

# Responses of litter-dwelling arthropods to four different thinning intensities in Douglas-fir forests of the Pacific Northwest, USA

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We investigated the response of litter-dwelling arthropods to the effects of four forestry thinning intensities (Control, Light Thin, Light Thin with Gap, and Heavy Thin). With the balance between timber demand and maintaining biodiversity in the forest ecosystem in mind, we examined the effects of thinning on the abundance, richness, and diversity of arthropods as an indicator of how ecological processes affect forest litter-dwelling fauna. Study sites were 40- to 60-year-old stands of typical Douglas-fir plantation in the Willamette National Forest, Oregon, USA. To examine the seasonal response of the litter-dwelling arthropods, litter debris and humus samples were collected in October 2000 (wet late-growing season, Late 2000), June 2001 (wet early-growing season, Early 2001), and August 2001 (dry mid-growing season, Mid 2001) and extracted with Tullgren funnels. The abundance and diversity of litter-dwelling arthropods decreased as thinning intensity increased. The decreases in both abundance and diversity of arthropods with limited mobility within the two heaviest thinnings were correlated with an increased heterogeneity of disturbance to the forest floor (patchy litter and moss cover removal), rather than responses to thinning itself at the scale of the entire stand. The litter-dwelling fauna correlated positively with litter moisture. Under control conditions, the abundance of predators and detritivores increased during the dry summer in August. Non-metric multidimensional scaling results showed distinct clusters for the three growing seasons. The wet early-growing season clustered with the dry mid-growing season, but not with the wet late-growing season. Moisture correlated highly with the ordination axes. This study showed that litter-dwelling arthropods were correlated with stand density and seasonal litter moisture of the forest floor.

## Introduction

Silvicultural thinning has become a significant part of the forest management plans in the Pacific Northwest, U.S.A., as the ratio of young managed forests to older forests has vastly increased and as biological diversity has become a major objective (Carey & Johnson 1995, Hayes *et al.* 1997, Graham 1999, Carey 2000, Sullivan *et al.* 2001a, 2001b, Hayes *et al.* 2003, Schowalter *et al.* 2003). Forest management plans simultaneously require the maintenance of biodiversity and increased thinning. The PNW Forest Management Plan has been applied to federal forests in the Pacific Northwest during the last decade, but testing is still needed on the ecological and silvicultural implications of the adopted protocols on forest biota (Hunter 1993, 2001, Rose & Muir 1997, Spence & Volney 1999, Halpern & McKenzie 2001).

The U.S. Forest Service's Young Stand Thinning and Diversity Study was designed to determine how different thinning treatments can accelerate the development of late-successional habitat, a primary requirement of the Forest Plan (USDI 1992, Hunter 1993, 2001, Han & Kellogg 2000, Lint 2005). Unlike the situation in most countries, where thinning is employed primarily to increase stem volume, in the Pacific Northwest, thinning is employed to provide growing conditions that more closely resemble those found historically to be conducive to the development of old growth (Tappeiner *et al.* 1997). These conditions are created by moving stands out of the closed-canopy competitive stage and accelerating the development of conditions found in late-seral forests (McComb *et al.* 1993, Bailey 1996, Carey & Curtis 1996, Hayes *et al.* 1997). The process of harvesting can disturb the litter layer, and deposition of logging slash can destroy plants and affect future establishment, but slash may have a positive influence on understory recovery by providing protection from excessive solar radiation (Tesch *et al.* 1986, Halpern 1989, McInnis & Roberts 1994), thus combating more extreme temperature ranges and the decrease in available shade (Matlack 1993, Chen *et al.* 1995). The greatest effects of thinning on the forest floor involve soil moisture, both by removal of live tree roots and their water

uptake and an increased amount of evaporation through increased solar radiation and air movement. In this study, we consider that the forest floor includes surface litter, the partially decomposed layer beneath it, and the humus layer. Litter plays a major role in the transfer of energy and nutrients in the forest ecosystem, and litter-fall data have been used to quantify the overall productivity of an ecosystem (Toky & Singh 1983, Ananthakrishnan 1996).

Forest management practices affect ground-dwelling arthropods and can affect the availability of prey for vertebrates (Jokimäki *et al.* 1998). Edenius and Elmberg (1996) reported negative effects in bird species from forest management in Sweden, but Sjöberg *et al.* (2007) emphasize that little is actually known about the effects of forestry activities on birds in the old-growth forests of northern Scandinavia. Stork and Brendell (1990) reported that 70% of all arthropods inhabit the soil and leaf litter in the rainforest ecosystem in southeast Asia; Southwood (1987) reported the same percentage in forest ecosystems in Europe. Besides being major engineers and potential regulators of ecosystem conditions (Schowalter 2000), the rapid response of arthropods to environmental change makes them useful indicators, as well (Peltonen *et al.* 1997). Arthropod diversity in litter depends on the type of litter and its complex microbial components, coupled with the heterogeneity of the litter layer (Ananthakrishnan 1996). In Oregon, seasonal abundance of the soil fauna varies with rainfall (Moldenke & Fichter 1988).

Although previous studies of arthropod responses to thinning apply to a wide range of conditions, the impact of forest thinning on animal assemblages, particularly litter-dwelling arthropods, is poorly documented and not well understood (Didham *et al.* 1996). In a companion study, Yi and Moldenke (2005) reported that thinning intensity was correlated with higher abundance and diversity of epigeic macroarthropods collected by pitfall-trapping. This increase was correlated with a decrease in litter moisture during the dry-season for four of the five principal groups of arthropods. Carabidae, the exception, preferred unthinned conditions and was significantly more abundant during the wet-season. We hypothesized that the increased arthropod

response to thinning was associated with either (1) increased forest-floor habitat heterogeneity (skid trails removing forest floor locally and intentional deposition of large amounts of slash throughout) in otherwise uniform young plantations or (2) possibly greater amounts of food resources in thinned areas (millipedes and camel-cricket have far more litter to feed upon; predaceous ants, spiders and carabids potentially correlated with an increased rate of litter decomposition and higher densities of springtails and mites). The increase in disturbance to the litter layer and the increase in slash and total litterfall are well-documented; unfortunately, there is no data on the availability of food for the larger predaceous arthropods aside from this study.

We examined the diversity and abundance of the litter-dwelling arthropod community in stands subjected to thinning treatments. The response of the litter-dwelling arthropods is expected to be season specific, and general increases in most faunal components is expected in the moist spring and early summer as a response to increased habitat heterogeneity and litter biomass. In the litter itself (not including the mineral soil), thinning is expected to promote dehydration with a consequent decrease in arthropods sensitive to drier conditions, while promoting arthropods that prefer dry habitats. In general, the three thinning treatments, excluding the forested control, should produce a graduated response in the arthropods as none of the treatments was especially severe.

## Materials and methods

### Study sites and experimental design

A total of 16 Douglas-fir (*Pseudotsuga menziesii*) stands in the Willamette National Forest (total treatment area 490 ha, 43°–45°N, 121°–123°W, elevation 430–900 m a.s.l.) on the western slope of the Cascade Mountain Range were examined in the Young Stand Thinning and Diversity Study. Replicate blocks, consisting of four stands each, were located in the Blue River Ranger, McKenzie, and Oakridge districts. The regional climate of the typical northwestern mesic forest zone is Mediterranean, with dry and hot sum-

mers, and wet and relatively warm winters. The annual growing season starts with the initiation of rain in October, slows during the cool rainy winter, peaks during the warmer rainy spring and sunny early summer; conditions become extremely dry during August and September. A more detailed site description is given in Yi and Moldenke (2005).

The thinning areas were selected for similarity of stand characteristics in age, stand index, soil class, spatial extent of treatment, dominant plant community type, slope, and elevation at each block (see Hunter 1993). Thinning treatments were implemented in 1993 and 1994 (see Han & Kellogg 2000 and Yi & Moldenke 2005 for a detailed description) and our study was conducted during the autumn of 2000 through the summer of the 2001 growing season. The age of the dominant conifer trees at the time of our study was 50 years old, and their height ranged between 18 to 27 m. The density of trees that were greater than 10 cm in diameter at breast height was 610 trees per hectare (stems/ha) prior to thinning. Deciduous trees averaged approximately 7% of the canopy cover (Bohac *et al.* 1997). A control unharvested stand and three thinning intensity treatments were selected in each of the four blocks (Hunter 1993, Han & Kellogg 2000). Each regional block had four treatments: Control (CN; 649 trees ha<sup>-1</sup>), Light Thin (LT; 271 trees ha<sup>-1</sup>), Light Thin with Gap (LT/G; 271 trees ha<sup>-1</sup> with gaps, equally spaced 0.2-ha patches representing 20% of the stand area were completely harvested), and Heavy Thin (HT; 123 trees ha<sup>-1</sup>) (see more detail in Yi & Moldenke 2005).

### Litter-dwelling arthropod sampling

Litter and humus from treatments on 14 October 2000 (late-growing season, Late 2000), 18 June 2001 (early-growing season, Early 2001), and 2 August 2001 (mid-growing/dry season, Mid 2001) were collected from two randomly selected squares (0.5 m × 0.5 m) with a scraper and put into plastic bags (50 l). In the LT/G treatment, samples were taken under the forest canopy at the edge of the gaps to minimize the effect of the gap itself (because we were inter-

ested in the effect of the gap on the species composition of the forest fauna, as opposed to which species inhabited only the gaps, which in Oregon are usually open-canopy species) (A. Moldenke unpubl. data). In the other three treatments, samples were collected from the center of the treatment block, avoiding special microhabitats (e.g., fallen logs, tree trunks, shrub thickets, etc.) in order to represent typical forest conditions. All samples were chilled at 5 °C until processed in Tullgren funnels (30 cm in diameter, 50 cm deep) and allowed to dry for at least two weeks under 65-watt bulbs (Macfadyen 1961, 1962). Except for mites (Acari) and springtails (Collembola), which were not included in this study, most litter arthropods were identified to the lowest possible taxonomic level with the available expertise. For comparison among treatments, the arthropod number divided by sample size provided a standard unit. All arthropod taxa were combined by family and ecological guilds for statistical analyses of abundance patterns (Schowalter & Ganio 1998). All arthropod specimens were verified against the H.J. Andrews Long-Term Ecological Research Collection and the Oregon State University Arthropod Collection in Corvallis, Oregon. Voucher arthropods were deposited at the Oregon State University collection.

Ecological guilds (i.e. functional groups: plant sucking herbivores, predators, and detritivores) were assigned for statistical analyses of abundance patterns (Schowalter & Ganio 1998). Five sub-samples of litter (approximately 20 g) were randomly extracted from the samples of each treatment to measure moisture content (Yi & Moldenke 2005). Litter samples were dried at 50 °C to a constant weight and then weighed again.

## Statistical analyses

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 was based on a 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 treat-

ments using the split plot in time approach by analyses of variance (ANOVAs), with 3 df for block, 3 df for treatment, and 2 df for seasons to test the effects of treatment and season on the litter arthropods. Abundance data were used as a response variable, and sites, treatments, seasons, and their interactions as predictor variables (Sokal & Rohlf 1994, SAS Inc. 2001). Separate ANOVA tests were performed on overall arthropod abundance, the abundance of various taxonomic groups and the abundance of the functional groups (Table 1). The arthropods at each treatment were averaged separately for each sampling season to compare the abundance and diversity of the samples (SAS Inc. 2001).

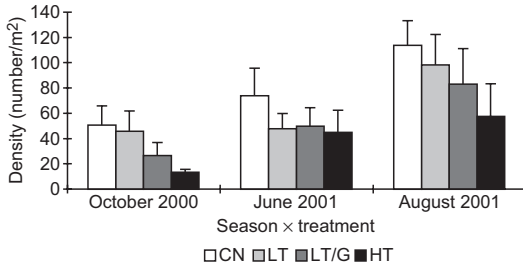
The averaged data were examined with PC-ORD v. 4.28 for multivariate analyses (McCune & Grace 2002). The main matrix for each arthropod sample had high beta diversity, moderate-to-extreme row and column skewness, and a high coefficient of variation (CV) among the sums of the columns (species) in the matrix. We deleted rare species that occurred in less than 5% of the samples and applied a logarithmic transformation. Nonmetric multidimensional scaling (NMS) was used to determine the number of factors structuring the complex arthropod community and to qualitatively summarize the overall distribution of species assemblages across the gradients of different thinning levels (Kruskal 1964, Mather 1976, Clarke 1993). NMS was used in lieu of other ordination methods because it avoids the zero-truncation problems of Beals (1984). Sorensen's distance measure was used in species space. We examined nine variables to find which had the highest correlation coefficients. The variables used included three categorical variables (date, site, thinning treatments) and six quantitative variables (elevation, slope, treatment area, stand age, litter moisture, litter depth).

$\alpha$ ,  $\beta$ , and  $\gamma$  diversity measures were calculated at the family-level resolution of the arthropods collected, since many species could not be identified to species level. In general, for this study  $\alpha$  diversity represents a measure of microhabitat diversity within a homogeneous community;  $\beta$  diversity represents a change between microhabitats within the homogeneous community, and  $\gamma$  diversity is the total diversity of all

**Table 1.** Overall mean litter-dwelling arthropod abundance and standard error in parenthesis from the forest litter samples in October 2000 (Late 2000), June 2001 (Early 2001), and July 2001 (Mid 2001). Bold numbers mean the sum of each functional group (Herbivores, Predators, Detritivores including total number) at each treatment column.

| Tested effects           | Late 2000          |                    |                    |                    | Early 2001          |                     |                      |                      | Mid 2001           |                    |                    |                    |
|--------------------------|--------------------|--------------------|--------------------|--------------------|---------------------|---------------------|----------------------|----------------------|--------------------|--------------------|--------------------|--------------------|
|                          | ON                 | LT                 | LT/G               | HT                 | ON                  | LT                  | LT/G                 | HT                   | ON                 | LT                 | LT/G               | HT                 |
| <b>Herbivores</b>        | <b>4.5 (1.3)</b>   | <b>6.5 (3.5)</b>   | <b>5.0 (1.2)</b>   | <b>7.0 (3.5)</b>   | <b>8.5 (4.7)</b>    | <b>8.5 (4.3)</b>    | <b>9.0 (4.0)</b>     | <b>9.0 (4.5)</b>     | <b>11.5 (4.4)</b>  | <b>20.0 (4.7)</b>  | <b>9.5 (5.9)</b>   | <b>6.0 (1.3)</b>   |
| Coleoptera               | 1.5 (1.0)          | 6.5 (2.5)          | 4.0 (1.5)          | 3.5 (2.9)          | 4.5 (1.5)           | 2.0 (0.8)           | 2.5 (1.5)            | 2.5 (1.0)            | 8.0 (4.5)          | 5.0 (1.3)          | 3.5 (2.9)          | 1.5 (1.0)          |
| Hemiptera                | 1.0 (0.6)          | 0.0 (0.0)          | 0.5 (0.5)          | 2.5 (2.5)          | 4.0 (3.0)           | 6.0 (3.5)           | 5.0 (2.5)            | 6.0 (3.0)            | 3.0 (1.5)          | 11.0 (6.5)         | 5.5 (4.5)          | 3.5 (2.0)          |
| Lepidoptera              | 2.0 (1.3)          | 0.0 (0.0)          | 0.5 (0.5)          | 1.0 (0.5)          | 0.0 (0.0)           | 0.5 (0.5)           | 0.5 (0.5)            | 0.5 (0.5)            | 0.5 (0.5)          | 4.0 (3.0)          | 0.5 (0.5)          | 1.0 (0.5)          |
| Thysanoptera             | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.0 (0.0)           | 1.0 (1.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| <b>Predators</b>         | <b>23.5 (4.8)</b>  | <b>20.0 (8.3)</b>  | <b>14.5 (6.7)</b>  | <b>18.5 (4.3)</b>  | <b>163.0 (28.2)</b> | <b>137.5 (30.0)</b> | <b>119.0 (41.6)</b>  | <b>86.5 (49.1)</b>   | <b>78.5 (27.3)</b> | <b>53.0 (29.7)</b> | <b>19.0 (12.1)</b> | <b>16.7 (2.0)</b>  |
| Pselaphidae              | 2.0 (2.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 10.5 (3.9)          | 3.5 (1.7)           | 1.5 (1.0)            | 0.5 (0.5)            | 1.5 (1.5)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Staphylinidae            | 1.5 (0.5)          | 2.0 (0.8)          | 0.0 (0.0)          | 3.5 (1.3)          | 7.0 (5.2)           | 2.0 (0.8)           | 0.5 (0.5)            | 1.0 (1.0)            | 2.0 (1.4)          | 6.5 (5.2)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Other Coleoptera         | 1.0 (1.0)          | 2.5 (1.5)          | 1.0 (0.5)          | 1.5 (1.5)          | 1.0 (0.5)           | 3.5 (2.9)           | 2.0 (0.0)            | 2.0 (0.8)            | 0.5 (0.5)          | 0.5 (0.5)          | 0.0 (0.0)          | 0.5 (0.5)          |
| Formicidae               | 1.5 (1.0)          | 2.0 (2.0)          | 0.0 (0.0)          | 0.5 (0.5)          | 47.0 (28.1)         | 59.0 (16.6)         | 81.5 (37.1)          | 66.5 (48.8)          | 23.5 (17.2)        | 25.0 (17.3)        | 16.0 (12.8)        | 8.7 (8.6)          |
| Other Hymenoptera        | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)          | 0.5 (0.5)          | 6.5 (2.6)           | 2.5 (1.5)           | 4.0 (1.6)            | 1.5 (1.5)            | 11.0 (8.5)         | 0.5 (0.5)          | 0.5 (0.5)          | 0.0 (0.0)          |
| Ophionenes               | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 1.0 (1.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 1.0 (1.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Raphidioptera            | 0.5 (0.5)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Chilopoda                | 7.5 (2.2)          | 2.5 (0.5)          | 8.0 (5.5)          | 8.5 (4.7)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.5 (0.5)            | 1.0 (1.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Geophilomorpha           | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 62.0 (22.3)         | 28.5 (6.9)          | 10.0 (3.5)           | 9.0 (2.4)            | 14.0 (5.4)         | 4.5 (2.6)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Libiomorpha              | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 6.0 (2.9)           | 1.0 (1.0)           | 8.5 (4.7)            | 1.0 (0.6)            | 0.5 (0.5)          | 0.5 (0.5)          | 0.5 (0.5)          | 1.0 (1.0)          |
| Scolopendromorpha        | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 5.0 (4.4)           | 6.0 (4.7)           | 2.5 (1.9)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.5 (0.5)          |
| Pseudoscorpiones         | 1.5 (1.0)          | 2.5 (2.5)          | 4.5 (2.6)          | 0.5 (0.5)          | 7.5 (3.0)           | 8.0 (4.7)           | 3.0 (1.9)            | 0.5 (0.5)            | 5.0 (1.9)          | 4.5 (2.6)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Thomisidae               | 0.5 (0.5)          | 0.0 (0.0)          | 0.0 (0.0)          | 1.0 (1.0)          | 1.5 (1.0)           | 0.5 (0.5)           | 0.5 (0.5)            | 1.5 (1.0)            | 3.5 (1.7)          | 2.0 (1.2)          | 0.5 (0.5)          | 2.0 (0.8)          |
| Other Spiders            | 7.5 (2.4)          | 2.5 (1.5)          | 2.0 (0.5)          | 2.5 (2.5)          | 8.0 (0.8)           | 23.0 (19.0)         | 3.0 (1.3)            | 2.0 (1.4)            | 16.0 (2.5)         | 9.0 (5.9)          | 1.5 (1.0)          | 4.0 (2.2)          |
| <b>Detritivores</b>      | <b>10.0 (2.5)</b>  | <b>8.0 (1.5)</b>   | <b>4.5 (3.8)</b>   | <b>5.0 (3.3)</b>   | <b>40.0 (10.2)</b>  | <b>36.5 (21.6)</b>  | <b>24.5 (5.9)</b>    | <b>5.5 (3.0)</b>     | <b>2.0 (0.8)</b>   | <b>6.0 (1.7)</b>   | <b>16.5 (12.7)</b> | <b>0.5 (0.5)</b>   |
| Tenebrionidae            | 0.0 (0.0)          | 1.5 (1.5)          | 0.0 (0.0)          | 0.0 (0.0)          | 3.0 (1.3)           | 2.5 (1.5)           | 3.5 (2.5)            | 1.5 (1.0)            | 1.0 (1.0)          | 0.5 (0.5)          | 15.5 (12.9)        | 0.0 (0.0)          |
| Other Coleoptera         | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)           | 0.5 (0.5)           | 0.5 (0.5)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.5 (0.5)          | 0.5 (0.5)          |
| Psocoptera               | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.5 (0.5)          | 1.5 (1.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Protura                  | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Dipluran                 | 0.0 (0.0)          | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)          | 5.0 (3.7)           | 3.0 (2.4)           | 9.5 (5.2)            | 1.5 (1.5)            | 0.0 (0.0)          | 1.5 (1.5)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Diplopoda                | 6.5 (2.6)          | 6.0 (1.8)          | 3.0 (3.0)          | 4.0 (2.5)          | 29.5 (12.8)         | 29.5 (19.6)         | 8.5 (4.9)            | 2.0 (1.4)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Spirrobolida             | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 2.0 (1.4)           | 0.0 (0.0)           | 1.0 (1.0)            | 0.0 (0.0)            | 0.5 (0.5)          | 0.5 (0.5)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Crustacea                | 0.0 (0.0)          | 0.0 (0.0)          | 1.0 (0.6)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Diptera                  | 4.0 (1.9)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.5 (0.5)           | 0.5 (0.5)           | 1.5 (1.0)            | 0.5 (0.5)            | 0.0 (0.0)          | 1.0 (0.6)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Orthoptera               | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.0 (0.0)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.5 (0.5)          | 0.0 (0.0)          | 0.0 (0.0)          |
| Machilidae               | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)          | 0.0 (0.0)           | 0.5 (0.5)           | 0.0 (0.0)            | 0.0 (0.0)            | 0.0 (0.0)          | 0.5 (0.5)          | 0.5 (0.5)          | 0.0 (0.0)          |
| <b>Total</b>             | <b>38.0 (11.4)</b> | <b>34.5 (14.2)</b> | <b>24.0 (20.2)</b> | <b>30.5 (21.2)</b> | <b>211.5 (78.0)</b> | <b>182.5 (99.2)</b> | <b>152.5 (109.7)</b> | <b>101.0 (100.3)</b> | <b>92.0 (62.1)</b> | <b>79.0 (60.7)</b> | <b>45.0 (41.6)</b> | <b>23.2 (14.8)</b> |
| Moisture (%)             | 69.8 (4.8)         | 67.6 (2.9)         | 58.5 (2.0)         | 54.2 (1.2)         | 43.1 (2.5)          | 35.3 (4.9)          | 38.6 (2.1)           | 29.3 (2.4)           | 18.2 (1.1)         | 12.8 (2.2)         | 10.2 (1.6)         | 11.5 (2.2)         |
| Species richness         | 8.5 (1.2)          | 6.4 (0.9)          | 5.8 (0.9)          | 6.0 (1.3)          | 11.1 (1.9)          | 9.8 (0.6)           | 10.9 (1.1)           | 7.1 (1.3)            | 8.2 (1.0)          | 6.9 (1.2)          | 3.4 (0.8)          | 4.0 (0.8)          |
| Shannon-Wiener Diversity | 1.5 (0.2)          | 1.5 (0.1)          | 1.2 (0.2)          | 1.3 (0.2)          | 1.9 (0.1)           | 1.8 (0.1)           | 1.8 (0.2)            | 1.5 (0.3)            | 1.7 (0.1)          | 1.4 (0.3)          | 0.8 (0.2)          | 0.8 (0.2)          |

T = Treatment, S = Season, I = Interaction, \* $P < 0.05$ , \*\* $P < 0.001$ , ns = not significant.



**Fig. 1.** Mean density of litter-dwelling arthropods in the different growing seasons and thinning treatments. CN = Control; LT = Light Thin; LT/G = Light with Gap; HT = Heavy Thin. Late 2000, Early 2001, Mid 2001.

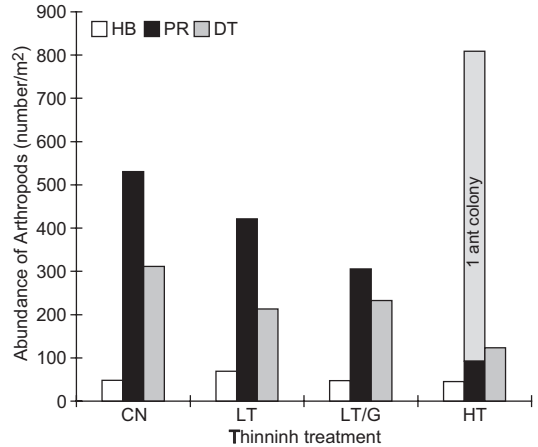
sampled communities within the entire study design (Cody 1986). To calculate  $\beta$  diversity, the total number of morph-species ( $\gamma$  diversity) was divided by the average number of morpho-species ( $\alpha$  diversity) per thinning treatment. The Shannon-Weiner and Simpson diversity indices were calculated by PC-ORD (McCune & Grace 2002).

## Results

### Abundance of arthropods

Late 2000 had the lowest mean abundance of litter-dwelling arthropods for each thinning treatment, and Early 2001 had the highest. Predaceous arthropods were the dominant group and were relatively the most abundant in Early 2001 (72%) and the least abundant in Mid 2001 (51%). The main predators in the litter layer were ants, spiders, and geophilomorph centipedes. Detritivores/fungivores were the second most abundant group. The main detritivore taxon was Diplopoda (Table 1).

In general, the abundance of litter arthropods decreased with thinning intensity (Table 1). Total abundance was significantly different between the CN and the HT for both the Early 2001 and Mid 2001; the two less severe thins were intermediate (Fig. 1). The same trend was found for both predators and detritivores (Fig. 2), though not significant for detritivores. The number of ants in a single sample of HT seriously affected the overall treatment comparison (Fig. 2) and was excluded from our analyses.



**Fig. 2.** Total abundance (excluding Collembola and mites) of functional groups of litter arthropods at each thinning treatment. HB = herbivores, PR = predators, DT = detritivores. As in Fig. 1, the effect of the inclusion of a single ant colony is specifically noted because it affects the interpretation significantly; the ants in this sample (one species) were excluded from analyses.

During the year, the average seasonal moisture content varied between 63% (Late 2000), 37% (Early 2001), and 13% (Mid 2001). Litter moisture decreased with increased thinning intensity (Tables 1 and 2). Moisture was highest for CN (43.7%) and lowest for HT (31.7%). Litter moisture was used as a covariate that explains overall arthropod abundance significantly ( $F_{1,94} = 18.01$ ,  $P = 0.0001$ ), and after adjusting for the covariate, thinning treatment was no longer significant ( $F_{3,86} = 2.63$ ,  $P = 0.06$ ). A positive relationship between  $\log(\text{arthropod abundance})$  and  $\log(\text{moisture})$  was found,  $\log(\text{abundance}) = 0.419 \times \log(\text{moisture}) + 2.419$  ( $r = 0.485$ ). In pair-wise comparisons (after accounting for site and season), we showed a significant difference in arthropod abundance between the CN and HT ( $F_{1,86} = 14.79$ ,  $P = 0.0002$ ) treatments and the LT and HT treatments ( $F_{1,86} = 7.00$ ,  $P = 0.01$ ). Pair-wise comparisons revealed no evidence of a difference in abundance among other treatments after accounting for site and season.

### Species richness and diversity

There were strong positive correlations between  $\log(\text{abundance})$  and  $\log(\text{species richness})$  (Fig.

3). The relationships were nearly identical between the four treatments, except that the LT/G and HT samples were more heterogeneous. Species richness followed a trend similar to that of total abundance; richness in the CN significantly exceeded that of HT during both Early 2001 and Mid 2001 (Table 2).

Differences in both the Shannon and Simpson diversity indices were significantly higher at the CN and LT treatments as compared with those at the heavier thinnings during the mid-season ( $P < 0.05$ ), but only suggestive at other seasons.  $\beta$ -diversity increased significantly with thinning intensity during all three seasons. Within any given season, there was no correlation between richness/diversity and moisture content of the litter (results not presented).

### Community composition

NMS analysis of the litter arthropod communities using 48 litter samples (four sites  $\times$  four thinning treatments  $\times$  three seasons) with nine variables (date, site, thinning treatments, elevation, slope, treatment area, stand age, litter moisture, litter depth) produced separate clusters for the three growing seasons (Late 2000, Early 2001, Mid 2001; Fig. 4). Other variables had exceedingly

weak correlations. Axis 1 explained 48% of the variance, and axis 2 explained 22% of the variance. The spring wet-season, Early 2001, clustered with the dry mid-season, Mid 2001, but not with the moist late-season, Late 2000. Moisture was correlated to axis 1 at 78% and to axis 2 at 48% of the variance (Fig. 4).

### Discussion

In temperate climates with a pronounced dry season, arthropod abundances and diversity are expected to vary throughout the year. Our NMS result confirms that arthropod communities are indeed distinct during the three seasons studied. It is well known that many, if not most, species of arthropods are differentially active during the year in the Pacific Northwest. Taxa, such as the Carabidae, are speciose in this environment with numerous species active at different times during the year (Thiele 1977, Halaj *et al.* 2008). Analyses at finer taxonomic resolutions should minimize the effect of individual species' activity patterns. With this caveat in mind, the fact that seasonal effects on the arthropod fauna exceed the effects of differing levels of thinning is important both in the design of experiments and in interpreting the scale of the effect.

**Table 2.** Average species richness per thinning treatment,  $\alpha$  diversity (average diversity in individual sample units),  $\beta$  diversity ( $\beta = \gamma\alpha$ , amount of compositional variation in a sample),  $\gamma$  diversity ( $\gamma = 61$ , landscape-level diversity), Shannon diversity ( $H'$ ) and Simpson diversity ( $D'$ ) of litter arthropods and litter moisture (%) at Willamette National Forest in 2000 and 2001. Growing seasons: Late 2000 (15 Oct. 2000), Early 2001 (19 June 2001), Mid 2001 (15 Aug. 2001).

| Growing season (mean litter moisture) | Diversity | Thinning treatments (mean litter moisture) |            |              |            |
|---------------------------------------|-----------|--|------------|--------------|------------|
|                                       |           | CN (43.7%)                                 | LT (38.6%) | LT/G (35.8%) | HT (31.7%) |
| Late 2000 (62.5%)                     | $\alpha$  | 8.5  | 6.4        | 5.8          | 6.0        |
|                                       | $\beta$   | 7.7  | 10.2       | 11.2         | 10.8       |
|                                       | $H'$      | 1.5  | 1.5        | 1.2          | 1.3        |
|                                       | $D'$      | 0.7  | 0.7        | 0.6          | 0.6        |
| Early 2001 (36.6%)                    | $\alpha$  | 11.1                                       | 9.8        | 10.9         | 7.1        |
|                                       | $\beta$   | 5.9  | 6.6        | 6.0          | 9.2        |
|                                       | $H'$      | 1.9  | 1.8        | 1.8          | 1.5        |
|                                       | $D'$      | 0.8  | 0.8        | 0.7          | 0.6        |
| Mid 2001 (13.2%)                      | $\alpha$  | 8.1  | 6.9        | 3.4          | 4.0        |
|                                       | $\beta$   | 8.0  | 9.4        | 19.1         | 16.3       |
|                                       | $H'$      | 1.7  | 1.4        | 0.8          | 0.8        |
|                                       | $D'$      | 0.8  | 0.6        | 0.4          | 0.4        |

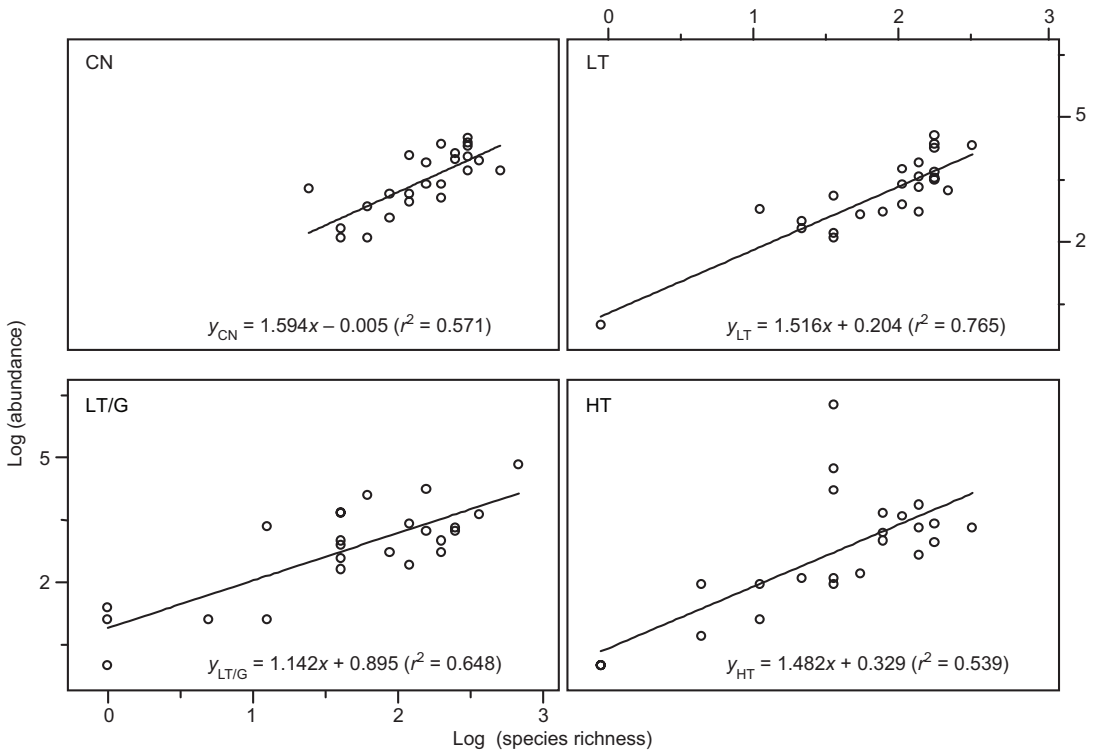


Fig. 3. Regression of log species richness versus log total abundance for the four thinning treatments.

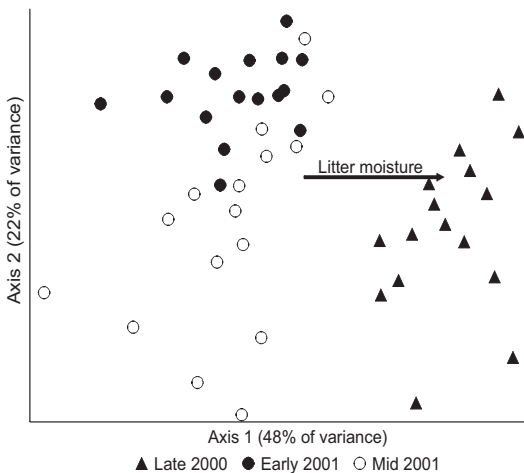


Fig. 4. Nonmetric Multidimensional Scaling (NMS) plot of the litter arthropods according to the growing seasons (Late 2000, Early 2001, and Mid 2001) in 48 litter samples from the thinning treatments. Growing seasons represented the sampling times during 2000 and 2001. (Moisture correlated with axis 1 at 78% and axis 2 at 48%; minimized final stress = 19.09%; Final instability = 0.00001; Monte Carlo 50 runs).

The response of soil moisture to thinning procedures is not well understood and doubtless varies with soil type and annual precipitation patterns (Matlack 1993, Chen *et al.* 1993, 1995). Ignoring localized physical trauma to the soil during the harvesting process, it is broadly hypothesized that soil (*not* litter) moisture availability should increase following canopy removal because transpiration from the removed trees is eliminated (Carlson & Groot 1997). In the case of gaps, total transpiration by the dense herbaceous/shrub growth is presumed to be considerably less than the transpiration loss from the trees that used to occupy the gaps.

It is expected that the smallest soil-dwelling arthropod fauna (principally Collembola and Cryptostigmata) would increase in relation to thinning intensity, because soil moisture would increase, and additional leaf litter (as a food resource) would be created during the thinning process (Huhta *et al.* 1967, Huhta 1976, Moldenke & Fichter 1988, Ananthakrishnan 1996).



Therefore, in this forest environment, the Collembola and Cryptostigmata are expected to increase significantly for several years following thinning, which would, in turn, provide an increase in food resources for the predaceous litter-dwelling arthropods. The number of larger detritivores in the litter would also be expected to increase with increased thinning because of a corresponding increase in the availability of resources. This increase in the microfauna would eventually decrease as the one-time litter resource is removed by decomposition.

We found, however, that an increase in the degree of thinning decreased the total abundance of litter-dwelling arthropods. This trend was significant for total arthropods and for the two most abundant feeding guilds: predators and detritivores. These differences were significant principally between the CN and HT, with little difference between the CN and LT, and the LT/G was nearly indistinguishable from the HT (Table 1). If this decrease in arthropods was within the soil itself, we might postulate compaction, associated with logging, as a cause, however, compaction would not occur in these litter/humus samples. We speculate that either (a) compaction of the soil beneath the litter/humus layer decreased the localized soil-dwelling springtail and mite abundances and, indirectly, the litter-dwelling arthropod predators, or (b) the decrease is from enhanced patchy litter dryness from the partial removal of the litter layer during the logging disturbance itself.

The physical characteristics of the litter layer were studied by Beggs (2004). She found that exposed sections of mineral soil (complete removal of the litter/humus layers) increased in the LT/G and HT relative to the CN, as collateral disturbance increased with logging intensity. She also documented that live moss ground cover decreased with logging intensity; live moss is a significant factor for water retention on the surface of the forest soil. The arthropods examined in this study are mostly characterized by limited mobility. Increased patchiness of disturbed conditions on the forest floor is expected to have significant localized effects on arthropod abundance and richness.

Current forest planning envisions the implementation of LT on a limited basis because it

only increases the growth rate of the remaining trees for approximately one decade and produces no measurable tendency to attain the old-growth conditions mandated by the Forest Plan (Hunter 1993, FEMAT 1994). Currently, thinning levels that exceed the intensity of HT are widely implemented to attempt to accelerate the managed production of big trees that once dominated these forests naturally. HT is no longer even referred to as "heavy thinning" (FEMAT 1994). Currently, the debate is whether any thinning whatsoever within an established stand can produce Douglas-fir with large branches beneath the crown. If these specialized growth requirements have to be met within the first 20–30 years of stand establishment, then familiar thinning protocols will be employed once again, primarily to regulate growth rate and control the build up of combustible materials. Whatever the rationale, LT versus HT treatments have different effects on the environment. Large-scale implementation of LT intensities should have a minimal effect on the arthropods, whereas HT will have to be studied carefully for the full range of its effects on numerous ecosystem components.

Although seasonal changes in the composition of the litter-inhabiting fauna are to be expected, the changes were only partially what we anticipated. Predators were expected to decline during the dry summer because the mite and springtail fauna upon which they feed decline to low levels (Moldenke & Fichter 1988). Detritivores were also expected to decline during the dry summer because increased insolation and air flow dries the litter and decreases fungal growth and the rate of decomposition. In this study, the total abundances of both predators and detritivores increased as the summer season progressively dried. The increase in abundance of these relatively small predators and detritivores, extracted by the Tullgren funnel, is directly opposite to the trend documented for relatively large predators captured by pitfall traps at the same research sites (Yi & Moldenke 2005). It appears that these smaller species of lower mobility, which are confined to the litter habitat, respond more strongly to higher temperature than to decreased moisture.

Most of the litter-dwelling arthropods collected from this study are too large to experi-

ence true soil conditions (few have the ability to burrow), and most are confined to the litter/humus environment or pre-existing fissures in the upper soil. In this study, thinning intensity was directly related to increased litter drying, which is likely because of the initial disturbance of logging, during which the deciduous shrub cover was both crushed by falling trees and actively reduced in order to stimulate understory conifer growth.

## Conclusion

This study demonstrates that the effects of thinning on the arthropod fauna of Pacific Northwest forests are complex. Because the arthropod fauna changes seasonally, it is critical to quantify treatment effects within a given season and compare treatment effects at different times of the year. Seasonal effects on arthropods are always large and expected to exceed treatment effects because, in general, the species that are active during the dry season are different from those active during the wet season. Comparisons between seasons can be facilitated by analyses at the functional guild or higher taxonomic level.

The litter-dwelling fauna are most closely tied to seasonal litter moisture. Even though seasonal differences are large, the indirect treatment effects of thinning on litter moisture significantly decrease both abundance and diversity proportional to thinning. There are no detectable differences between the CN and LT, and the LT/G is generally not distinguishable from HT. This decrease in the low-mobility litter-dwelling arthropod fauna may be correlated to the heterogeneity and intensity of the disturbance (amount of mineral soil exposed, death of moss ground cover), rather than to the effects of stand-level thinning treatments.

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