 \pm 1.2	5.1 \pm 1.3	NS	*
<i>Odontodamaeus verornatus</i> (Higgins)	6.6 \pm 1.3	6.6 \pm 1.1	NS	NS	4.4 \pm 1.6	3.1 \pm 1.5	NS	NS
<i>Oppliella nova</i> (Oudemans)	42.7 \pm 11.1	121.0 \pm 30.8	June**	*	152.0 \pm 27.8	175.0 \pm 32.3	June**	NS
<i>Quadropia quadricarinata</i> (Michael)	0.8 \pm 0.6	11.3 \pm 5.1	—	—	11.2 \pm 5.6	16.4 \pm 7.3	June**	NS
<i>Scheloribates pallidulus</i> (Koch)	19.3 \pm 6.3	28.6 \pm 7.7	NS	NS	46.7 \pm 10.6	26.7 \pm 5.9	NS	*
<i>Suctobelba</i> sp.	0.8 \pm 0.6	2.5 \pm 1.3	—	—	38.0 \pm 11.0	35.3 \pm 10.0	Oct.**	NS
<i>Tectocephus velatus</i> (Michael)	14.1 \pm 3.7	21.8 \pm 6.5	NS	NS	56.7 \pm 12.9	24.9 \pm 10.2	NS	**
<i>Trhypochthonius tectorum</i> (Berlese)	10.2 \pm 3.3	0.9 \pm 0.9	NS	**	23.4 \pm 15.0	0.3 \pm 0.3	June*	**

June and October sample dates have been combined to show treatment means but were separated for ANOVA analyses. NS, not significant; *, 0.05 < P < 0.10; **, < 0.05.

^a Species not analyzed statistically: *Achiptera* sp., *Ametroproctus* sp., *Aphelacarus acarinus* (Berlese), *Atopochthonius artiodactylus* Grandjean, *Autogneta* sp., *Belba* sp., *Camisia horrida* (Hermann), *Cam. spirifer* (Koch), *Carabodes* sp., *Ceratoppia bipilis* (Hermann), *Ceratozetes pacificus* Behan-Pelletier, *Cosmoethonius lanatus* (Michael), *Epidamaeus coxalis* (Hammer), *Ep. hammerae* Behan-Pelletier & Norton, *Ep. koyukon* Behan-Pelletier & Norton, *Eremaeus californiensis* Behan-Pelletier, *Er. gracilis* Behan-Pelletier, *Er. orebites* Behan-Pelletier, *Er. sp.*, *Hermannella robusta* Ewing, *Kodiakella lutea* Hammer, *K. sp.*, *Lepidozetes trifolius* (Fujikawa), *Liacarus latus* Ewing, *Licnodamaeus* sp., *Liebstadia similis* Michael, *Maerkelotritia alaskensis* Hammer, *Moritzoppia clavigera* (Hammer), *Mycobates conitus* Hammer, *Nanhermannia elagantula* Berlese, *Nortonella gildersleeveae* (Hammer), *Nothrus* sp., *Palaeacarus* sp., *Phthiracarus anonymous* Grandjean, *Propelops canadensis* (Hammer), *Pr. groenlandicus* (Sellnick), *Scheloribates rotundatus* Hammer, *Zachwatikinibates* sp., *Zygoribatula* sp.

^b Too few individuals were collected to test for statistical differences.

prostigmatid mites, because Eupodidae and Rhagidiidae were more numerous in June, whereas Nanorchestidae and Tydeidae were more numerous in October. An abundance of juveniles in October samples resulted in greater overall numbers on this date. Oribatid mites and Collembola were most numerous in June in both horizons. For astigmatid mites, no seasonal difference was found in the forest floor, but greater densities were found in October in the soil.

Thinning had a greater impact on microarthropod densities in the forest floor than in the soil (Table 2). Within the forest floor, oribatid mites, mesostigmatid mites, prostigmatid mites, and astigmatid mites were significantly more abundant in unthinned stands than in thinned stands, although the difference was marginal for prostigmatid mites. In contrast, no significant thinning effect within soil was found at the suborder level for mites. For mesostigmatid mites in the forest floor, both Ologamasidae and Zerconidae were more abundant in unthinned stands than in thinned stands, whereas for prostigmatid mites, Alicorhagiidae were more numerous in unthinned stands. Within soil, Eupodidae and Nanorchestidae were more common in thinned stands. Although this difference was marginal for Eupodidae, >6 times more individuals were collected in thinned sites than in unthinned sites. No difference between thinned and unthinned sites was found within either horizon for Collembola.

No significant relationship was found between time since thinning and the abundance of oribatid mites, mesostigmatid mites, prostigmatid mites, astigmatid

mites, or Collembola within the forest floor on either sample date.

Oribatid Mites. Fifty-five species of oribatid mites from 33 families were collected in thinned and unthinned sites. Most species were found in both stand types, with 53 and 48 species collected in thinned and unthinned sites, respectively. Species overlap between horizons was also high, with 42 species (76.4%) found in both the forest floor and soil. *Oppliella nova* dominated the samples, comprising 30.4% of all adult oribatid mites collected (25.3% in forest floor and 33.9% in soil), followed by *Scheloribates pallidulus* (7.5%), *Tectocephus velatus* (7.3%), *Brachychthonius* sp. (7.0%), and *Gustavia* sp. (6.3%). Most species were relatively rare, because 39 species each comprised <1% of the total.

Seventeen species of oribatid mites were abundant enough to analyze statistically. Significant seasonal abundance patterns were found for some taxa in both the forest floor and soil (Table 3). In the forest floor, *Brachychthonius* sp., *Epidamaeus arcticolus*, *Gustavia* sp., *Metrioppia oregonensis*, and *O. nova* were all significantly more abundant in June than in October. In contrast, *Eueremaes stiktos* and *Neorizetes rugosula* were more abundant in October than in June. Within the soil, *Brachychthonius* sp., *O. nova*, *Quadropia quadricarinata*, and *Trhypochthonius tectorum* were more abundant in June, whereas *Liacarus bidentatus* and *Suctobelba* sp. were more abundant in October.

Densities of several oribatid mite species differed between thinned and unthinned sites (Table 3).

Table 4. Comparison of mean \pm SEM densities (no./400 cm² surface area) of the most abundant collembolan species in forest floor and soil between thinned and unthinned stands

Species ^a	Forest floor				Soil			
	Thinned	Unthinned	P value		Thinned	Unthinned	P value	
			Date	Treatment			Date	Treatment
<i>Anurophorus septentrionalis</i> Palissa	1.3 \pm 0.5	1.7 \pm 0.9	June**	NS	5.5 \pm 2.2	7.8 \pm 2.2	Oct.**	NS
<i>Entomobrya confusa</i> Christiansen	16.7 \pm 2.7	33.2 \pm 6.8	NS	NS	7.6 \pm 1.9	6.4 \pm 1.4	Oct.**	NS
<i>Folsomia candida</i> (Willem)	0.0 \pm 0.0	0.1 \pm 0.1	— ^b	—	16.4 \pm 5.4	26.3 \pm 5.8	June**	**
<i>Folsomia ozeana</i> Yosii	0.3 \pm 0.3	0.0 \pm 0.0	—	—	6.2 \pm 2.4	15.4 \pm 7.8	Oct.*	* ^c
<i>Hypogastrura virga</i> Christ. & Bellinger	2.1 \pm 0.8	4.4 \pm 1.6	June**	*	7.4 \pm 1.6	10.3 \pm 1.8	June*	NS
<i>Hypogastrura vulgaris</i> Yosii	1.8 \pm 0.7	3.0 \pm 1.1	June**	NS	9.1 \pm 3.8	8.8 \pm 2.9	June**	NS
<i>Isotoma</i> sp. nr. <i>macleani</i> Fjellberg	3.7 \pm 1.0	6.0 \pm 3.5	NS	NS	0.0 \pm 0.0	1.9 \pm 1.3	—	—
<i>Isotoma sensibilis</i> Tullberg	18.0 \pm 7.5	21.9 \pm 8.0	June**	NS	66.0 \pm 19.4	63.5 \pm 16.0	June**	NS
<i>Onychiurus cocklei</i> (Folsom)	0.1 \pm 0.1	0.6 \pm 0.4	—	—	4.7 \pm 2.2	5.7 \pm 2.1	Oct.**	NS
<i>Onychiurus eisi</i> Rusek	0.0 \pm 0.0	0.0 \pm 0.0	—	—	23.5 \pm 5.3	30.4 \pm 6.8	Oct.**	NS
<i>Onychiurus eous</i> Christ. & Bellinger	5.3 \pm 1.9	18.8 \pm 8.9	June**	NS	0.0 \pm 0.0	0.0 \pm 0.0	—	—
<i>Onychiurus flavescens</i> Kinoshita	0.0 \pm 0.0	0.0 \pm 0.0	—	—	6.0 \pm 2.1	14.3 \pm 8.0	June**	NS
<i>Onychiurus folsomi</i> (Shäffer)	3.9 \pm 1.6	4.8 \pm 2.5	June**	NS	0.0 \pm 0.0	0.0 \pm 0.0	—	—
<i>Onychiurus millsi</i> Chamberlain	1.1 \pm 0.5	3.6 \pm 2.4	NS	NS	66.6 \pm 15.6	114.1 \pm 26.9	June**	*
<i>Onychiurus ramosus</i> Folsom	9.1 \pm 3.7	9.1 \pm 3.8	June**	NS	0.0 \pm 0.0	0.0 \pm 0.0	—	—
<i>Tomocerus vulgaris</i> (Tullberg)	3.8 \pm 1.0	8.0 \pm 2.0	June**	NS	2.9 \pm 1.3	1.7 \pm 0.8	June**	NS
<i>Tullbergia nulla</i> Christ. & Bellinger	0.0 \pm 0.0	0.0 \pm 0.0	—	—	11.8 \pm 3.6	12.4 \pm 2.2	June**	*

June and October sample dates have been combined to show treatment means but were separated for ANOVA analyses. NS, not significant; *, 0.05 < P < 0.10; **, < 0.05.

^a Species not analyzed statistically: *Arrhopalites diversus* Mills, *Bourletiella lurida* Snider, *Cryptopygus decemoculatus* (Folsom), *Entomobrya atrocineta* (Schott), *E. griseoolivata* (Packard), *E. sp.*, *E. triangularis* Schott, *Folsomia macroseta* Ford, *F. nivalis* (Packard), *F. sp. A.*, *F. sp. B.*, *F. stella* Christiansen and Tucker, *Hypogastrura brevis* Christiansen and Bellinger, *H. isabellae* Fjellberg, *H. pratorum* (Packard), *H. pseudarmata* (Folsom), *H. horrida* Yosii, *H. krafti* (Scott), *H. sp. A.*, *H. sp. B.*, *Isotoma albella* Packard, *I. arborea* (L.), *I. brucealla* Wray, *I. sp. nr. communis* MacGillivray, *I. japonica* Yosii, *I. monochaeta* Kos, *I. neglecta* (Schaffer), *I. pseudocinerea* (Fjellberg), *I. sp.*, *Metisotoma grandiceps* (Reuter), *Morulina* sp., *Neamura frigida* Yosii, *Neelus minimus* Willem, *Odontella coronifer* Mills, *Onychiurus* sp., *Orchesella albosa* Guthrie, *Proisotoma minuta* (Tullberg), *Pseudachorutes simplex* Maynard, *Sminthurinus henshawi* (Folsom), *S. maculosus* Snider, *S. sp.*, *Tafallia robusta* (Scott), *Tomocerus grahami* Christiansen, *To. sp.*, *To. nr. wilkeyi* Christiansen, *Xenylla* sp.

^b Too few individuals were collected to test for statistical differences.

^c A significant (P < 0.05) date by treatment interaction was found. *F. ozeana* was significantly (P < 0.05) more abundant in unthinned stands in June, but more abundant (but not significantly) in thinned stands in October.

Within the forest floor, *E. arcticolus*, *Eremaeus occidentalis*, and *Eremaeus stiktos* were found in significantly greater densities in unthinned stands compared with thinned stands. Only *T. tectorum* was more abundant in thinned stands. Within the soil, *Nycobates incurvatus*, *T. velatus*, and *T. tectorum* were more abundant in thinned stands, whereas *Neorizetes rugosala* was marginally more abundant in unthinned stands.

Ordination revealed no obvious separation between thinned and unthinned stands for oribatid mite species in either the forest floor or soil. Variation among sites was relatively high because the cumulative amount of variation explained by Principal Coordinate axes one and two was 53.1% in the forest floor and 51.7% in the soil. Overall, MANOVA failed to find differences between centroid values representing oribatid mite communities in thinned and unthinned stands for either the forest floor ($F = 2.93$; $df = 10, 5$; $P = 0.12$) or the soil ($F = 2.18$; $df = 10, 5$; $P = 0.20$).

Collembola. Overall, 61 species of Collembola from seven families were identified. Slightly more species were found in unthinned sites than in thinned sites, with 54 and 46 species identified, respectively. Species overlap between horizons was lower than that for oribatid mites, with 25 species (41.0%) found in both the forest floor and soil. *Onychiurus millsi* was most abundant species, comprising 23.1% of the fauna, followed by *Isotoma sensibilis* (21.1%), *Entomobrya confusa* (7.9%), and *Onychiurus eisi* (6.7%). Most species

were uncommon or rare, as 44 species each comprised <1% of the total collected.

Seasonal differences in density were found in one or both horizons for 16 of the 17 Collembola species abundant enough to be analyzed statistically (Table 4). Within the forest floor, eight of 11 species showed significant seasonal differences in density; all eight species were collected in greater numbers in June than in October. The seasonal pattern was even stronger in the soil, with differences in density found for all 13 species analyzed. In contrast to the forest floor, however, five species were more abundant in October than in June. Only one species, *Anurophorus septentrionalis*, revealed seasonal patterns that differed between horizons, with a significantly greater density found in June in forest floor and in October in soil.

Thinning impacted only a few species of Collembola (Table 4). Within the forest floor, only *Hypogastrura virga* was affected, being marginally less abundant in thinned sites than in unthinned sites. Similarly within soil, *Folsomia candida*, *O. millsi*, and *Tullbergia nulla* were found in fewer numbers in thinned sites than in unthinned sites. A significant date by treatment interaction was found for *Folsomia ozeana*; significantly more individuals were collected in unthinned sites in June but on average (but not statistically different), more individuals were collected in thinned sites in October.

Collembolan communities from the forest floor and soil did not ordinate consistently within groups representing thinned and unthinned stands. Rather, adjacent thinned and unthinned stands often placed similarly in space along axes one and two suggesting high community similarity between some stands. The first two Principal Coordinate axes accounted for more of the variance in the forest floor than in soil (61.7 and 47.9%, respectively). Collembolan community composition did not differ significantly between thinned and unthinned stands in either the forest floor or the soil (MANOVA; $F = 0.88$; $df = 10, 5$; $P = 0.60$ and $F = 2.08$; $df = 10, 5$; $P = 0.22$, respectively).

Discussion

Our results indicate that late-successional stands thinned 16–41 yr prior support lower densities of mites within the forest floor than unthinned stands of similar age, but mite densities in the upper 5 cm of soil were largely unaffected by thinning. Densities of oribatid, mesostigmatid, prostigmatid, and astigmatid mites were all lower in thinned stands, indicating that longer term effects of thinning is widespread among mite taxa. In contrast, the overall abundance of Collembola did not differ between stand types, suggesting that current conditions within thinned stands were not sufficiently different from unthinned stands to result in differences in their abundance.

To a limited degree, our findings corroborate those of others. Within coastal redwood forests of central California, a study comparing forest floor arthropods within uncut old-growth, mature second growth (≥ 80 yr old), and second growth stands (≥ 60 yr old) selectively harvested 14 yr before the study, found only predatory arthropods (which included spiders, centipedes, and pseudoscorpions as well as many mesostigmatid mites) to be significantly lower in abundance in thinned stands than in unthinned stands (Hoekstra et al. 1995). Micro- and pan-phytophagous arthropods (mostly oribatid and prostigmatid mites and Collembola) did not differ in abundance among the three stand types. In a multiregional study within coniferous forests of western Oregon, Madson (1998) found no significant differences in the abundance of microarthropods within the forest floor and soil among old-growth, mid-aged pole stands (50–90 yr old), and pole stands thinned 5–23 yr before the study.

Physical changes on the forest floor associated with thinning may influence microarthropod communities in a variety of ways. For example, thinning can result in more extreme temperatures and an increase in the rate at which the forest floor desiccates during dry periods (Abbott et al. 1980). Microclimatic conditions during these times may approach the tolerance limits of many species (Woodring and Cook 1962, Madge 1965). Seastedt and Crossley (1981) found significantly lower densities of microarthropods in litterbags, and to a lesser extent in the upper 5 cm of litter and soil, in clearcut stands than in uncut stands. Their data suggested that temperatures on the forest floor might have surpassed critical thresholds for survival,

suppressing microarthropod abundances. Bird and Chatarpaul (1986) found mites within litter to be significantly less abundant in whole-tree harvested plots than in uncut and conventionally harvested plots but found a decrease in moisture to be more strongly associated with reduced mite abundance than temperature. In contrast, Marra and Edmonds (1998) found moisture and temperature to have had little influence on microarthropod densities in clearcut forests on the Olympic Peninsula of western Washington, although climatic conditions in their study area are moderate compared with many other temperate environments. Changes in microclimatic conditions within our thinned stands may have been less severe than in the clearcuts discussed above, but they still may have approached tolerance limits for some species. Data from a nearby weather station indicated that July temperatures reached 35.8°C, with five consecutive days being at least 31.4°C. In addition, little rain fell on the sites between mid-June and mid-August, likely causing moisture stress. Our late June and early October samples were not taken during periods of greatest climatic stress, but lower numbers of mites collected in thinned stands may reflect a generalized response to less favorable conditions.

The amount of organic matter on the forest floor also has been shown to influence the microarthropod community. Seastedt and Crossley (1981) found a positive correlation between microarthropod abundances and increased organic matter following timber harvest, and proposed that when physiological tolerances are not exceeded, the amount and distribution of organic matter within soil can be an accurate predictor of microarthropod abundances. Similarly, Mitchell (1978) found significant positive correlations between abundances of three oribatid mite species and the depth of organic matter within fermentation and humus layers of Aspen woodlands soil. In our study, amounts of fine wood (<2.5 cm in diameter) and partially decomposed organic material were significantly greater in unthinned stands compared with thinned stands (Peck and Niwa 2005). These differences were due to the higher abundance of trees and greater extent of canopy cover in unthinned stands. It is unclear how organic matter may have influenced microarthropod abundances, but plausible explanations include greater amounts of microbial food inhabiting the surface of the organic matter (Seastedt and Crossley 1981) or a buffering of temperature and moisture stresses (Mitchell 1978).

Although thinning reduced the abundance of many taxa, ordination and MANOVA revealed that the overall composition of the microarthropod community differed little between stand types. Most species were found in both thinned and unthinned stands; 85% of oribatid mites and 64% of Collembola were found in both stand types. In some cases, greater similarity existed between adjacent thinned and unthinned stands than within either stand type. Marra and Edmonds (1998) also found broad overlap in species composition between clearcut and uncut stands, with 47 of 62 species of oribatid mite common to both stand

types. And Madson's (1998) landscape-level study of microarthropod response to forest thinning found geographic affinities to be of greater importance in determining community composition than was stand structure.

The fact that no significant relationships were found between time since thinning and the abundance of any of the mite suborders or Collembola suggests that recovery from thinning is not progressing at a steady rate over time. It is likely that temporal changes in microarthropod abundance after thinning is influenced by a variety of complex factors, including the extent and spatial pattern of tree harvest as well as the rate that the vegetation changes over time. It is possible that a greater sampling effort, representing additional thinned stands of varying age, would have revealed more clear relationships between microarthropod abundance and time since thinning.

It is clear from our results as well as those of others (Luxton 1981, Bird and Chatarpaul 1986, Moldenke and Fichter 1988, Moldenke and Thies 1996, Marra and Edmonds 1998) that forest microarthropod abundances fluctuate considerably over the course of the year. Of the 17 most common collembolan species collected, 16 differed significantly in abundance in either the forest floor or soil between June and October. Oribatid mite abundances were only slightly more similar over time, with 11 of 17 species differing between dates. Species-specific life history strategies may influence the extent to which seasonal differences are detected. For example, oribatid mites have relatively low metabolic rates, long developmental times, and low fecundity. Some species take a year or more to complete development (reviewed by Luxton 1981), and some females lay fewer than 100 eggs in a lifetime (Saichuae et al. 1972). Because egg laying generally occurs over the entire season (Luxton 1981), adults and juveniles are likely to be encountered at any time. In contrast, many Collembola and prostigmatid and astigmatid mites are relatively shorter lived and are more fecund, often completing multiple generations within a single season (Crossley 1977, Dindal 1990). Because these latter taxa are better able to respond more quickly to changes in resource availability, such as rapid growth of fungal mycelia after snow melt or fall rain, temporal differences in abundance are more likely to occur (Crossley 1977). This reproductive trait also may explain why such a high percentage of prostigmatid mites collected ($\approx 90\%$) were juveniles. Due to potentially rapid population changes of many species, we concur with Moldenke and Thies (1996) that it is important to sample on multiple occasions throughout the year to measure the response of microarthropods to forest treatments.

Seasonal migration within and between the forest floor and soil is a common response to heat and desiccation stress (Dowdy 1944, Usher 1970, Hassall et al. 1986) and may help explain some of the differences we observed between stand types. However, we were unable to detect abundance patterns that would suggest that microarthropods migrated vertically to a greater extent in thinned stands than in unthinned

stands. Deeper and more frequent sampling may have detected seasonal vertical migrations if they had occurred.

Understanding the functional role of microarthropods within forest ecosystems is important to interpreting the results of studies involving impacts due to management practices. Although great strides have been made determining and classifying the diets of many microarthropods (Luxton 1972, Behan-Pelletier and Hill 1983, Wallwork 1983, Walter 1987, Kaneko 1988), current levels of knowledge limit our ability to accurately place many forest microarthropod taxa, particularly mites, into specific functional groups (Dindal 1990, Moldenke and Thies 1996). Primary challenges include understanding the extent of omnivory (Walter et al. 1986, Walter 1987), understanding how seasonal changes in resource availability affect diet (Anderson 1975, Rockett 1980, Behan-Pelletier and Hill 1983, Walter and Ikonen 1989) and determining how diets change as species mature (Walter 1987). Largely due to these limitations, we did not analyze our results at the functional level. However, it is clear that thinning reduced numbers of both microphytophagous (fungi and bacteria feeders; sensu Luxton 1972) and predaceous mites within the forest floor. In particular, densities of oribatid mites, generally the dominant fungivorous microarthropod group within many forest ecosystems, were lower in thinned stands than in unthinned stands. Densities of mite taxa that are primarily predaceous, such as the Ologamasidae and Zerconidae (Mesostigmata) and Alicorhagiidae and Rhagidiidae (Prostigmata), were also lower in thinned stands. Considering the roles that microarthropods play in nutrient cycling, determining the relationship between forest management practices, such as thinning, and the functional response of affected microarthropod populations is critical to effective ecosystem management. Further research is necessary to better understand these complex interactions.

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