Response of Ground-Dwelling Arthropods to Different Thinning Intensities in Young Douglas Fir Forests of Western Oregon

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ABSTRACT We evaluated the effect of four different forest management techniques, unthinned control and three thinning intensities (light, light with gaps, and heavy thin), on arthropod abundance, diversity, and community structure as an indicator of ecological processes affecting other forest fauna. Ground-dwelling arthropods were collected during 2000–2001, with pitfall traps in June (warm-wet season) and August (hot-dry season) 5 yr after a thinning treatment in 40- to 60-yr-old Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees in the Willamette National Forest. We found arthropod abundance and diversity was higher in heavy and light/gap thinning treatments than the other treatments. Additionally, four groups (ants, spiders, camel-crickets, and millipedes) preferred the more intense thinning treatment areas. The abundance of carabids, the third most abundant group, was higher at the unthinned control than any thinning treatment during the wet season, but not during the dry season. Although the immediate disturbance associated with thinning might be expected to decrease population density of fauna such as ground beetles, we hypothesized that the principal effect of thinning was to increase habitat heterogeneity in these uniform plantations and indirectly increase species richness and abundance of soil-dwellers. Nonmetric multidimensional scaling (NMS) of overall arthropod community composition revealed that both seasonality and thinning were highly significant, resulting in four separate clusters of points, with season dominating thinning. Both variables were correlated with litter moisture. The NMS results indicated that ants preferred heavy thinning intensity. Spiders, carabids, and millipedes were positively associated with litter moisture, and camel-crickets were negatively associated with litter moisture. Overall, our results suggest that some dominant groups of ground-dwelling arthropods are sensitive indicators of environmental change, such as forest thinning.

KEY WORDS abundance, arthropods, diversity, forest ecosystem, thinning

OVER THE PAST HALF-CENTURY, several million hectares of mature and old-growth forests have been harvested in western Oregon and Washington and converted to young stands (Hunter 1993, 2001). Over time, the proportion of older forests in the landscape has steadily decreased, whereas the amount of young managed forests has vastly increased (Hunter 1993); therefore, the need for information on impacts of silvicultural practices has become a significant part of the prospective forest management plan in the Northwest Forest Plan. Young Stand Thinning and Diversity Study (United States Department of Agriculture) and the Density Management Study (United States Department of the Interior) are designed to determine how different thinning treatments can accelerate the development of late-successional habitat, a primary requirement of the Northwest Forest Plan (Han and Kellogg 2000).

The overall long-term goals of the multidisciplinary Young Stand Thinning and Diversity Study are to determine to what extent management strategies will (1) accelerate the return of old-growth characteristics in younger managed stands and (2) promote more biologically diverse young forests (Hunter 1995, 2001). Forest management through the application of thinning protocols can alter species composition and stand structure (Graham 1999). Thinning can also create more disease- and insect-resistant stands (Berryman 1986).

Although both unmanaged and managed forest ecosystems show variation in structure and composition, the greatest difference between unmanaged and managed stands is the lower density and volume of large snags and logs, as well as the lower number of trees and lower basal area of live trees in managed plantations (Spies et al. 1988, Spies and Franklin 1991, Hunter 1993). Thinning young stands may provide growing conditions that more closely approximate those conditions historically found in developing old-growth stands (Tappeiner et al. 1997). Thinning can move

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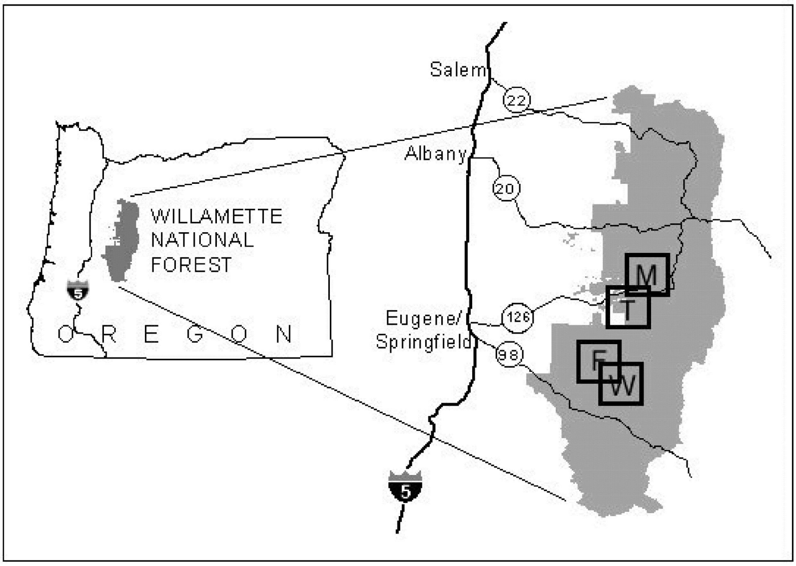

Fig. 1. Map of four study blocks (rectangles), TAP (T), MILL (M), FLAT (F), WALK (W), in Willamette National Forest in Oregon. Major highways and cities are indicated for reference.

stands out of the closed-canopy competitive stage and accelerate the development of conditions found in late seral forests (Bailey 1996, Hayes et al. 1997).

Arthropods are one of the most speciose groups on earth, accounting for >70% of all described species, including insects, which account for 56% of all described species (Groombridge 1992, Pollock 1998, Schowalter 2000). Arthropods represent the vast majority of recognized species in terrestrial ecosystems (Schowalter 2000). The diversity of arthropod species largely reflects an equivalent variety of physiological and behavioral adaptations to environmental conditions (Schowalter and Sabin 1991, Niemelä et al. 1992, Niemelä and Spence 1994). This capacity for rapid response to environmental change allows many arthropods to be useful indicators of change, as well as major engineers and potential regulators of ecosystem conditions (Schowalter 2000).

Interpreting the responses of a diverse arthropod community to multiple interacting environmental factors in integrated ecosystems requires new approaches, such as multivariate statistical analysis and modeling (Liebhold et al. 1993, Gutierrez 1996). Such approaches may benefit from avoidance of species-level resolution, using instead the combination of species into phylogenetic or functional groupings. An ecosystem approach provides a framework for integrating arthropod ecology with the changing patterns of ecosystem structure and function.

Although previous studies of arthropod responses to thinning apply to a wide range of 20- to 120-yr-old stands (Schowalter 1995), there is a lack of arthropod community data for 40- to 60-yr-old managed Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae)] forests, which are becoming as important a portion of the Northwest Forest as the widespread young stand areas (Hunter 1993, Schowalter 1995). For this study, four thinning treatments were applied to young stands of 40- to 60-yr-old plantations.

The objective of this study was to determine the diversity and abundance of ground-dwelling arthropods in young stands of Douglas fir that had been subjected to thinning treatments. Our specific hypothesis is that there will be treatment differences (directly correlated with intensity of disturbance) during each of the two principal growing seasons of the year (wet spring and dry summer). Furthermore, we expect that the effects of thinning would be greatest during the dry season. Our rationale is based on the widely documented observation (Bohac et al. 1997, Hayes et al. 1997, Tappeiner et al. 1997, Hunter 2001) that young managed plantations are characterized by homogeneous canopy tree species cover, minimal shrub and herb cover, and lack of snags and downed coarse woody debris. Because all three thinning intensities employed in this study are relatively benign, we expect that the principal effect of thinning will be to increase heterogeneity on the forest floor, thereby increasing arthropod diversity without drastically reducing the fauna by physical disturbance alone. We expect that the differences in entomofauna will be greater during the dry season because moisture will be affected by thinning treatments more substantially is the dry season than in the wet season.

Materials and Methods

Study Sites. The study was conducted in 2000 and 2001 at four study blocks located in the Blue River, McKenzie, and Oakridge Ranger Districts in the Willamette National Forest (44°07′30″ N, 122°15′00″ W) on the western slope of the Cascade Mountain Range

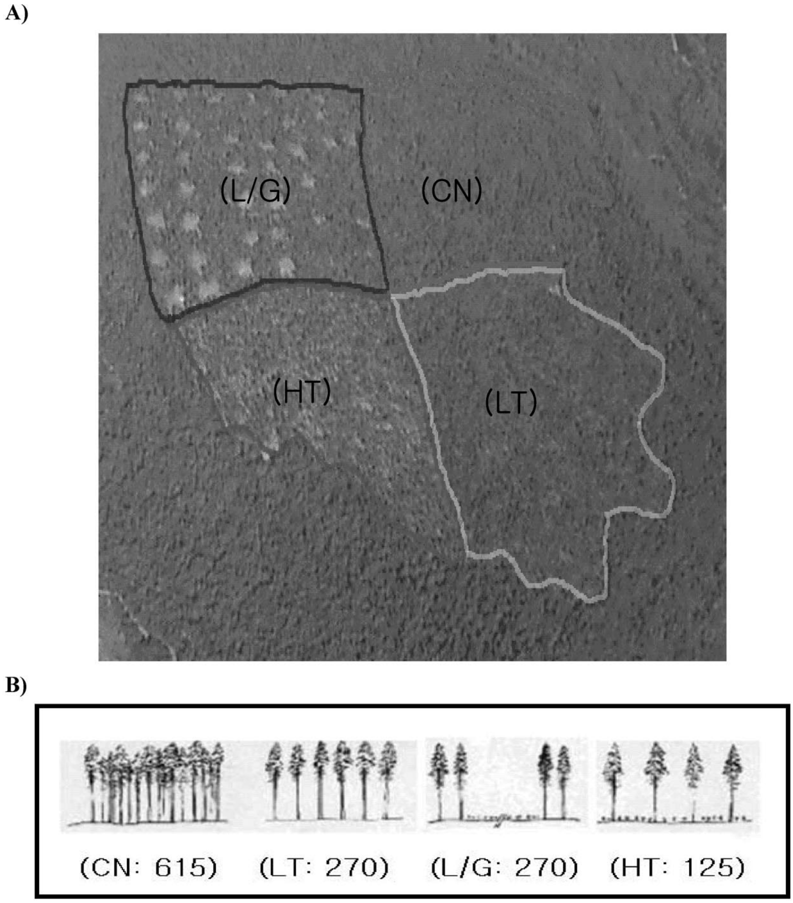

Fig. 2. (A) An aerial photo of four thinning treatments in landscape view at FLAT block (adapted from a photo taken by Sonja Weber). (B) A schematic of four thinning treatments. Numbers indicate the number of trees per hectare (tph; CN, control; LT, light thin; L/G, light with gap thin; HT, heavy thin).

in Oregon (Fig. 1). This region receives 2,000–4,000 mm of rainfall annually, with only 5% falling between 1 July and 31 October. The average yearly temperature is 10.1°C, with 1.6°C in January and 18.9°C in July. Soils are generally well developed on a tertiary volcanic substrate (Zobel et al. 1976). The forest overstory is dominated by two conifer species: Douglas fir and western hemlock [*Tsuga heterophylla* (Raf.) Sarg. (Pinaceae)] (Franklin and Dyrness 1973). The regional climate of the typical northwestern mesic forest zone is Mediterranean, with relatively warm wet winters and hot dry summers.

Thinning Treatments. Four thinning treatments were selected at each of four blocks (Han and Kellogg 2000). The four blocks were the MILL, TAP, FLAT, and WALK thinning areas in the Willamette National Forest (Hunter 1993) (Fig. 1). The four stands in each block were randomly assigned for the four thinning treatments, which were unthinned control (CN; 649 residual trees per hectare [TPH]), light thin (LT; 271 TPH), light thin with gap (L/G; 271 TPH with gaps, equally spaced 0.2-ha patches representing 20% of the stand area were completely harvested and underplanted), and heavy thin (HT; 123 TPH with underplanting; Fig. 2). The thinning treatment areas were selected for stand characteristic homogeneity of age, stand index, soil class, treatment size, dominant plant community type, slope, and elevation at each block (Hunter 1993). The age of the dominant conifer trees at the study site is 40–60 yr old, and their height is 18–27 m. Stands averaged ≈610 trees/ha >10 cm diameter breast height. Deciduous trees average ≈7% of the canopy cover (Bohac et al. 1997). The L/G treatment was the same as LT except that ≈20% of the stand consisted of 0.2-ha openings. The WALK block is somewhat more mesic than the others because of its north-facing aspect and is thus dominated by *Rhododendron macrophyllum* D. Don (Ericaceae) and *Gaultheria shallon* Pursh (Ericaceae).

Thinning treatments were implemented in 1993–1994 for precommercial thinning, and woody material was left on the site, both downed and standing, for reasons of structural diversity, animal habitat needs, and long-term site productivity (Hunter 1995). Ground-based skidding, cable, and mechanized (harvester-forwarder) harvest systems were used (Han and Kellogg 2000). After harvest, heavy and light thin w/gap treatments were underplanted with coniferous species.

Litter Collecting and Litter Moisture Measure. To measure moisture content (%) of the litter, five subsamples of litter (≈20 g) were chosen from randomly selected locations within each treatment. We collected the litter samples above the soil layer and placed the samples in plastic bags to maintain the original moisture conditions until the samples could be measured. The litter sampling periods co-occurred with arthropod sampling seasons in June and August in 2000–2001. The fresh litter subsamples were weighed soon after collecting from the treatments, and the samples were transferred into small envelopes and dried at 50°C to a constant weight. The litter moisture contents were calculated into percentages from the difference of fresh weight and dry weight.

Ground-dwelling Arthropod Sampling. We conducted a 2-yr study to monitor response of ground-dwelling arthropods to thinning treatments. Samples were taken using pitfall traps over the intervals 15 June to 29 June (warm wet season) and 27 July to 11 August (hot dry season) in 2000, and 18 June to 3 July and 2 August to 18 August in 2001. Each pitfall trap consisted of two plastic cups (12.5 cm in diameter by 8 cm deep) stacked and buried flush within the soil surface. The upper cup, containing propylene glycol as a preservative, was used for trapping, while the bottom cup remained in place to reduce local soil disturbance between collection dates. Each trap was covered by a metal cover (13 by 13 cm) to prevent rain from diluting the preservative and supported by four nails, leaving a space of ~3 cm between the cover and the rim of the cup, which was at ground level. Five pitfall traps set out in a pentagon-shaped transect per treatment were maintained for 2 wk per sampling period.

Pitfall trapping represents abundances of arthropods encountering the traps, and therefore, captures represent activity rather than density (Schowalter et al. 2003). Pitfall trap data provide useful evidence of change in relative abundance or activity that results from environmental changes (Work 2000). To minimize the edge effect of each thinning treatment, the trap grid was located close to the center of each treatment along a transect (arranged 3 by 3 cross) with 5-m intervals (Nakashizuka and Stork 2002). In theory, the three forms of thinning treatments should produce a graduated response of the ground-dwelling arthropods, because none of the thinning treatments is particularly severe. The direct effects of gaps are minimized in this research because sampling is confined to the circumference of the gaps and not within the gaps per se; any effect of gaps would be at the stand level.

Samples collected from each treatment site were taken to the laboratory and identified with a dissecting microscope to as fine a taxonomic resolution as possible. The identified sample data were pooled to compare abundance and diversity of arthropods under the separate treatments. Ground beetles (carabids), widely employed in biodiversity studies, were keyed to species level (Lindroth 1969). Separate analyses were performed on (1) total taxa with individual analysis of Formicidae, Araneae, Gryllacrididae, and Polydesmida and (2) Carabidae.

Statistical Analyses. Species diversity was measured by α, β, and γ diversity. In general, at the resolution of this study, α diversity is a measure of microhabitat diversity within a homogeneous community; β diversity is change between communities or change between microhabitats within homogeneous communities; and γ diversity is total diversity of all sampled communities within a geographic area (Cody 1986). To calculate β diversity, the total number of species (γ diversity) was divided by the average number of species (α diversity) per each thinning treatment. The Shannon-Weiner diversity index was calculated, with evenness included, as well as the Simpson diversity index (McCune and Grace 2002).

These thinning treatments were assigned to stands in a randomized block design. Each of the four study areas was considered a regional replicate (block), and the statistical analysis of this study was based on nested experimental design. Given the randomized block design of the experiment, we initially evaluated responses of individual taxa and groups to site (block) and thinning treatments using the split plot in time approach by analyses of variance (ANOVAs), with 3 df for block, 3 df for treatment, and 1 df for time (seasons) (Sokal and Rohlf 1981). ANOVA was used to test the differences in mean abundance, mean species richness, and mean species diversity for the ground-dwelling arthropod community (SAS Institute 2001). F-statistics were calculated for site, thinning treatment, season, and interactions. The Tukey-Kramer procedure was used to compare treatment means. In all analyses, the level of significance was at least $P = 0.05$ (SAS Institute 2001).

Ordination analyses were done using PC-ORD version 4.28 (McCune and Mefford 1999, McCune and Grace 2002). The pooled main matrices for each arthropod sample had high β diversity, moderate to extreme row and column skewness, and a high coefficient of variation among the sums of the columns (species) in the matrix. Thus, rare species that occurred in <5% of the samples were deleted, and the data were transformed by taking logarithms. Relativization by column (species) maxima was then done to equalize the weights between abundant and less abundant species. The Sorensen distance measure was used for all analyses. The transformed data were used for ordination analysis at this point.

Nonmetric multidimensional scaling (NMS) (Mather 1976, Kruskal 1964, Clarke 1993) is an iterative method based on rank distances between sample units. It is useful for ecological gradient studies because of its general robustness and lack of assumptions about the distribution or type of data. Therefore, NMS was used to determine the number of factors structuring the complex arthropod community structure and to qualitatively summarize the overall distribution of species assemblages across the gradients of different thinning levels. NMS was used in lieu of other ordination methods because it avoids the “zero-truncation

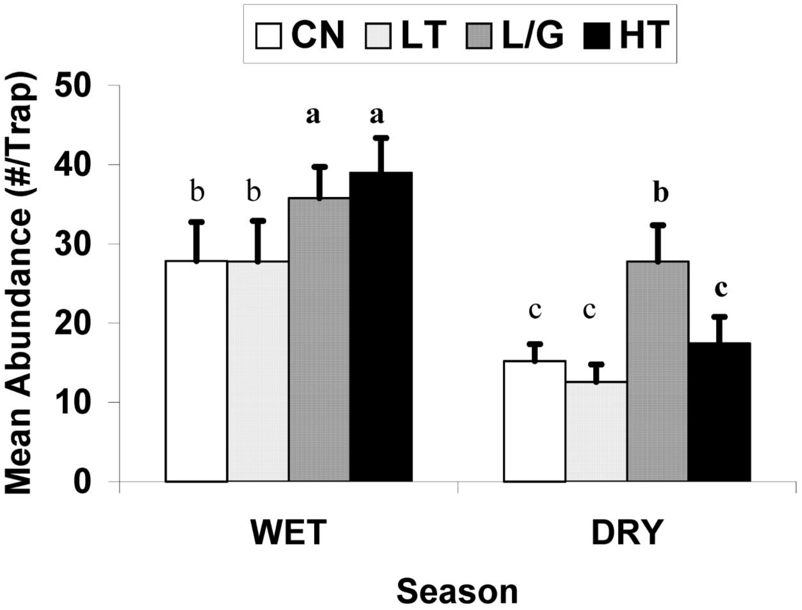

Fig. 3. Mean abundance and SE of ground-dwelling arthropods at each treatment during wet and dry seasons in 2000 and 2001. Bars having different letters differ significantly (by Tukey-Kramer procedure).

problems" of Beals (1984). We used 10 variables to determine which of the variables had high correlation coefficients. The variables we used for NMS analysis are four categorical variables (year, season, site, thinning treatments) and six quantitative variables (elevation, slope, area, stand age, litter moisture, litter depth).

Our randomized block experiments and simple repeated-measure designs, which are common in ecology, required blocked multi-response permutation procedures (MRBP) (McCune and Grace 2002). The MRBP analysis reassigned randomly the observed values to different treatments in each block, and the analysis required a balanced design: there must be one sample unit for each combination of block and treatment. Additionally, the number of treatments must be the same among blocks, and each treatment must be present in each block. Using MRBP focuses the analysis on block differences, presumably because of the treatment alone (McCune and Grace 2002). Because our research fitted well to the analysis, we could use MRBP. This procedure was useful for analyzing ecological data because it did not require assumptions of normality and constant variance (Biondini et al. 1988, McCune and Mefford 1999).

The analysis of indicator species by the method of Dufrêne and Legendre (1997) provided a simple, intuitive solution for identifying which species might serve as indicators of a particular environmental condition. This method calculated the proportional abundance of a particular species in a particular group relative to the abundance of that species in all groups. The method calculated the relative abundance of a certain species in a certain group and calculated the proportional frequency of the species in each group. These percentages were regarded as the faithfulness or constancy of presence within a particular group. The two proportions were multiplied to yield a percentage, used as an indicator value for each species in each group. Because the component terms are multiplied, both indicator criteria must be high for the overall indicator value to be high. The highest indicator value for a given species across groups is saved as a summary of the overall indicator value (IV) of that species and evaluated by a Monte Carlo method with randomly reassigned sample units to groups 1,000 times. The probability of type I error was the proportion of times that the IV from the randomized data set equals or exceeds the IV from the actual data set. The null hypothesis is that IV is no larger than would be expected by chance (McCune and Grace 2002).

Results

Thinning Treatment and Seasonal Effects on Arthropod Species Abundance. The mean abundance of arthropods was statistically different between CN, LT, and L/G and HT thinning treatments, and it seemed to be correlated directly to thinning intensity during the warm wet season but did not show a consistent treatment effect during the dry season (Fig. 3). The mean abundance of arthropods in the warm wet season was higher than that in the hot dry summer for all treatments ($F_{1,128} = 31.55$; $P = 0.0001$).

The mean abundance of captured arthropods was significantly greater in L/G than in CN or LT during both seasons (Fig. 3). Results in HT were the same as LT during the spring and the same as LT/CN during the dry summer. The mean abundance of arthropods in each of the treatments was greater during the spring

Table 1. Pairwise comparison of thinning treatments for ground-dwelling arthropods

	CN	LT	L/G	HT
CN		0.5819	$<0.0001^a$	0.0062^b
LT			$<0.0001^a$	0.0011^b
L/G				0.1766
HT				

Values are P values.
^{a} $P < 0.001$; ^{b} $P < 0.01$.

than during the dry summer (Fig. 3). For the data analysis of season (S) and thinning treatment (T), each proved statistically significant for all taxa ($P <$ 0.0001), but their interaction effect was not statistically significant for all taxa ($P = 0.128$).

To quantify how much the thinning treatments differ for total fauna, a pairwise comparison was conducted (Table 1). It was found that there was a significant difference between L/G and HT treatments relative to both CN and LT, respectively. There was no evidence of a difference in abundance in LT treatment relative to CN or between L/G and HT.

We also examined separately the five dominant taxa: Formicidae (ants), Araneae (spiders), Carabidae (ground beetles), Gryllacrididae (camel-crickets), and Polydesmida (millipedes) (Fig. 4). The relative abundances of Formicidae and Araneae were 25 and 16%, and the relative abundances of three taxa, Carabidae, Gryllacrididae, and Polydesmida, were 9, 8, and 7.5%, respectively. Formicidae and Araneae, (Fig. 4A and B) showed higher mean abundance during the wet season. The mean abundance for both taxa generally increased with the intensity of thinning during both seasons but not significantly for ants. The third most abundant group, Carabidae, showed a higher mean abundance during the wet season; however, its mean abundance decreased with the intensity of thinning (Fig. 4C). Gryllacrididae showed higher abundance during the dry season (Fig. 4D), and Polydesmida showed a higher mean abundance during the wet season (Fig. 4E). The mean abundance for Araneae, Gryllacrididae, Polydesmida, and Formicidae generally increased with the intensity of thinning during the wet season (but not significantly for ants). Gryllacrididae was the only major taxon to increase with the intensity of thinning during the dry season.

Species Diversity and Richness. Although mean species richness of arthropods did not show a statistical difference among thinning treatments at each season, a nonsignificant increasing trend of mean species richness (α) was shown with the intensity of thinning ($\text{CN} = \text{LT} < \text{L/G} = \text{HT}$) within each season (Table 2). Mean β diversity calculated from total species ($\gamma = 73$) and species richness (α) decreased with thinning intensity, but not significantly (data not shown). Shannon diversity and Simpson diversity showed a significant difference between seasons but did not show any difference among treatments during each season. Simpson diversity of the three thinning treatments relative to the CN during the wet season showed a statistically inconclusive increase (Table 2).

Community Response of Arthropods. The patterns generated by NMS in overall arthropod community composition revealed that both season (wet [W] and dry [D]) and thinning treatment (L [CN and LT] and H [L/G and HT]) were important variables in determining community composition (Fig. 5). The NMS result revealed four separate clusters of points with moisture dominating thinning along axis 2.

In this NMS ordination, axis 1 and axis 2 explained 19 and 40% of the variance between sampling points ($P = 0.02$ from the Monte Carlo test based on 50 randomizations). Regarding the 10 variables, composed of 4 categorical variables and 6 quantitative variables, that we used for NMS ordination, our results showed that both axis 1 and axis 2 were positively correlated to litter moisture and negatively correlated to stand age (Table 3). It is likely that litter moisture was sensitive to both season and thinning intensity. Of the dominant taxa, Formicidae were negatively associated with axis 1 ($r = -0.572$); Araneae, Carabidae, and Polydesmida (*Harpaphe haydeniana*) were negatively associated with axis 2 ($r = -0.418$, -0.722, and -0.0745, respectively); and Gryllacrididae (*Pristoceuthophilus* spp.) were positively associated with axis 2 ($r = 0.516$).

The MRBP test was used to find statistically explicit differences among treatments within blocked sites with the graphical results shown by the NMS ordination (Fig. 5). Thinning treatments were grouped, and the paired sites were blocked at both years. This test was run using the 2-yr matrix. The test showed a statistically significant difference for the matrix (T-statistics $= -4.36$, A-statistic; chance corrected within-group agreement $= 0.131$, $P = 0.0006$).

Indicator Taxon Analysis. The indicator analysis of Dufrêne and Legendre (1997) examined the responses of individual taxa to both thinning treatments and seasonal abundance (Table 4). Generally, treatment effects occurred only when seasonal effects were absent (10 of 15 examples). Heavier thinning favored Lygaeidae, Cicadellidae, Formicidae, Acrididae, Thomisidae, and miscellaneous spiders; Lygaeidae and Acrididae are taxa indicative of early succession (A.M., unpublished data). Less intense thinning favored snails (mollusks) and Curculionidae.

Eight arthropod groups were chosen as indicators for the June wet season (all have over 40% of IV, all $P <$ 0.05). Two families were indicators for the August dry season: Cicadellidae and Gryllacrididae (*Pristoceuthophilus* sp.; Table 4). The June wet season was characterized by four times as many indicator taxa as the August dry season.

One of the dominant families, Carabidae, was analyzed by thinning intensity and season; there were no carabid indicator species for thinning intensity. There were four indicator species, *Cychrus tuberculatus* Harris, *Omus dejeani* Reiche, *Promecognathus crassus* LeConte, and *Pterostichus lama* Menetries, for the wet season (Table 4).

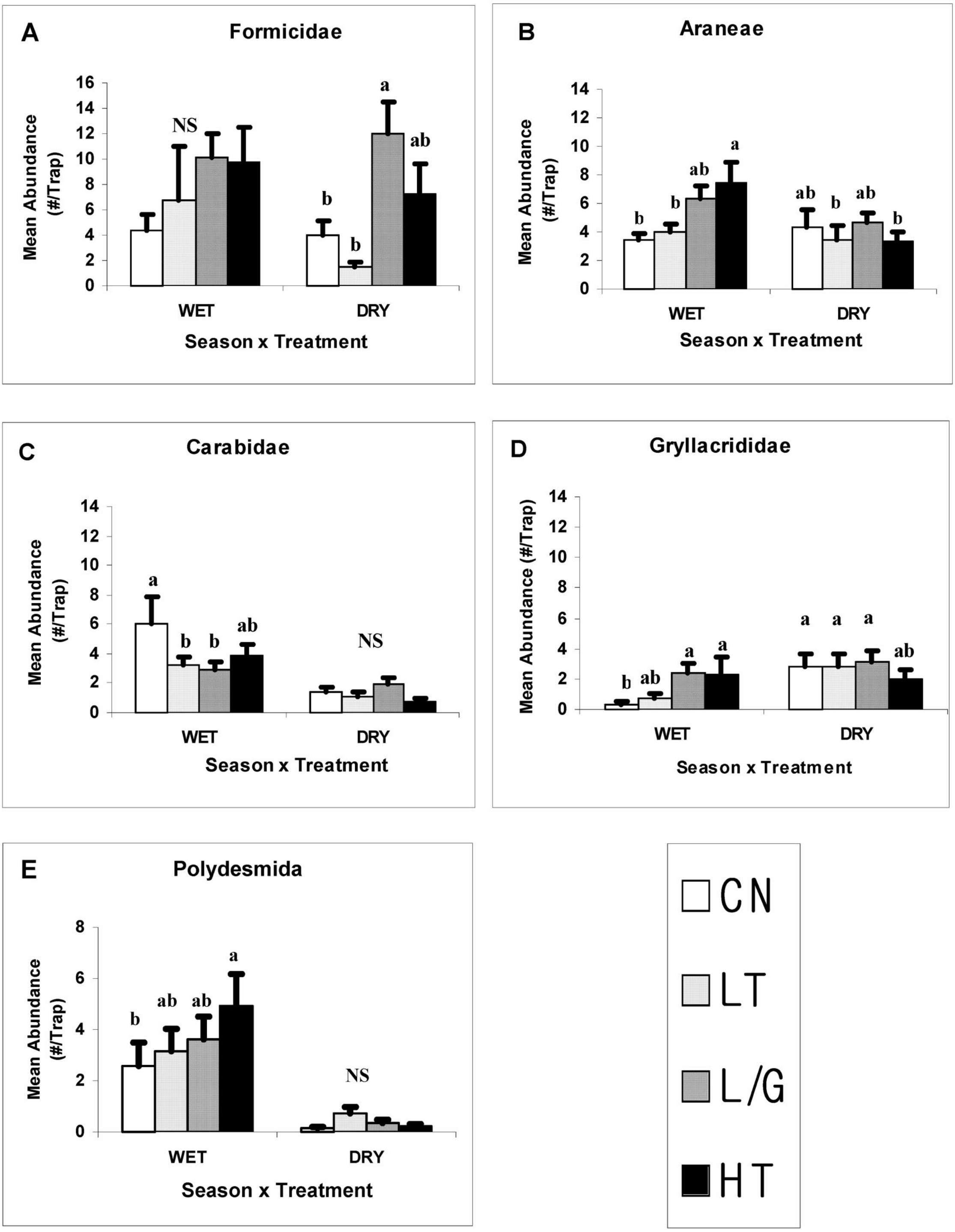

Fig. 4. Relative abundance of dominant taxa. The five dominant taxa comprise over 67% of all taxa. Mean abundance with SE bars of each taxa, shown separately for both seasons, warm wet spring and hot dry summer, with four thinning treatments in 2000 and 2001. Bars having different letters were statistically different ($P < 0.05$). ab, no statistically significant difference between letters a and b ($P > 0.05$). NS indicates no statistically significant difference ($P > 0.05$).

Table 2. Mean arthropod abundance, species richness, and Shannon and Simpson diversity indices of ground-dwelling arthropods for thinning treatments in 2000 and 2001

Season	Treatment	S ± SE	α ± SE	H' ± SE	D' ± SE
Wet	CN	27.83 ± 4.92b	20.13 ± 1.72a	2.17 ± 0.09a	0.79 ± 0.03ab
	LT	27.78 ± 5.13b	20.50 ± 1.85a	2.23 ± 0.15a	0.81 ± 0.03a
	L/G	35.78 ± 3.92a	21.63 ± 1.74a	2.17 ± 0.08a	0.81 ± 0.02a
	HT	38.98 ± 4.37a	23.13 ± 1.36a	2.19 ± 0.08a	0.82 ± 0.03a
Dry	CN	15.20 ± 2.15c	13.38 ± 1.89b	1.82 ± 0.07b	0.75 ± 0.03b
	LT	14.68 ± 1.29c	14.38 ± 1.44b	2.03 ± 0.10b	0.80 ± 0.02ab
	L/G	27.78 ± 4.56b	16.63 ± 1.66b	1.92 ± 0.08b	0.76 ± 0.02b
	HT	17.43 ± 3.37c	15.25 ± 1.31b	1.91 ± 0.09b	0.76 ± 0.03b

Within a column, means followed by the same lowercase letter are not statistically different (Tukey-Kramer's test).
Total taxa = $\gamma = 73$.
S, mean abundance; α, species richness; H', Shannon diversity; D', Simpson diversity.

Discussion

Species Abundance, Richness, and Thinning Effect. Heavier thinning is associated with a higher abundance of large ground-dwelling arthropods than lighter thinning, a response detectable during both the spring wet season and summer dry season. The abundance of four dominant taxa, Formicidae, Polydesmida, Gryllacrididae, and Araneae, were all significantly higher in the heavier thinning treatments. This trend parallels species richness, and it might be explained simply by either an increase in resources or habitat heterogeneity correlated with increasing thinning intensity.

The problem is that it is not easy to quantify the total number of potential habitats or niches under comparative conditions. Ecologists usually assume that higher species richness requires a greater number of microhabitats, proving the causality is daunting when arthropod diversity is analyzed. It is possible, however, to rule out the possibility that total food resources (i.e., total soil-dwelling Collembola and Oribatida) are greater in proportion to thinning intensity. From a parallel study on litter-dwelling microarthropods, Yi (2003) found both abundance and richness decrease significantly with thinning intensity.

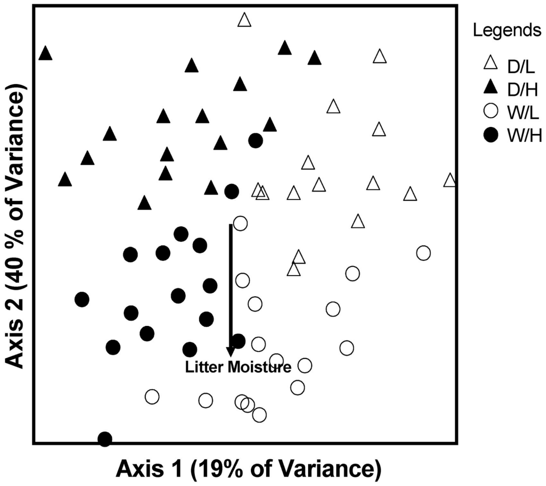

Fig. 5. NMS ordinations of pitfall arthropod samples for season (W, wet; D, dry) and thinning treatments (L, CN and LT; H, L/G and HT) in 2000 and 2001 (minimized final stress, 20%; final instability, 0.00002).

Although we hypothesized initially that the responses to thinning would be more evident during the dry season because the differential effects of thinning would be more significant, we have no direct evidence for this. Ants, spiders, and Gryllacridids were the only taxa to be collected in sufficient numbers during the dry season for analysis; of these taxa, only ants showed a greater treatment response during the dry season.

Thinning Effects on the Seasonal Occurrence of Ground-dwellers. The abundance of ground-dwelling arthropods reveals strong differences between two seasons: warm wet season and hot dry season. Large arthropod abundance, measured by pitfall trapping, of the wet season is higher than that of the dry season. Although a seasonal trend in total abundance of arthropods captured was apparent, it is difficult to explain the difference in terms of the distribution of individual taxa among treatments (Greenberg and Thomas 1995, Greenberg and McGrane 1996). In this study, the dominant predaceous taxa (e.g., Formicidae, Carabidae, and Araneae) have higher abundances in wet season than in dry season, and they numerically drive the entire faunal response.

Taxonomic Composition. NMS for ground-dwelling arthropods also documents a thinning response that is much less than that for seasonal change. Even though the thinning treatment is relatively weak, many of the species that invade the HT are unique and are normally found in an open-canopy situation (and never in the denser forests). Thus, twice as many taxa were indicators of HT than of LT (e.g., Lygaeidae, Cicadellidae, Formicidae, Thomisidae, and other Araneae; see Table 4). The gaps created by L/G and HT are influenced by direct sunlight and the drying effect of winds, and thus, these treatments cause the most se-

Table 3. Correlation coefficients between variables used for NMS analysis

Variables	Axis 1		Axis 2	
	r	r^2	r	r^2
Stand age (yr)	−0.380	0.144	−0.317	0.100
Litter moisture (%)	0.449	0.202	0.319	0.102

Table 4. Monte Carlo test of significance level of indicator values >40% or lower *P* value for some important taxa and carabids

Taxon	Thinning degree		Season	
	Light	Heavy	Wet	Dry
Carabidae	—	—	75.5^b	—
Curculionidae	54.3^c	—	63.9^b	—
Staphylinidae	—	—	60.3^b	—
Lygaeidae	—	56.9^b	—	—
Cicadellidae	—	57.7^b	—	48.0^b
Formicidae	—	69.5^b	—	—
Pristoceuthophilus spp.	—	—	—	65.0^c
Chordeumatida	—	—	60.7^b	—
Harpaphe haydeniana	—	—	89.4^b	—
Tylobolus deces	—	—	44.4^b	—
Lithobiomorpha	—	—	67.4^b	—
Xysticus spp.	—	34.3^c	41.8^b	—
Other spiders	—	58.3^c	—	—
Snails (*Haplotrema*, *Vespericola* sp.)	46.6^b	—	—	—
Carabidae				
Cychrus tuberculatus	—	—	41.8^b	—
Omus dejeani	—	—	65.7^b	—
Promecognathus crassus	—	—	40.6^b	—
Pterostichus lama	—	—	55.8^b	—

^{a} $P < 0.001$; $^bP < 0.01$; $^cP < 0.05$; —, not significant.
Light, CN and LT; Heavy, L/G and HT.

vere and rapid effects on the forest floor arthropod fauna, which are most often detected by an increase of open-habitat species (Koivula 2002). Herbivores, such as the Lygaeidae and Cicadellidae, invade the heavy thinning treatments as a heliophilic herb layer establishes after thinning. Predators, such as spiders and ants, presumably respond secondarily to all the herbivorous species precluded from the closed-canopy environment by the lack of an herb layer.

Lindroth (1969) and Work (2000) reported carabid beetles among the many forest-dwelling taxa with various forest ecosystem effects. While distribution of these species may be caused in part by microclimate changes resulting from tree harvest effects, they may also indirectly reflect prey availability across the gradient (Parsons et al. 1991). Parsons et al. (1991) also indicated the role prey availability plays in the presence of *Scaphinotus angusticollis* Harris, *S. marginatus* Fisher, and *Promecognathus crassus* LeConte. In this study, the prey of the different species of carabids are not well understood. *P. crassus* LeConte and its prey [Polydesmida: Harpaphe haydeniana (Wood)] are correlated, and both are tied to ground moisture contents.

Arthropods and Vertebrates on Thinning Treatment. Epigeic macroarthropods (the species generally caught in pitfall traps) responded to thinning with increased abundance. We have hypothesized that the increase in the pitfall-trapped macroinvertebrate fauna is related to the increase in the amount of slash and ground disturbance caused by the logging. This increases the heterogeneity of the environment greatly and provides refuges for the larger species (mostly predators) to hide successfully from their own vertebrate predators. This increase in heterogeneity is obvious to anyone visiting the plot, but is difficult to quantify in a meaningful manner for arthropods whose limiting factors are imprecisely known. Mammalogists cite the same factor as a limiting factor for small mammals in Northwest forests but can seldom successfully correlate it directly to abundance patterns (Garman 2001). Whether this means that the generally held hypothesis of limiting refuges is incorrect or that the appropriate descriptors again have not been used is unknown. It is clear that this type of thinning disturbance certainly increases prey availability for all the insectivorous vertebrates foraging on the forest floor. Deciduous shrub growth after thinning also increases the food resources for insectivorous vertebrates in the Northwest (Hagar and Starkey 2002, Hagar 2003, Yi 2003).

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References Cited

Bailey, J. D. 1996. Effects of stand density reduction on structural development in western Oregon Douglas-fir forests—a reconstruction study. PhD dissertation, Oregon State University, Corvallis, OR.

Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Adv. Ecol. Res. 14: 1–55.

Berryman, A. A. 1986. Forest insects: principles and practices of population management. Plenum, New York.

Biondini, M. E., P. W. Mielke, and K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio. 75: 161–168.

Bohac, S. A., M. D. Lattig, and G. F. Tucker. 1997. Initial vegetative response to alternative thinning treatments in second growth Douglas-fir stands of the Central Oregon Cascades. The Evergreen State College, Olympia, WA.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117–143.

Cody, M. L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions, pp. 122–152. *In* M. E. Soulé (ed.), Conservation biology, the science of scarcity and diversity. Sinauer, Sunderland, MA.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Garman, S. L. 2001. Response of ground-dwelling vertebrates to experimental levels of downed woody debris. Long Term Ecosystem Productivity Study. Willamette National Forest, Blue River, OR.

Graham, R. T. 1999. The effects of thinning and similar stand treatments on fire behavior in western forests. U.S. Dep. Agric. Forest Service, Pacific Northwest Research Station, Portland, OR.

Greenberg, C. H., and A. McGrane. 1996. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. For. Ecol. Manage. 89: 31–41.

Greenberg, C. H., and M. C. Thomas. 1995. Effects of forest management practices on terrestrial coleopteran assemblages in sand pine scrub. Fla. Entomol. 78: 271–285.

Groombridge, B., ed. 1992. Global biodiversity, status of the earth's living resources. Chapman & Hall, London, UK.

Gutierrez, A. P. 1996. Applied population ecology: a supply-demand approach. Wiley, New York.

Hagar, J. 2003. Linkage among birds, arthropods, and understory vegetation in western Oregon Douglas-fir forests. PhD dissertation, Oregon State University, Corvallis, OR.

Hagar, J., and E. Starkey. 2002. Birds, pp. 37–40. *In:* P. S. Muir, R. L. Mattingly, J. C. Tappeiner II, J. D. Bailey, W. E. Elliott, J. C. Hagar, J. C. Miller, E. B. Peterson, E. E. Starkey (eds.), Managing for biodiversity in young Douglas-fir forests of western Oregon. Biological Sciences Report USGS/BRD/BSR-2002–0006. U.S. Department of Interior.

Han, H. S., and L. D. Kellogg. 2000. Damage characteristics in young Douglas-fir stands from commercial thinning with four timber harvesting systems. West J. Appl. For. 15: 27–33.

Hayes, J. P., S. S. Chan, W. H. Emmingham, J. C. Tappeiner, L. D. Kellogg, and J. D. Bailey. 1997. Wildlife response to thinning young forests in the Pacific Northwest. J. For. 95: 28–33.

Hunter, M. G. 1993. Young managed stands. Communiqué. Cascade Center for Ecosystem Management, Blue River Ranger District, Willamette National Forest, Blue River, OR.

Hunter, M. G. 1995. Residual trees as biological legacies. Cascade Center for Ecosystem Management. Blue River Ranger District, Willamette National Forest, Blue River, OR.

Hunter, M. G. 2001. Management in young forests. Cascade Center for Ecosystem Management. Blue River Ranger District, Willamette National Forest, Blue River, OR.

Koivula, M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). For. Ecol. Manage. 167: 103–121.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika. 29: 115–129.

Liebhold, A. M., R. E. Rossi, and W. P. Kemp. 1993. Geostatistics and geographic information systems in applied insect ecology. Annu. Rev. Entomol. 38: 303–327.

Lindroth, C. H. 1969. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Opuscula Entomol. Suppl. 35: I–XLVIII.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. Wiley, London, UK.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design. Gleneden Beach, OR.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0. MjM Software Design, Gleneden Beach, OR.

Nakashizuka, T., and N. Stork 2002. Biodiversity research methods. Kyoto University Press, Kyoto, Japan.

Niemelä, J., D. Langor, and J. R. Spence. 1992. Effects of clear-cut harvesting on boreal ground beetle assemblages in western Canada. Conserv. Biol. 7: 551–561.

Niemelä, J., and J. R. Spence. 1994. Distribution of forest dwelling carabids: spatial scale and concept of communites. Ecography. 17: 166–175.

Parsons, S. L., G. Cassis, A. R. Moldenke, J. D. Lattin, N. H. Anderson, J. C. Miller, P. Hammond, and T. D. Schowalter. 1991. Invertebrates of the H. J. Andrews Experimental Forest, Western Cascade Range, Oregon. V: an annotated list of insects and other arthropods. U.S. Dep. Agric. Forest Service, Pacific Northwest Research Station, Portland, OR.

Pollock, M. M. 1998. Biodiversity, pp. 430–452. *In* R. J. Naiman and R. E. Bilby (eds.), River ecology and management: lessons from the Pacific coastal ecoregion. Springer, New York.

SAS Institute. 2001. PROC user's manual, 6th ed. SAS Institute, Cary, NC.

Schowalter, T. D. 1995. Canopy arthropod communities in relation 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, San Diego, CA.

Schowalter, T. D., and T. E. Sabin. 1991. Litter microarthropod response to canopy herbivory, season and decomposition in litterbags in a regenerating conifer ecosystem in western Oregon. Soil Biol. Fert. 11: 93–96.

Schowalter, T.D., Y. L. Zhang, and J. J. Rykken. 2003. Litter invertebrate responses to variable density thinning in Washington forest. Ecol. Appl. 13: 1204–1211.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York, NY.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth forests in Oregon and Washington, pp. 91–109. *In* L. F. Ruggiero, K. A. Aubry, A. B. Carey, and M. H. Huff (eds.), Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Dep. Agric. Forest Service, Pacific Northwest Research Station, Portland, OR.

Spies, T.A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology. 69: 1689–1702.

Tappeiner, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27: 638–648.

Work, T. T. 2000. Edge effects of clearcut harvesting on ground arthropod species composition and predator community structure in old-growth Douglas-fir forests. PhD dissertation, Oregon State University, Corvallis, OR.

Yi, H. B. 2003. Response of arthropods to different intensities of thinning in Oregon. PhD dissertation, Oregon State University, Corvallis, OR.

Zobel, D. B., A. McKey, G. H. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western cascades of Oregon. Ecol. Monogr. 46: 135–156.

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