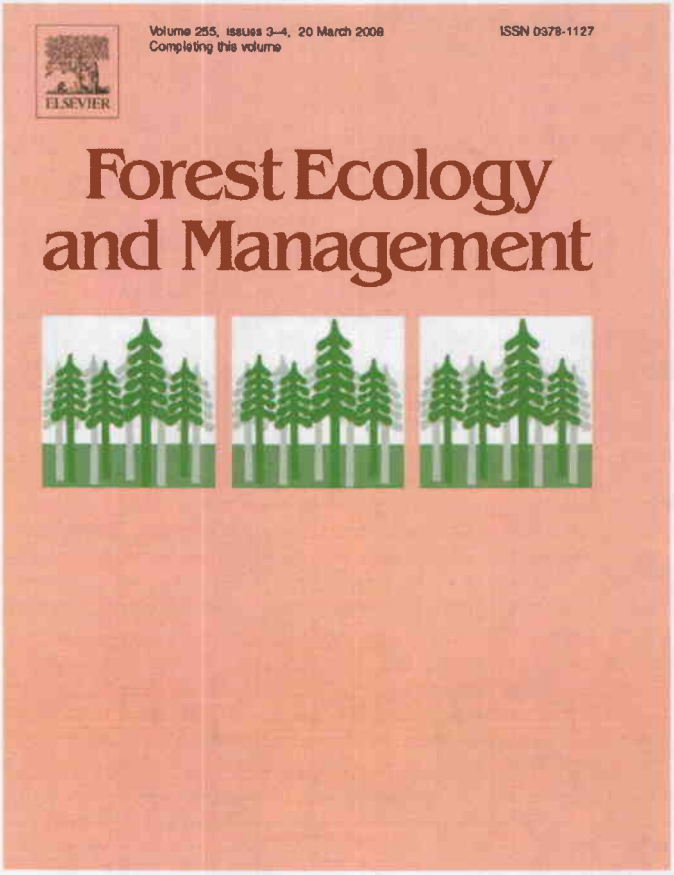

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Responses of litter-dwelling spiders and carabid beetles to varying levels and patterns of green-tree retention

Juraj Halaj [a], Charles B. Halpern [b,*], Hoonbok Yi [c,1]

[a] Cascadien, Inc., Corvallis, Oregon 97330-1016, USA
[b] College of Forest Resources, Box 352100, University of Washington, Seattle, Washington 98195-2100, USA
[c] Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, USA

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Abstract

We studied effects of timber harvest with green-tree retention on litter-dwelling predatory arthropods (spiders and carabid beetles). Arthropods were sampled with pitfall traps at four experimental blocks in western Oregon and Washington. Within each block, arthropods were collected 5–7 years after treatment in five 13-ha harvest units including a control and four that represent contrasts in retention level (15 vs. 40% of original basal area) and spatial pattern (dispersed vs. aggregated in 1-ha patches). More than 47,000 arthropods were collected during two 6-week periods in 2003 and 2004. All harvest treatments had positive effects on the activity-density (relative abundance) of spiders. Groups typically associated with open habitats showed particularly large responses (6.3–7.5 greater abundance than in controls). In contrast, species characteristic of old forest exhibited 57–84% lower abundance in harvest treatments than in controls. Abundance of carabid beetles was 60% lower among harvest treatments than controls reflecting declines in forest-dependent taxa. Among harvest treatments we did not detect a significant effect of level or pattern of retention for most groups of predatory arthropods. However, we documented significant variation in response within aggregated treatments. As a group, spiders were more abundant at edge and intermediate positions (15 m from edge), than at the centers of aggregates. In contrast, carabids showed significant declines at the edge. Correlation and ordination analyses revealed significant relationships between local abundance/composition of arthropod taxa and selected habitat attributes (e.g., tree density and basal area, cover of disturbed soil and herbs), consistent with treatment effects. Our results suggest that 5–7 years after harvest, habitat conditions were not suitable in any treatment to support the abundance and diversity of taxa present in late-seral forests.

Keywords: Arthropod community structure; Carabid beetles; Forest litter; Spiders; Variable-retention harvest

1. Introduction

In forests of the Pacific Northwest, structural retention has become the standard method of regeneration harvest on federally administered lands within the range of the northern spotted owl (Franklin et al., 1997; Aubry et al., 1999). Standards and guidelines in the Northwest Forest Plan stipulate retention of overstory trees in at least 15% of each harvest unit with the expectation that residual trees will moderate effects on microclimate and provide habitat features that ensure persistence of late-seral species and promote their subsequent recovery (USDA and USDI, 1994). These standards further require that 70% of this retention occurs in patches of undisturbed forest or "aggregates" of 0.2–1.0 ha. Effective implementation of these practices, however, requires an understanding of the minimum habitat requirements of forest species and an assessment of the variation in habitat quality created by different levels and patterns of retention.

Forest litter invertebrates are useful indicators of environmental changes because of their sensitivity to changes in temperature and moisture, or to changes in the amount or quality of resources associated with habitat alteration. After timber harvest, forest litter can experience biologically significant changes in temperature and moisture content (Bird and Chatarpaul, 1986; Thibodeau et al., 2000). Soil biological activity may also be stimulated by input of organic matter (Huhta et al., 1967; Bird and Chatarpaul, 1986), which may

* Corresponding author.
E-mail addresses: chalpern@u.washington.edu (C.B. Halpern), yih@kribb.re.kr (H. Yi).
[1] Present address: Bio-evaluation Center, Korea Research Institute of Bioscience and Biotechnology, Daejeon 305-333, South Korea.

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affect the dynamics of food-webs. Litter arthropods can be sensitive to changes habitat structure, including cover and diversity of understory plants (Heliölä et al., 2001; Heyborne et al., 2003), amount or quality of litter (Uetz, 1991), and abundance of coarse woody debris (Martikainen et al., 2000; Latty et al., 2006). These provide nutrition, serve as refugia, or ameliorate environmental stress (Strong et al., 1984) and can vary with stand age or disturbance history (e.g., Harmon et al., 1986; Halpern and McKenzie, 2001; Halpern et al., 2005).

Most evidence for effects of timber harvest on soil and litter arthropods derives from studies that address responses to clearcut logging (Huhta, 1971, 1976; McIver et al., 1992; Niemelä et al., 1993; Greenberg and McGrane, 1996; Marra and Edmonds, 1998; Heliölä et al., 2001, Koivula et al., 2002). Studies of less intensive methods of harvest are not as common (Koivula, 2002; Moore et al., 2002; Siira-Pietikäinen et al., 2003; Pihlaja et al., 2006) and focus primarily on responses to silvicultural thinning in younger forests (e.g., Huhta et al., 1967; Yi and Moldenke, 2005). A common conclusion is that timber harvest leads to loss of forest-dependent species and colonization of open-habitat taxa; the consequences for total abundance, however, can be highly variable.

Our study is part of a broader experiment, Demonstration of Ecosystem Management Options (DEMO), which evaluates some basic ecological assumptions of variable-retention harvests in Pacific Northwest forests (Aubry et al., 1999). In particular, it is designed to test the sufficiency of the 15% minimum standard of retention, and the ability of relatively small (1 ha) forest aggregates to serve as temporary refugia and ultimately, as sources for dispersal of forest-dependent species into adjacent harvest areas. Here we examine responses of two major groups of epigeal arthropods, spiders (Araneae) and carabid beetles (Carabidae). We chose these groups because both are abundant, generalist predators in temperate litter communities, are sensitive to environmental changes associated with habitat modification (Huhta, 1971; Thiele, 1977; Uetz, 1991; Niemelä et al., 1993), and are integral in the dynamics of litter food-webs, decomposition, and nutrient cycling (Wise et al., 1999; Halaj and Wise, 2002; Moore et al., 2002; Scheu, 2002). We postulated that variation in the density and distribution of residual trees would elicit significant responses among predatory litter arthropods by changing soil/litter temperature, moisture availability, and vegetation structure. We tested the following specific hypotheses:

Hypothesis 1. *Effects of level of retention.* Arthropods favoring open or disturbed habitats will increase in treatments with lower levels of retention; those adapted to interior forests will decline in these habitats. Richness of carabid beetles will increase at lower levels of retention, reflecting an influx of open-habitat taxa.

Hypothesis 2. *Effects of pattern of retention.* Dispersed treatments will support greater abundance of arthropods adapted to warmer/drier conditions, reduced abundance of forest-interior taxa, and greater richness of carabids than aggregated treatments.

Hypothesis 3. *Responses to habitat edges in aggregated treatments. 3a:* Abundance of forest-interior taxa will decrease with proximity to the edge of forest aggregates reflecting increases in light and temperature and declines in soil moisture. In contrast, taxa adapted to warmer/drier conditions will increase near the edge, as will richness of carabid beetles. *3b*: As a consequence of these edge effects, abundance of forest-interior species will be lower and open-habitat species higher in forest aggregates than in controls.

Hypothesis 4. *Responses to local habitat structure.* Local (plot-scale) abundance of arthropods will be positively correlated with cover of understory vegetation and fine litter (intact forest floor), surrogates of habitat quality. Correlations with overstory density and basal area will be positive for forest-dwelling taxa and negative for open-habitat taxa.

2. Methods

2.1. Study sites

We utilized four of the six experimental blocks that comprise the DEMO study. All occur between ~800 and 1300 m elevation in the Cascade Range: one in southwestern Oregon (Watson Falls) and three in southwestern Washington (Butte, Little White Salmon, and Paradise Hills). The region is characterized by a maritime climate with warm, dry summers and cool, wet winters with most precipitation falling between October and April (Franklin and Dyrness, 1973). *Pseudotsuga menziesii* was the dominant overstory species in all blocks although stand age, structure, and composition varied among blocks. Detailed information on physical environment, forest structure, and disturbance history is presented in Aubry et al. (1999) and Halpern et al. (2005).

2.2. Experimental design

The full experiment consists of a randomized block design with six 13-ha experimental units (Aubry et al., 1999; Halpern et al., 2005). We utilized five of these treatments: a control (100% retention) and four that represent strong contrasts in level of retention (15 vs. 40% of original basal area) and/or spatial pattern (trees dispersed vs. aggregated in 1-ha patches). In dispersed treatments (15%D and 40%D), dominant or co-dominant trees were retained in a dispersed fashion throughout the harvest unit. In aggregated treatments, two (15%A) or five (40%A) 1-ha circular forest aggregates were retained at fixed locations and all merchantable trees (>18 cm dbh) were removed from adjacent harvest areas using either ground-based or helicopter-yarding systems. Harvest treatments were completed in 1997 or 1998. Details on harvest treatments and post-harvest management activities are presented elsewhere (Halpern and McKenzie, 2001; Halpern et al., 2005).

2.3. Field sampling

Within each experimental unit a systematic grid of permanent sample points (8 × 8 or 7 × 9 with 40-m spacing) was established before treatment to facilitate sampling and integration among studies (Aubry et al., 1999). Sampling of litter arthropods was linked to permanent vegetation plots established at a subset of these points, with the number and distribution of plots varying by treatment (Halpern et al., 2005). In control and dispersed treatments, plots were established at alternate points (32 plots per treatment). In aggregated treatments, plots were established at all points within forest aggregates and at a subset of points in the surrounding harvest area (32–37 plots per treatment).

Litter-dwelling spiders and carabid beetles were sampled with pitfall traps installed within 1 m of the center of a vegetation plot. In dispersed treatments and controls, traps were established at 15 randomly selected grid points with vegetation plots (~56–80 m apart). In aggregated treatments, traps were installed at various positions relative to forest aggregates: at the *center* of each aggregate ($n = 2$–5 per treatment); at *intermediate* positions (~40 m from the center and ~15 m from the edge, $n = 3$–4 per treatment); on the *edge* ($n = 6$–8 per treatment); or in the *harvest area* (~20–100 m from the edge, $n = 8$ per treatment). In total, 89 traps were established per block.

Following the design of Yi and Moldenke (2005), each pitfall trap consisted of two plastic cups with a diameter of 12.5 cm. A larger ("sleeve") cup, 8 cm deep, was buried flush with the soil surface to form a receptacle for a smaller collecting cup containing propylene glycol preservative. A metal roof (13 cm × 13 cm) was installed at a height of 3–5 cm above each trap. All traps were installed in June 2003 and arthropods were sampled for two weeks in June, July, and August in 2003 and 2004. Traps were repaired or replaced as needed at the beginning of each collecting interval. Collections were preserved in ethanol and identified to the lowest taxon possible; here we report only on the major predaceous groups, including Araneae (spiders), Opiliones (harvestmen), and Carabidae (ground beetles).

2.4. Measures of habitat structure

Several measures of forest structure, understory vegetation, and ground conditions were used as potential predictors of arthropod abundance at a local (plot) scale. These were derived from a comprehensive sampling of permanent vegetation plots in 2003 and 2004. Tree density and basal area were computed from measurements of stems ≥5 cm dbh within a circular, 0.04 ha plot. Total cover of herbs (herbaceous and woody plants <1 m tall), fine litter (intact forest floor), coarse litter (≥10 cm diameter), and mineral soil was obtained by averaging estimates from 24 microplots (0.2 m × 0.5 m) per plot. Total cover of tall shrubs (≥1 m tall), understory hardwoods, and understory conifers (<5 cm dbh) was estimated by the line-intercept method using four, 6-m long transects per plot. Volume of coarse woody debris (CWD, ≥10 cm dbh) was estimated with the line-intersect method of Brown (1974) using the same transects. Sampling details are provided in Halpern and McKenzie (2001) and Halpern et al. (2005).

2.5. Data analyses

We express the response of litter arthropods as an "activity-density index of relative abundance" (number of arthropods collected/trap/day), henceforth abundance. This index is commonly used because the total area of sampled habitat and the absolute abundance of arthropods cannot be reliably ascertained with pitfall traps (Niemelä et al., 1990; Spence and Niemelä, 1994). Species richness of carabid beetles was expressed as the number of species collected/trap/day; richness of spiders was not considered because they were not identified to species. Abundance and species richness values from individual traps were averaged for each treatment unit; means for aggregated treatments were calculated as weighted averages of plots representing aggregates and harvest areas to account for differences in the area and sampling intensities of these environments. All univariate analyses were limited to taxa that comprised >5% of individuals within each community (spiders or carabid beetles).

To test for effects of level and pattern of retention on arthropod abundance (Hypotheses 1 and 2), data were modeled as a randomized block, split-plot design with treatment as the whole-plot and time (year) as the split-plot. The variance–covariance matrix for the two years was modeled as unstructured, allowing different variance among the measurements in each year, permitting direct comparisons of treatments within and between years. Responses to harvest, and to level and spatial pattern of retention in particular, were then evaluated through a series of *a priori* contrasts conducted as *t*-tests. Contrasts were conducted on pooled data (2003 and 2004) where there were no significant time-by-treatment interactions and on individual years where interactions were significant.

A series of separate ANOVAs were used to test for effects of habitat edge within aggregated treatments (Hypothesis 3). Data were analyzed as a randomized block, split–split-plot design with treatment (15%A and 40%A) as the whole-plot, trap position (center, intermediate, edge, and harvest area) as the first sub-plot, and time (year) as the split-plot. Because we planned for all possible comparisons among positions within treatments, a Dunn–Sidak adjustment (Ury, 1976) was applied to comparisons of means to achieve an overall alpha level of 0.05. Contrasts were conducted on pooled data where there were no significant time-by-position interactions and on individual years where interactions were significant. Logarithmic transformations were applied to abundance data, as appropriate, to satisfy the assumptions of ANOVA

Two types of analyses were conducted to explore relationships between arthropods and habitat structure (Hypothesis 4). Pearson correlations were used to assess the direction and magnitude of association between individual taxa and measures of habitat structure (overstory, understory, and ground condition variables). Blocks were analyzed separately due to

marked variation in the frequency and abundance of these variables. Prior to analysis, arthropod abundance data were averaged for the two sampling years. Data were combined from all treatments within a block ($n = 75$–77 plots per block), however, edge plots were excluded because they lacked corresponding vegetation data.

In addition to these univariate tests, we used non-metric multidimensional scaling (NMS; Kruskal, 1964) to assess gradients in community composition and their correlations with habitat structure. NMS was performed on a matrix of 36 samples (block-by-treatment or position-within-treatment) and 12 taxa using Sørensen's distance measure. In the control (100%) and dispersed treatments (15%D and 40%D), samples represented the average of all traps; in the aggregated treatments (15%A and 40%A), they represented the average of trap positions (center, intermediate, or harvest area). As with Pearson correlations, edge positions were not included. Prior to analysis, data were averaged for the two years, log-transformed, and relativized by column (species) maxima to equalize the weighting of abundant and less abundant species. We used the "slow and thorough" autopilot of PC-ORD (McCune and Mefford, 1999) conducting 70 runs that yielded one- to three-dimensional solutions. Each run continued for as many as 500 iterations or until an instability threshold of 0.00001 was reached. We selected a final two-dimensional solution with a stress of 11.50 (final instability = 0.00004) based on comparisons of final stress values for the best solutions at each dimensionality. A Monte Carlo test was performed to compare the stress of the final solution with those obtained from 50 runs of randomized data (McCune and Grace, 2002). Pearson correlations between sample scores on the NMS axes and habitat variables were displayed as a biplot of vectors on the sample ordination (McCune and Grace, 2002); only variables with strong correlations ($r > 0.50$) are reported. Multivariate analyses were conducted with PC-ORD version 4.28 (McCune and Mefford, 1999); all other analyses were performed with SAS version 9.1 (SAS Institute, Inc. 2003).

3. Results

3.1. Overall abundance and community composition

Two years of trapping yielded >25,000 spiders (at least 19 families) and >12,000 carabid beetles (at least 31 species) (Appendix A). More than half of all spiders belonged to the family Lycosidae (diurnal running, or wolf spiders), followed by Gnaphosidae (nocturnal running spiders; 14%), Linyphiidae (sheet-web builders; 6%), Agelenidae (funnel-web builders; 6%) and Antrodiaetidae (burrowing trap-door spiders; 6%). Most remaining families each comprised <3% of individuals. *Pardosa dorsalis* and *P. dorsuncata*, characteristic of disturbed habitats, dominated the Lycosidae (93%) and were the most common taxa overall (49%). Among Gnaphosidae, the habitat generalists, *Zelotes fratris* (29%) and *Z. puritanus* (23%), were most numerous and together with *Pardosa* spp. accounted for ~60% of spiders. Opiliones (harvestmen) comprised 26% of all arachnids.

More than 85% of carabid beetles were comprised of five species: *Scaphinotus angusticollis* (a snail-feeding specialist, 39%), *P. herculaneus* (16%), *Carabus taedatus* (14%), *P. protractus* (12%) and *Zacotus matthewsii* (5%) (Appendix A). All but *C. taedatus* (which is common in open, grassy habitats) are typical of forest-interior environments.

3.2. Responses to level and pattern of retention

As a group, spiders responded positively to harvest. Their abundance among harvest treatments averaged >50% higher than controls in 2003, and more than twice as high as controls in 2004 (Table 1; Fig. 1). Lycosidae and Gnaphosidae, characteristic of open or xeric habitats, showed large increases in abundance (6.3–7.5 times greater than in controls). In contrast, Linyphiidae, Hahniidae, and Opiliones, characteristic of interior forest, were sensitive to harvest. In 2003, their abundances were 57–84% lower than in controls

Table 1
Results of split-plot ANOVA testing effects of treatments on activity-density of predatory litter arthropods

Arthropod category	Treatment ($F_{4,12}$)	Year ($F_{1,15}$)	Treatment × year ($F_{4,15}$)
Araneae (total spiders)	8.63*	24.75*	4.50*
Lycosidae	9.57*	0.24	2.84
Linyphiidae	18.11*	19.85*	4.43*
Gnaphosidae	8.66*	4.33	0.99
Hahniidae	6.29*	14.69*	5.55*
Agelenidae	4.61*	25.91*	0.88
Antrodiaetidae	1.99	18.49*	0.39
Opiliones	10.37*	41.21*	3.37*
Carabidae (total carabids)	4.81*	1.62	2.85
Scaphinotus angusticollis	6.54*	0.21	2.39
Pterostichus herculaneus	3.56*	13.37*	1.31
Carabus taedatus	1.11	1.74	1.87
Pterostichus protractus	2.87	0.57	0.05
Zacotus matthewsii	14.76*	1.65	0.31
Species richness (Carabidae)	7.07*	4.28	0.68

Asterisks (*) denote significant effects ($P < 0.05$). Analyses were limited to taxa that comprised >5% of individuals within a community (spiders or carabid beetles). Taxa are ordered as in Figs. 1 and 2.

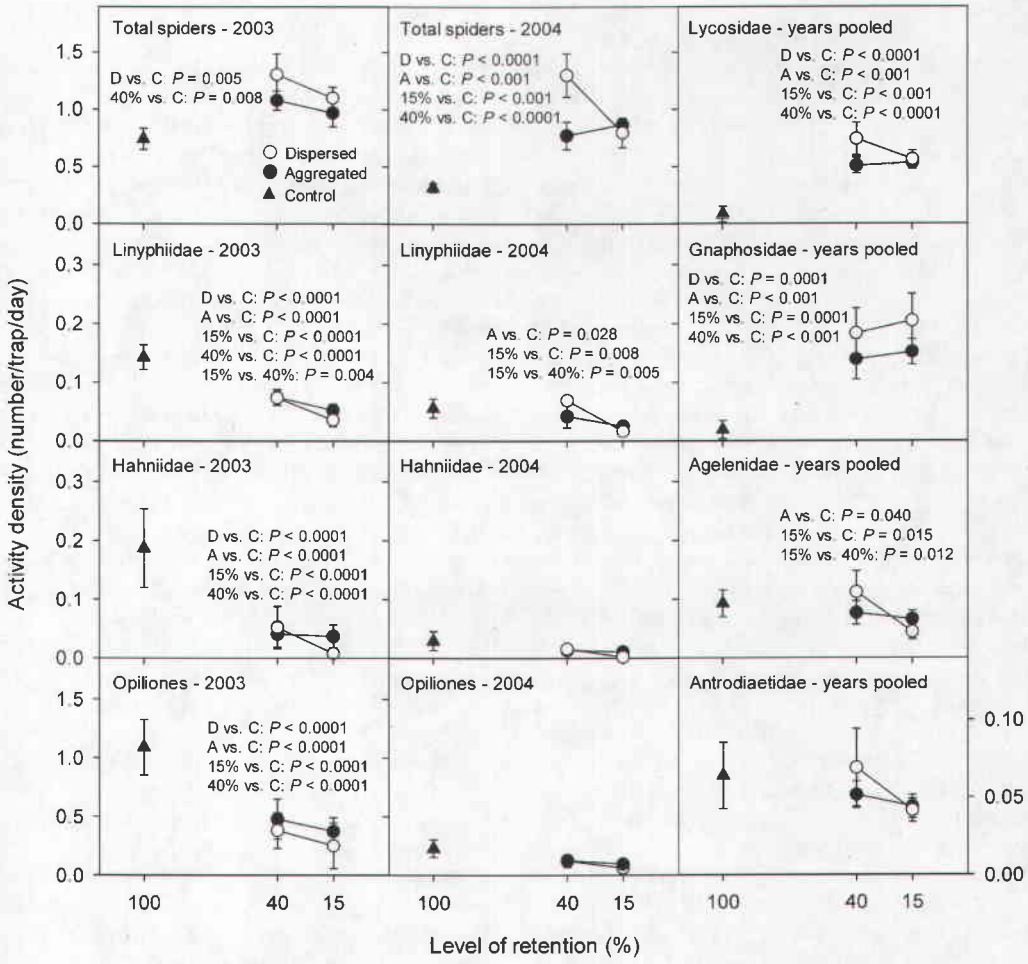

Fig. 1. Abundance (mean ± 1 S.E.; $n = 4$) of arachnids among treatments. Data from 2003 and 2004 are shown separately for groups with a significant treatment-by-year interaction in the split-plot ANOVA (see Table 1). *P* values are from *a priori* contrasts (*t*-tests). Treatment codes: C, control; A, aggregated retention; D, dispersed retention; 15%, 15% retention; 40%, 40% retention.

(Fig. 1). Increases were less evident in 2004, largely due to declines in the controls. Level of retention, however, had surprisingly little affect on the magnitude of response (Hypothesis 1). Only two groups, Linyphiidae and Agelenidae, had significantly lower abundance at 15 than at 40% retention (Fig. 1). Contrary to our prediction (Hypothesis 2), pattern of retention had no effect on the abundance of any group of spiders (Fig. 1).

In contrast to expectation, carabid species showed significant declines in the harvest treatments, both in abundance and richness (Table 1; Fig. 2). On average, abundance was 60% lower in harvest treatments than controls, reflecting declines in the two most common forest species, *S. angusticollis* and *P. herculaneus* (Fig. 2). Similarly, richness (no. species/trap/day) was ~40% lower in harvest treatments than in controls. Similar to spiders, level and pattern of retention had little effect on the magnitude of response. Only *Z. matthewsii* showed lower abundance at 15 than at 40% retention and there were no differences in richness or abundance of carabids between aggregated and dispersed treatments.

3.3. Responses to habitat edges in aggregated treatments

As predicted, we observed significant variation in abundance of arthropods across the edges of forest aggregates (Hypothesis 3) (Figs. 3 and 4); effects were comparable at both levels of retention (non-significant treatment-by-position interaction; Table 2). As a group, spiders showed greater abundance at intermediate and edge positions than at aggregate centers (Fig. 3). These trends reflected the combined responses of Lycosidae and Gnaphosidae—consistent with our prediction that taxa adapted to warmer/drier conditions would increase near the edge (Hypothesis 3a). Conversely, the remaining groups, characteristic of interior forest, showed gradual declines with proximity to edge (Fig. 3). The most pronounced effects were observed for Hahniidae (all *Cryphoeca exlineae*) and Opiliones (2003); their abundances declined by as much as 60% at intermediate positions (~15 m from the edge; Fig. 3). As a result of these edge effects, open-habitat species (Lycosidae and Gnaphosidae) were 2.1–2.4 times as abundant in forest aggregates as in controls, and forest-interior species (Opiliones,

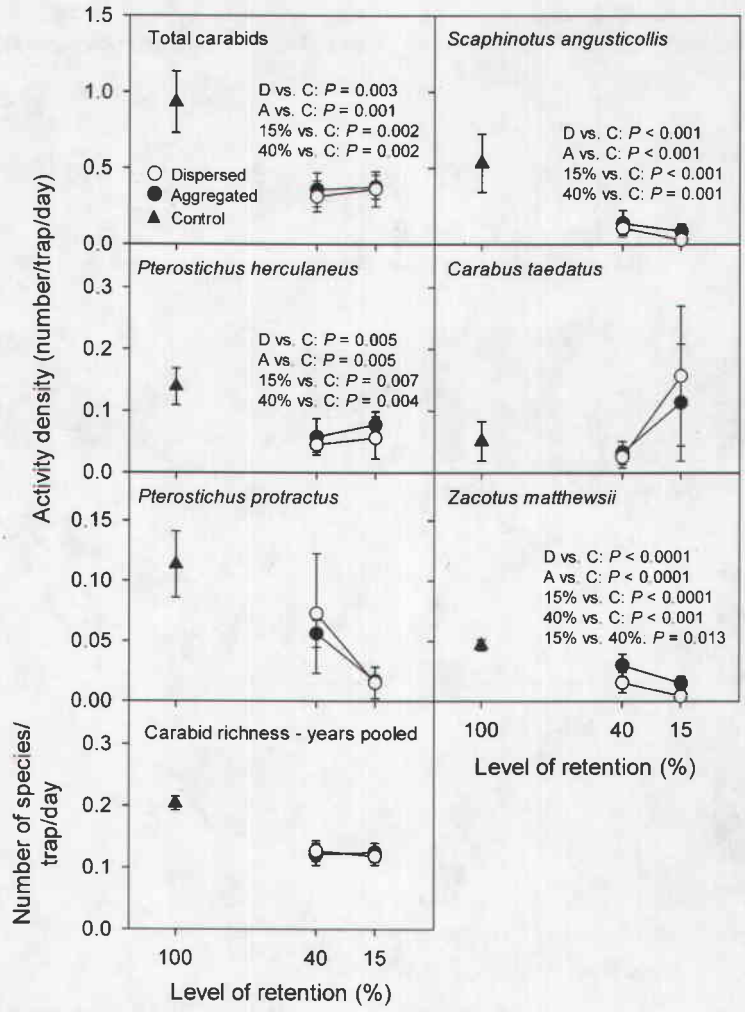

Fig. 2. Abundance and species richness (mean ± 1 S.E.; $n = 4$) of carabid beetles. See Fig. 1 for other details.

Table 2
Results of split–split-plot ANOVA testing predatory litter arthropod responses within aggregated-retention treatments

Arthropod category	Treatment ($F_{1,3}$)	Position ($F_{3,18}$)	Treatment × position ($F_{3,18}$)	Year ($F_{1,24}$)	Treatment × year ($F_{1,24}$)	Position × year ($F_{3,24}$)	Treatment × position × year ($F_{3,24}$)
Araneae (total spiders)	0.15	5.81*	0.16	29.94*	2.55	2.68	0.37
Lycosidae	0.00	9.55*	0.04	0.06	6.83*	1.25	0.12
Gnaphosidae	0.01	13.04*	0.31	13.18*	0.68	1.38	0.60
Linyphiidae	1.61	8.76*	0.23	13.70*	0.07	0.81	0.48
Agelenidae	0.27	9.83*	0.37	10.97*	0.01	0.56	0.17
Antrodiaetidae	0.23	1.84	0.38	11.61*	0.18	0.31	0.18
Hahniidae	0.17	5.52*	0.46	12.93*	0.10	4.30*	0.10
Opiliones	0.01	8.79*	0.34	57.90*	0.00	3.88*	0.58
Carabidae (total carabids)	0.01	7.29*	1.14	0.00	1.14	1.03	0.43
Scaphinotus angusticollis	0.36	3.38*	0.98	0.72	0.03	0.24	0.78
Pterostichus protractus	7.02	7.21*	2.46	3.33	1.11	2.31	1.32
Zacotus matthewsii	5.31	13.30*	0.78	3.21	0.35	0.81	0.08
Carabus taedatus	0.71	2.73	0.26	1.00	2.37	0.21	0.94
Pterostichus herculaneus	0.60	1.94	0.03	12.45*	0.00	1.40	0.27
Species richness (Carabidae)	0.18	13.47*	1.40	0.99	0.91	0.99	0.02

Asterisks (*) denote significant effects ($P < 0.05$). Analyses were limited to taxa that comprised >5% of individuals within a community (spiders or carabid beetles). Taxa are ordered as in Figs. 3 and 4.

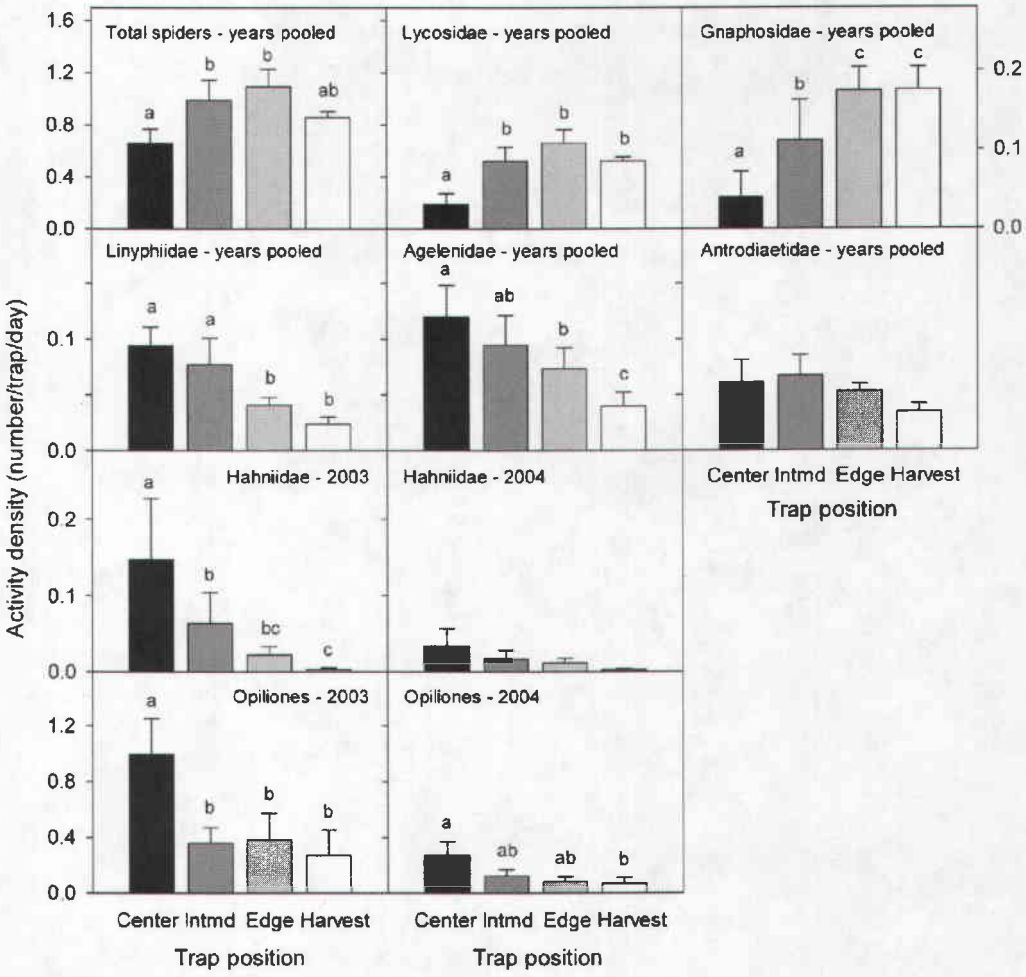

Fig. 3. Abundance (mean + 1 S.E.; $n = 4$) of arachnids among trap positions within aggregated treatments. Data from 2003 and 2004 are shown separately for groups with a significant position-by-year interaction in the split–split-plot ANOVA (see Table 2). Data from both treatments (15%A and 40%A) were pooled because treatment-by-position interactions were non-significant. Positions with different letters are significantly different at $\alpha = 0.05$ based on *a priori* contrasts with a Dunn–Sidak multiple-comparison adjustment. Trap position codes: Center, aggregate center; Intmd, intermediate (~40 m from center, ~15 m from edge); Edge, edge; Harvest, harvest area.

Linyphiidae, and Hahniidae) were 38–45% less abundant, consistent with our prediction (Hypothesis 3b).

Carabids also showed a significant responses to edge (Table 2, Fig. 4). Consistent with expectation, abundance of three forest-dependent species (*S. angusticollis*, *P. protractus*, and *Z. matthewsii*), was greater at center and/or intermediate positions than at edge and/or harvest-area positions (Fig. 4). However, similar trends were not apparent for *C. taedatus* and *P. herculaneus* (non-significant effect of position; Table 2; Fig. 4). Although we predicted greater carabid richness (no. species/trap/day) near the edge (Hypothesis 3a), we observed the opposite trend (Table 2, Fig. 4).

3.4. Responses to local habitat structure

3.4.1. Individual taxa

We detected significant correlations between the abundance of individual arthropod groups and local measures of habitat structure (Fig. 5). Tree density and basal area were the strongest and most consistent predictors of arthropod abundance. As predicted (Hypothesis 4), forest-dwelling species were positively correlated with both overstory variables, but open-habitat species, including spiders as a group, Gnaphosidae, and Lycosidae, showed negative correlations. In addition, with a few exceptions (Gnaphosidae and *C. taedatus* at Paradise Hills), arthropods exhibited positive correlations with cover of fine litter (intact forest floor). Conversely, most groups showed negative correlations with cover of mineral soil; Gnaphosidae was the only group that was positively correlated with mineral soil. Hahniidae, Linyphiidae, Opiliones, and most carabid taxa—groups adversely affected by harvest—displayed significant negative correlations with herb cover. In contrast, open-habitat taxa showed positive correlations with herb cover. Correlations with most other habitat variables (tall shrubs, understory hardwoods and conifers, coarse litter, and volume of CWD) were less frequent and less consistent among blocks.

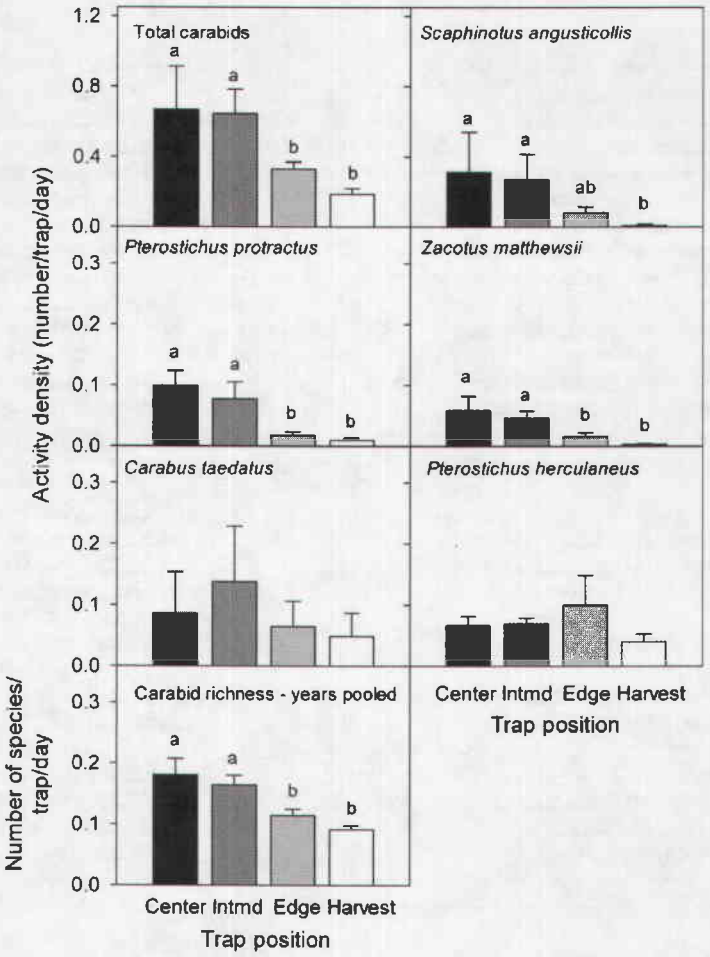

Fig. 4. Abundance and species richness (mean + 1 S.E.; $n = 4$) of carabid beetles among trap positions within aggregated treatments. See Fig. 3 for other details.

3.4.2. Community composition

Axes one and two of the NMS ordination accounted for 53 and 41% of the total variation in the data (Fig. 6). Samples representing harvest areas or low levels of dispersed retention (15%D) had low scores on NMS1 and were highly correlated with cover of mineral soil. Taxa associated with these samples included Gnaphosidae, Lycosidae, and *C. taedatus*. Samples representing controls (100% retention) and center or intermediate positions within aggregates had higher scores on NMS1 (although their overall spread was fairly large). These samples were highly correlated with tree density and basal area, as well cover of fine litter and tall shrubs. Associated taxa included Agelenidae, Antrodiaetidae, Hahniidae, Linyphiidae, Opiliones and forest-dwelling carabids, *S. angusticollis*, *P. herculaneus*, *P. protractus* and *Z. matthewsii*. Finally, samples representing moderate levels of dispersed retention (40%D) exhibited intermediate scores on NMS1. Volume of CWD and cover of herbs, understory hardwoods, understory conifers, and coarse litter all showed weak correlations with both ordination axes ($r < 0.5$).

4. Discussion

4.1. Arthropod responses to level and pattern of retention

Harvest treatments had large, but highly variable effects on litter arthropods, indicating that taxa responded differently to changes in habitat conditions. Densities of Lycosidae and Gnaphosidae, both dominated by species with an affinity for open and xeric habitats, increased dramatically in all harvest treatments. Other less common taxa, including jumping spiders (Salticidae) and crab spiders (Thomisidae), were also more numerous in open habitats, whereas forest specialists such as Linyphiidae and Opiliones declined. These changes are very similar to those documented by McIver et al. (1992) who studied succession of litter spiders 4–31 years after clearcut logging of 29 sites in western Oregon. Huhta (1971, 1976) reported similar changes 3–13 years after clear-cutting and thinning in boreal forests of Finland—namely, disappearance of forest species and arrival of open-habitat species (although total abundance of spiders decreased). Likewise, Greenberg and

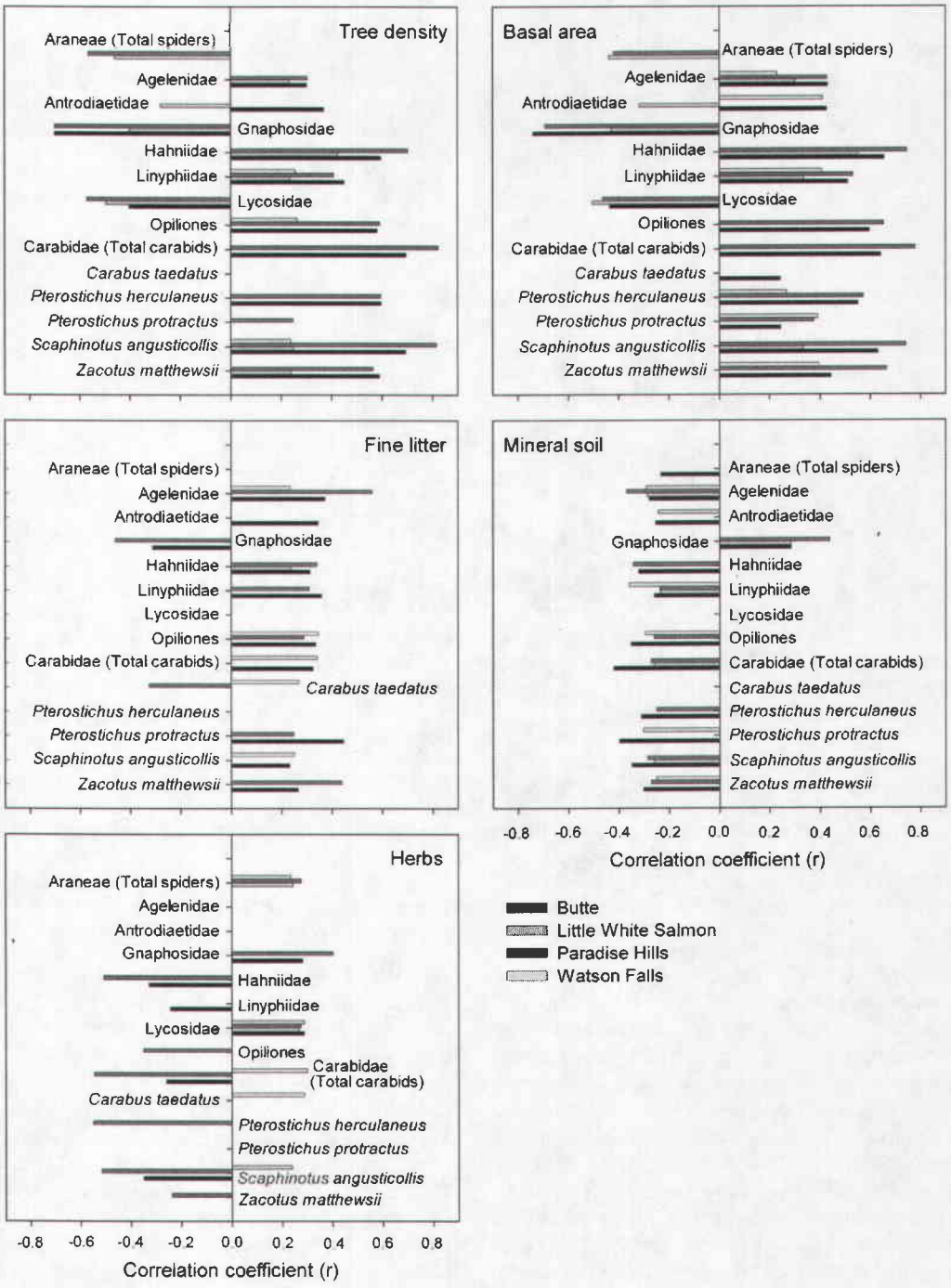

Fig. 5. Pearson correlation coefficients between activity-density of predatory litter arthropods and selected habitat variables. Plot-level data were averaged for both sampling years and combined from all treatments in each block (n = 75–77 per block). See *Data analyses* for other details. Results are shown only for habitat variables present in >10% of plots across blocks; taxa are limited to those that comprised >5% of individuals within a community (spiders or carabid beetles); only significant correlations ($P < 0.05$) are shown.

McGrane (1996) found significantly lower abundance of Opiliones and *Lycosa* spp. in clearcuts (5–7 years old) than in mature pine forest of Florida.

Total abundance and richness of carabids declined significantly in all harvest treatments. These declines did not support our prediction, nor are they consistent with previous studies that documented both short- and longer-term increases in carabid abundance and/or richness after forest cutting or fragmentation, primarily due to influx of open-habitat species (Niemelä et al., 1993; Heliölä et al., 2001; Koivula et al., 2002).

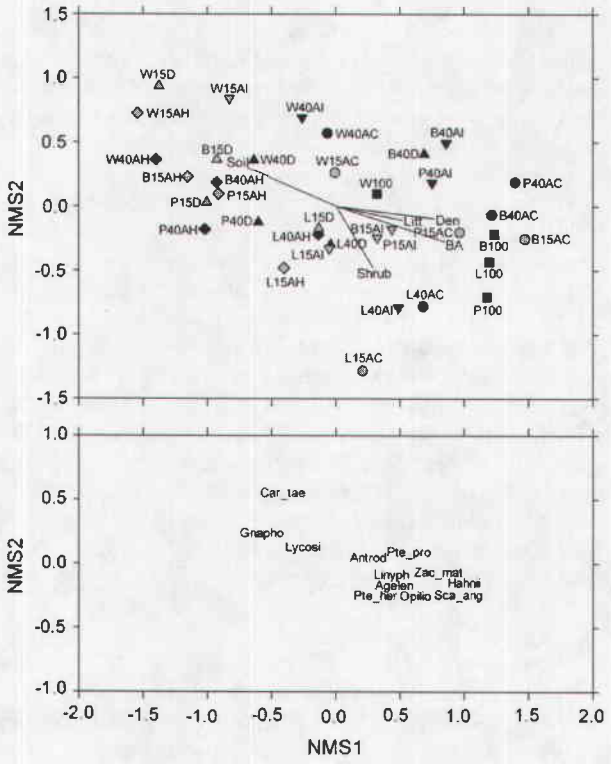

Fig. 6. NMS ordination of predatory litter arthropod samples (upper panel) and taxa (lower panel). Samples represent the average composition of traps within a block-by-treatment (or position-within-treatment); data from 2003 and 2004 were pooled. Pearson correlations between habitat variables and ordination axes are represented by vectors on the sample ordination; only variables with strong correlations ($r \geq 0.5$) are presented. Samples are coded by block (B, Butte; P, Paradise Hills; L, Little White Salmon; W, Watson Falls); level of retention (15, 15%; 40, 40%); pattern of retention (A, aggregated; D, dispersed); and position within aggregated treatments (C, center; I, intermediate; H, harvest area). Edge positions were not included (see *Data analyses*). Habitat variable codes: BA, basal area; Den, tree density; Litt; cover of fine litter; Shrub, cover of tall shrubs; Soil, cover of mineral soil. Codes for taxa: Agelen, Agelenidae; Antrod, Antrodiaetidae; Gnapho, Gnaphosidae; Hahnii, Hahniidae; Linyph, Linyphiidae; Lycosi, Lycosidae; Opilio, Opiliones; Car_tae, *Carabus taedatus*; Pte_her, *Pterostichus herculaneus*; Pte_pro, *Pterostichus protractus*; Sca_ang, *Scaphinotus angusticollis*; Zac_mat, *Zacotus matthewsii*.

Interestingly, early-seral species were present on our sites (e.g., *Trachypachus holmbergi*, *Calosoma tepidum*, *Harpalus affinis*, and *Amara patruelis*; Appendix A), but were too infrequent 5–7 years after harvest to balance the loss of more common forest taxa. Declines among forest specialists were consistent with previous studies (Niemelä et al., 1993; Heliölä et al., 2001; Koivula et al., 2002). Although they maintained limited presence in all treatments, possibly an adaptation to natural disturbance (Koivula, 2002), their long-term persistence is uncertain. In boreal forests of western Canada, Niemelä et al. (1993) reported almost complete disappearance of mature-forest specialists 2–9 years after clear-cutting, with no sign of recovery after 27 years.

Despite significant responses of many groups to harvest, level of retention generally had little effect on the magnitude of response. However, several forest specialists (Linyphiidae, Agelenidae, and *Z. matthewsii*) showed greater declines at 15 than at 40% retention, suggesting worsening of habitat conditions for these disturbance-sensitive species. Determining the level of retention or size of opening that does not result in adverse effects may be difficult. For example, in Douglas-fir plantations in western Oregon, Yi and Moldenke (2005) documented declines in carabids 5–7 years after thinning to 40% of initial density, but no difference in decline between stands thinned to 40 and 20%. Similarly, although the predator assemblage differed from that of uncut *Picea* forests in southern Finland (Koivula, 2002), Pihlaja et al. (2006) found no differences in abundance or richness of carabids between small clearcuts (2 ha) and artificial gaps (0.16 ha).

Surprisingly, pattern of retention was not a significant determinant of arthropod response. We expected dispersed treatments to support greater abundance of species adapted to warmer/drier conditions and lower abundance of forest-interior taxa, but we were unable to detect these effects. Two trends may explain this result. First, in these forests, summer microclimates (air and soil temperatures and soil moisture) are surprisingly similar among dispersed treatments (15%D and 40%D) and the harvested areas of aggregated treatments (Heithecker and Halpern, 2006). Thus, responses of open-site species to increases in temperature are likely to be similar. Second, the potential for 1-ha sized aggregates to support forest-interior species was compromised by edge effects (see below), yielding generally similar declines within aggregated and dispersed treatments.

4.2. Arthropod responses to habitat edges

We observed strong gradients in arthropod response within forest aggregates, consistent with patterns documented in studies of clearcut-forest edges (Work, 2000; Heliölä et al., 2001; Baker et al., 2007). Based on extensive trapping along transects from clearcut into old-growth Douglas-fir forests in Oregon, Work (2000) identified four types of edge response: (1) "edge-input" taxa showed greatest abundance in clearcuts and declined with distance into forest, (2) "edge-phobic" taxa displayed the opposite trend—peak abundance in old-growth and declining abundance toward the edge, (3) "edge-philic" taxa displayed maximum abundance at the edge, and (4) "edge-insensitive" taxa showed equal probability of capture across the entire gradient. In our study, Lycosidae and Gnaphosidae were the only major taxa that displayed an edge-input response, which may reflect their preference for drier and warmer habitats (Parsons et al., 1991; McIver et al., 1992; Work, 2000). Although Work (2000) characterized *C. taedatus* as an edge-input species, we were unable to detect a significant response to edge in these forests.

As expected, *P. protractus*, *S. angusticollis*, and *Z. matthewsii*, carabid species that are adapted to climatically more stable habitats of interior forest (Lindroth, 1969), showed clear edge-phobic responses, consistent with the findings of Work (2000). For *S. angusticollis*, this trend may also reflect its predation of mollusks (Lindroth, 1969; Parsons et al., 1991; Work, 2000), which are typically found in cooler,

moister habitats. Similar to previous studies (Work, 2000; Heliölä et al., 2001; Baker et al., 2007) we found no clear edge specialists.

Variation in response to habitat edges may reflect gradients in abiotic and biotic factors (Spence et al., 1996; Work, 2000). For example, at our sites, solar radiation and air and soil temperature were elevated at the edge, but declined steeply, stabilizing within 15–30 m at levels comparable to those in undisturbed forest; in contrast, soil moisture showed little edge-related variation (Heithecker and Halpern, 2007). Changes in plant abundance and composition were largely limited to the edge: incursion of early-seral species and declines among herbs and liverworts extended only 5–10 m (Nelson and Halpern, 2005a,b). These were also the distances to which harvest operations resulted in deposition of slash and disturbance of the forest floor. Smaller-scale manipulative experiments may be necessary to understand the relative importance of these and other factors for shaping edge-related responses of litter arthropods

As predicted, forest-dependent taxa including Hahniidae and *P. herculaneus* were 30 to as much as 50% less abundant in forest aggregates than in controls. These trends suggest that 1-ha aggregates may not be sufficient to maintain late-seral species at levels found in undisturbed forest. In a study of edge effects on ground-dwelling beetles in Tasmanian eucalyptus forest, Baker et al. (2007) documented declines in abundance that extended 10–25 m, leading to a similar conclusion—small, <1 ha forest remnants may provide almost no unaffected, interior habitat for forest-dependent arthropods. At the same time that forest-interior species showed declines within our aggregates, species characteristic of open-habitats were caught in higher numbers than in controls; abundance of Lycosidae and Gnaphosidae more than doubled. Spence et al. (1996) observed similar patterns of incursion among carabid habitat generalists in boreal forest fragments in Canada.

4.3. Relationships with habitat structure

Despite our inability to detect strong effects of level or pattern of retention on treatment-scale responses of arthropods, we detected strong correlations at a local (plot) scale with many components of habitat structure. It is unclear whether habitat variables were of direct ecological benefit or were simply indicators of habitat conditions either favored or avoided by particular taxa. For example, Hahniidae, Linyphiidae, *S. angusticollis*, *P. herculaneus*, and *Z. matthewsii* were positively correlated with tree density and basal area, but negatively correlated with cover of herbs (which were more abundant in harvest treatments than controls). On the other hand, Lycosidae and Gnaphosidae were positive correlated with herb cover, but negatively correlated with measures of overstory structure, supporting the general affinity of these taxa for open habitats. As expected, forest-dependent taxa consistently showed positive correlations with cover of fine litter and negative correlations with mineral soil. Gnaphosidae was the only group associated with mineral soil, suggesting a strong preference for disturbed habitats.

The results of NMS underscore these findings. Samples representing low levels of dispersed retention or harvest areas within aggregated treatments were characterized by open-site species and greater cover of mineral soil. In contrast, samples from controls and forest aggregates were characterized by forest specialists and greater cover of forest litter.

With the exception of tree density and basal area, the predictive power of most habitat variables in our study was generally low. This may indicate a limitation in our sampling design, namely the different scales at which arthropods and habitat structure were measured. Arthropods were collected with a single small trap, whereas vegetation structure and ground conditions were sampled with multiple subplots over greater areas (Halpern et al., 2005). It is also possible that habitat variables were only partly successful at capturing the ecological factors most relevant to these arthropods. Prey supply (McIver et al., 1992; Koivula et al., 2002) or interference with other predators such as ants (McIver et al., 1992; Heliölä et al., 2001; Koivula, 2002; Koivula et al., 2002) may also shape the distributions of litter predators.

4.4. Management implications

This large-scale experiment provides a unique opportunity to assess responses of litter-dwelling spiders and carabid beetles to levels and patterns of retention relevant to forest management. A cursory assessment of the general increase in arthropod abundance would suggest favorable effects of harvest. Clearly, however, these positive effects were limited to several groups, indeed several species, of early-seral spiders that dominated our samples, namely *Pardosa* spp. and *Zelotes* spp. that are common in clearcuts and other disturbed sites in this region (Parsons et al., 1991; McIver et al., 1992; Work, 2000). However, the Northwest Forest Plan and accompanying prescriptions for retention harvest emphasize maintenance of species associated with late-seral forests (USDA and USDI, 1994). Our results suggest that 5–7 year after harvest, none of the treatments, including those with levels of retention as high as 40%, provide suitable habitat for the forest-dependent arthropod predators that we studied. Moreover, the strong edge-related declines in aggregates as large as 1 ha suggest that smaller (0.2–1.0 ha) aggregates permitted under current federal standards are unlikely to support many taxa characteristic of older forests.

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Appendix A

See Table A1.

Table A1
Total number of predatory litter arthropods by treatment or position within treatment

Arthropod taxa		40%A					15%A					
	100% (60)	Center (19)	Intmd (13)	Edge (32)	Harvest (32)	40%D (60)	Center (8)	Intmd (16)	Edge (24)	Harvest (32)	15%D (60)	Total
Araneae (total spiders)	2,416	887	941	2,603	1,872	6,079	393	1,159	2,024	2,125	4,528	25,027
Lycosidae	286	280	493	1,568	1,138	3,409	114	628	1,267	1,287	2,652	13,122
Gnaphosidae	72	52	80	387	334	809	20	140	309	463	991	3,657
Agelenidae	446	164	102	183	94	540	69	101	131	99	215	2,144
Linyphiidae	483	129	78	116	70	336	48	78	64	48	130	1,580
Antrodiaetidae	301	75	60	129	92	333	41	74	92	69	196	1,462
Hahniidae	517	101	40	58	4	172	64	53	17	11	24	1,061
Thomisidae	75	17	36	43	28	203	7	39	47	27	90	612
Other	148	39	28	38	40	127	18	17	40	36	55	586
Amaurobiidae	57	23	14	22	7	99	9	16	14	17	25	303
Salticidae	8		2	29	39	23	2	4	23	37	111	278
Theridiidae	12	2		17	9	9		1	5	7	22	84
Liocranidae	8	3	2	6	2	8		3	4	2	6	44
Philodromidae	3	1	3	5	4	5		1	4	3	8	37
Anyphaenidae			1		5	2		1	5	6	1	21
Clubionidae					4	3				4	1	12
Corinnidae								3	2	4	1	10
Araneidae			2	2	1	1	1					7
Oxyopidae					1					3		4
Dictynidae		1								2		3
Opiliones	3,191	822	216	631	472	1,224	392	365	371	354	748	8,786
Carabidae (total carabids)	4,503	779	695	691	344	1,543	537	625	676	499	1,521	12,413
Scaphinotus angusticollis (F)	2,700	355	420	274	45	525	291	175	101	3	142	5,031
Pterostichus herculaneus (F)	635	73	45	187	71	202	49	104	199	125	268	1,958
Carabus taedatus (O)	199	40	71	46	46	133	95	227	205	137	569	1,768
Pterostichus protractus (F)	548	172	67	48	25	380	39	28	28	16	72	1,423
Zacotus matthewsii (F)	202	93	51	48	11	77	30	38	20	3	21	594
Trachypachus holmbergi (O)		2	1	33	63	36			12	37	126	310
Scaphinotus marginatus (F)	67	9	21	14	13	33	4	14	22	9	37	243
Calosoma tepidum (O)				1	5		2		33	72	86	199
Pterostichus lama (F)	20	2	3	10	26	21	1	6	18	24	43	174
Omus dejeani (F)	71					20	4	17	13	4	22	151
Harpalus affinis (O)			3	1	9	18			2	14	48	95
Cychrus tuberculatus (F)	7	3	1	10	4	14	1	1	5	11	14	71
Scaphinotus rugiceps (F)	9	5	1			27	8	5	7		5	67
Syntomus americanus (O)				6	6	7			2	26	16	63
Pterostichus inanis (F)	9	16	6	2		17	2	1		1	2	56
Pterostichus tuberculofemoratus (F)	18	4	5	4		12	3	1	4	2	3	56
Notiophilus sylvaticus (O)	9	1		4		7	3	4	2	4	2	36
Amara patruelis (O)						1				3	23	27
Pterostichus lattini (F)	6	3				7	2	1				19
Cicindela longilabris (O)				2	5	1				1	9	18
Amara latior (O)					9					3	3	15
Promecognathus crassus (G)				1	1	1	2	1	2	3	3	14
Pterostichus amethystinus (F)	1	1							1		4	7
Scaphinotus angulatus (F)	2					3	1				1	7
Harpalus viridiaeneus (O)					3					1		4
Pterostichus melanarius (O)					1			1				2
Calathus fuscipes (O)											1	1
Calosoma luxatum (O)											1	1
Nebria sp. (G)					1							1

Table A1 (*Continued*)

Arthropod taxa		40%A					15%A					
	100% (60)	Center (19)	Intmd (13)	Edge (32)	Harvest (32)	40%D (60)	Center (8)	Intmd (16)	Edge (24)	Harvest (32)	15%D (60)	Total
Pterostichus adstrictus (G)								1				1
Pterostichus pumilus (F)						1						1

Includes data from 2003 and 2004. Positions within aggregates are center, intermediate (Intmd), edge, or harvest areas (Harvest). Sample sizes are in parentheses and represent the total number of traps in all four blocks. Letters in parentheses after carabid taxa indicate habitat preference: F, forest; O, open habitat; G, habitat generalist.

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