

Effects of green-tree retention on abundance and guild composition of corticolous arthropods

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ABSTRACT

Corticolous, or bark-dwelling, arthropods may be useful indicators of environmental changes associated with variable-retention harvests. We studied the effects of varying levels and patterns of green-tree retention on the community composition of bark-dwelling arthropods. Arthropods were sampled with crawl traps installed on 280 live trees and 260 snags (all Douglas-fir) at three locations (experimental blocks) in the western Cascade Range of Oregon and Washington. Sampling coincided with the breeding season of the brown creeper (*Certhia americana*), a primary avian predator, in 2003 and 2004. Within each block, arthropods were collected in five, 13-ha experimental units—a control (uncut forest) and four treatments representing one of two levels of retention (15% vs. 40% of original basal area) and one of two spatial patterns (trees dispersed vs. aggregated in 1-ha patches). In total, 166,234 arthropods – predominantly Collembola (70%) – were collected over the course of study. With the exception of Collembola, arachnids were the most abundant arthropods (23% of individuals); spiders (Araneae) accounted for >95% of arachnids. Other common insect orders included adult Coleoptera (16%), Hemiptera (15%), and Diptera (12%). For all insects combined (excluding Collembola), activity-density (daily catch per trap, an index of abundance) was significantly greater in harvest treatments than in controls. The greatest increases were found at 15% retention-densities were 2.6 times greater than in controls and 1.8 times greater than at 40% retention. Pattern of retention did not affect abundance of most arthropod groups, although two families of spiders (Linyphiidae and Thomisidae) were more abundant in dispersed than in aggregated treatments. Traps on live trees yielded 2.2 times more arthropods than did traps on snags likely reflecting differences in food resources. A high proportion of herbivorous taxa showed negative associations with local density and basal area of overstory trees and positive associations with cover of herbs, suggesting that many corticolous arthropods originate in the understory and respond positively to increases in vegetation cover following retention harvests. The numerical dominance of Collembola and high abundance of Diplopoda also suggest important ecological ties between communities of corticolous and detrital (litter-dwelling) arthropods.

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1. Introduction

Green-tree or structural retention, in which live trees and snags are retained through timber harvest, has become an increasingly common method of managing forests for both production and ecological values (Franklin et al., 1997; Aubert et al., 1999, in press; Vanha-Majamaa and Jalonen, 2001; Beese et al., 2003; Rosenvald

and Lohmus, 2008). Live trees and snags are retained within harvest units to moderate microclimatic conditions, to enrich the structural and biological diversity of the regenerating forest, and to enhance connectivity with the larger landscape (Franklin et al., 1997). Clearly, the degree to which these goals are achieved will depend on the amount of structure retained (or removed), the characteristics of these structures, their spatial arrangement, and other factors.

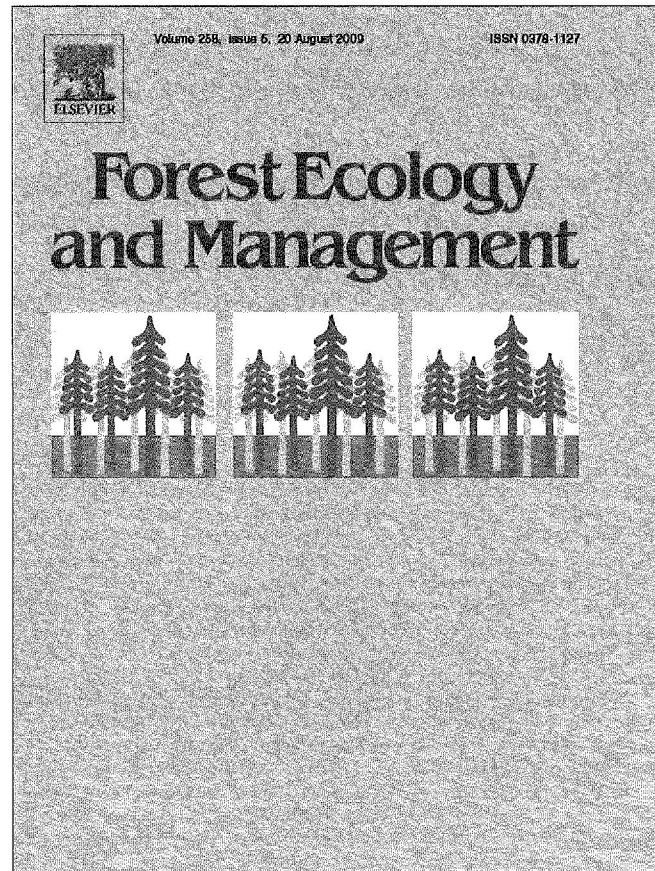
Over the past two decades, considerable research has been devoted to understanding the responses of forest organisms to green-tree retention in temperate and boreal ecosystems (see review in Rosenvald and Lohmus, 2008). However, the vast majority of research has been directed at wildlife (e.g., Chambers et al., 1999; Sallabanks et al., 2000; Schieck et al., 2000; Sullivan

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and Sullivan, 2001; Citzén et al., 2007) and ground vegetation (e.g., Beese and Bryant, 1999; Deal, 2001; Halpern et al., 2005; MacDonald and Fenniak, 2007). Arthropods are less well studied, despite their significant contributions to biological diversity, and most work to date has focused on litter arthropods (Huhta et al., 1967; McIver et al., 1992; Niemela et al., 1993; Hoekstra et al., 1995; Koivula, 2002; Moore et al., 2002; Siira-Pietikainen et al., 2003; Halaj et al., 2008). In comparison, corticolous, or bark-dwelling, arthropods have received minimal attention despite their direct dependence on the structures targeted for retention (live trees and snags).

Past research suggests that bark-dwelling arthropods may be sensitive indicators of the environmental changes that result from manipulation of forest structure. For example, Duguay et al. (2000) reported a significant decrease in the biomass of bark-dwelling arthropods on remnant trees in clearcuts (relative to undisturbed forests), but an increase in selectively harvested (seed-tree) stands. Peck and Niwa (unpublished data) observed higher densities of spiders, ants, and mites on tree boles in thinned than in unthinned stands, but lower densities of Collembola and insect larvae. Changes in arthropod composition and abundance may reflect altered microclimates (e.g., increased radiation, heating, or air movement), or indirect effects on understory habitats that serve as sources for colonization of trees. Correlative studies further suggest that corticolous arthropods are sensitive to habitat features that are influenced by stand structure, including tree diameter (Mariani and Manuwal, 1990; Adams and Morrison, 1993; Hanula et al., 2000), bark thickness (Mariani and Manuwal, 1990; Hanula et al., 2000), and diversity or density of understory vegetation (Duguay et al., 2000; Collins et al., 2002).

Effects of retention harvests on corticolous arthropod communities may have broader ecological significance as well, through effects on higher trophic levels (e.g., avian predators). Bark-dwelling arthropods are important in the diets of bark-gleaning birds such as the brown creeper (*Certhia americana*) (Williams and Batzli, 1979; Kuitunen and Tormala, 1983; Mariani and Manuwal, 1990; Suhonen and Kuitunen, 1991). Changes in food supply may be one of several mechanisms by which changes in forest structure affect avian communities (Marzluff et al., 2000; Sallabanks et al., 2000).

In this study, we examine the responses of bark-dwelling arthropods to varying levels and spatial patterns of green-tree retention in mature, coniferous forests of western Oregon and Washington. We use a subset of experimental treatments from a regional study of structural-retention harvests, the Demonstration of Ecosystem Management Options (DEMO) Study (Aubry et al., 1999, 2004, in press). Our primary objectives are threefold: (1) to compare responses of corticolous arthropod communities to contrasting levels and patterns of overstory retention, (2) to identify the contributions of live trees and snags to these responses, and (3) to evaluate the importance of local habitat variables (e.g., tree diameter, overstory density and basal area, and cover of various understory strata) to arthropod abundance.

2. Methods

2.1. Study sites

For this study we selected three of the six experimental blocks that comprise the DEMO experiment: Watson Falls and Dog Prairie on the Umpqua National Forest in southwestern Oregon, and Little White Salmon on the Gifford Pinchot National Forest in southwestern Washington (Aubry et al., 1999). The climate of this region is characterized by warm, dry summers and cool wet winters. Annual precipitation ranges from ca. 1440 to 1970 mm (DAYMET, Thornton et al., 1997); most precipitation falls between October

and April (often as snow) resulting in an extended period of summer drought. Elevations range from 825 to 1710 m and topography varies among blocks.

Forests ranged in age from 110 to 165 years. Although the climax species differed among blocks, all stands were dominated by *Pseudotsuga menziesii* (Douglas-fir) (Halpern et al., 2005). Additional details on forest structure, understory composition, physical environment, and disturbance history can be found in Aubry et al. (1999) and Halpern et al. (2005).

2.2. Experimental design

The full design consists of six treatments randomly assigned to 13-ha experimental units in each block. Treatments differ in the level of retention (proportion of original basal area) and/or the spatial pattern in which trees are retained (dispersed vs. aggregated) (Aubry et al., 1999). We use five of these treatments in this study: an untreated control (100% retention) and four that represent factorial combinations of retention level (15% vs. 40%) and spatial pattern (trees uniformly dispersed vs. aggregated in circular 1-ha patches) (Fig. 1). In dispersed treatments (15%D and 40%D), dominant and co-dominant trees were retained in a dispersed fashion. In aggregated treatments, two (15%A) or five (40%A) patches were retained at fixed locations and all merchantable trees (>18 cm dbh) were removed from adjacent harvest areas. Harvests were completed during summer or early fall 1998.

Federal safety requirements required felling of older snags within the treated areas of all harvest units (but not within the retention patches). Thus, to meet standards of the Northwest Forest Plan, 6.5 snags/ha were subsequently created in the harvested areas of both aggregated and dispersed treatments. These were chosen from among dominant and co-dominant stems and, to the extent possible, from decadent or broken-topped trees. Mortality was induced by girdling stems at ca. 1 m height. Trees were girdled during spring or summer 1999, 1 year after harvest treatments and 4–5 years before sampling. Given the bias toward damaged trees, created snags did not differ markedly from natural snags in their bole and bark characteristics. Additional details on treatment implementation and post-harvest management activities can be found in Halpern and McKenzie (2001) and Halpern et al. (2005).

2.3. Sampling design

Arthropods were sampled with crawl traps installed on tree boles following the design of Hanula and New (1996). This highly effective technique utilizes drift fences to guide crawling arthropods upward on a tree into a collecting cup filled with preservative solution. Traps were placed 1.5–2 m from the ground surface, facing a randomly chosen direction.

Traps were installed on a random selection of 20 live trees and 20 snags in each of the control, 15%D, 40%D, and 40%A treatments. In 15%A, where fewer trees were retained in closer proximity (two 1-ha patches), sample sizes were halved to approximate the sampling effort in the other treatments. Even so, it was not possible to maintain a 1:1 ratio of live trees to snags due to small numbers of snags in some experimental units.

Trees and snags were selected using three criteria: (1) Douglas-fir only, (2) diameter (dbh) 2:50 cm, and (3) located within a previously established vegetation plot (Halpern et al., 2005). Large Douglas-fir were chosen because they are the preferred feeding substrate for bark-gleaning birds in forests of this region (Lundquist and Manuwal, 1990; Mariani and Manuwal, 1990; Weikel and Hayes, 1999). Placement within pre-existing vegetation plots permitted use of existing understory data to assess effects of local habitat structure (see Section 2.4); vegetation plots

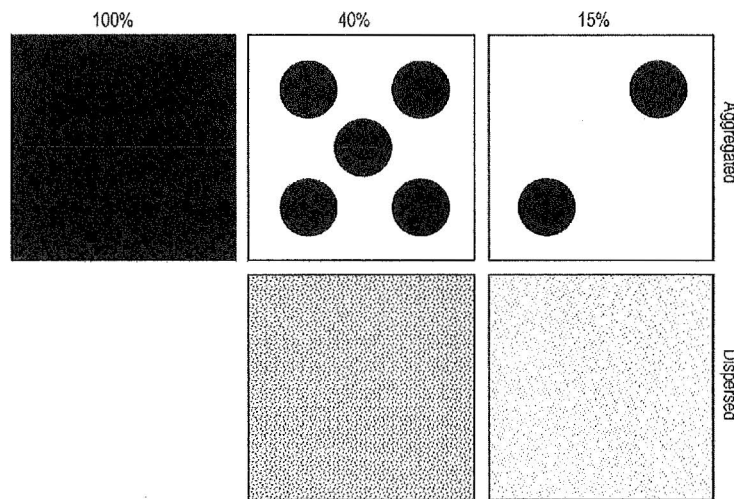


Fig. 1. Schematic representation of the five experimental treatments. Each 13-ha unit was replicated once at each block. Treatments are 100% (uncut control), 40% aggregated retention, 15% aggregated retention, 40% dispersed retention, and 15% dispersed retention. Circles in aggregated treatments represent 1-ha (56-m radius) retention patches; all merchantable trees in the surrounding matrix were cut.

were arrayed on a systematic grid of sample points spaced 40 m apart.

In aggregated treatments snags were restricted to retention patches (as were live trees); thus, all snags were remnants of the original forest. In dispersed treatments, however, many remnant snags were felled during timber harvest. To obtain a sufficient sample in these treatments, remnant snags were supplemented by snags created through girdling of live trees (35–80% of snags per experimental unit). In total, we sampled 280 live trees and 260 snags (199 remnant and 61 created snags).

Traps were installed between April and May 2003. Arthropods were collected four to six times from May through August in both 2003 and 2004 (5 and 6 years after harvest), coincident with the breeding season of the brown creeper. Traps remained open for 2–4 weeks during each sampling period. Collections were identified in the laboratory; spiders were identified to the lowest taxon possible, but non-arachnids were identified to order. Arthropod abundance was expressed as an activity-density index of relative abundance (number of individuals collected/trap/day), henceforth "abundance."

2.4. Measurements of local habitat structure

To evaluate the importance of local habitat variables on arthropod abundance, we used data from permanent vegetation plots sampled in 2003 or 2004 (Halpern et al., 2005; Maguire et al., 2006). Seven variables were considered: (1) diameter (dbh) of the sampled tree or snag; (2) density (stems/ha) and (3) basal area (m^2/ha) of overstory trees (>5 cm dbh) within a circular 0.04 ha plot; (4) total cover (%) of herbs (<1 m tall) estimated as the mean of 24, 0.2 m \times 0.5 m quadrats per plot; and total cover (%) of (5) tall shrubs (>1 m tall), (6) understory hardwoods, and (7) understory conifers (<5 cm dbh) estimated by line-intercept along four, 6-m lines per plot.

2.5. Data analysis

To examine responses to retention treatments, arthropod data from individual traps (sampling units) were averaged for all trees (or snags) within each experimental unit. Because some collections were lost to trap damage, data from each trap were first averaged among collecting dates within each year. Analyses were conducted

for individual arthropod groups that constituted at least 5% of all collections. We limit the taxonomic resolution of analyses to major arthropod orders, but apply greater taxonomic resolution to spiders, which were identified to family. These common predators are prominent in the diets of *Certhia* species (Williams and Batzli, 1979; Kuitunen and Tormala, 1983; Mariani and Manuwal, 1990; Suhonen and Kuitunen, 1991) and are excellent indicators of changes in the structural complexity of forest habitats (Gunnarsson, 1990, 1996; Halaj et al., 1998, 2000).

Abundance data were analyzed as a randomized block, split-split-plot ANOVA, with treatment as the whole-plot, tree status (live tree or snag) as the first sub-plot, and time (year) as the split-plot. Logarithmic transformations were applied as appropriate to satisfy the assumptions of ANOVA. Effects of retention level and spatial pattern on arthropod abundance were then tested with a series of a priori contrasts conducted as *t*-tests. Among the full set of ANOVA models (15 arthropod taxa tested), only one yielded a significant interaction (treatment \times status for Linyphiidae). Thus, contrasts were conducted on pooled data representing the average of all live trees and snags over both sampling years.

To explore relationships between arthropod abundance and variation in local habitat features - finer scale relationships that might explain responses to retention treatments - we used Pearson correlations between arthropod abundance and each of the seven measures of local habitat structure. Abundance data were averaged for the two sampling years and separate correlations were run for live trees and snags. Sample sizes varied for correlations with understory strata ($n = 188$ –214) because not all strata were present in all vegetation plots. All analyses were conducted with SAS Version 9.1 (SAS Institute, 2003).

3. Results

3.1. Overall arthropod abundance and community composition

In total, 166,234 arthropods were collected over the course of study. The vast majority (70.0%) were Collembola (springtails) (Table 1). Other important groups included arachnids (23.0%), adult Coleoptera (beetles, 15.8%), Hemiptera (plant bugs, 14.6%) and Diptera (flies, 11.7%). Each of the remaining arthropod orders comprised $<3.0\%$ of the overall assemblage.

Table 1

Total counts of bark-dwelling arthropods collected from live Douglas-fir trees and snags.

Arthropod taxa	Treatment										Total (540)
	100%		40%A		40%D		15%A		15%D		
	Live (60)	Snag (60)	Live (61)	Snag (59)	Live (60)	Snag (60)	Live (39)	Snag (21)	Live (60)	Snag (60)	
Collembola	14,351	7,866	14,609	3,268	19,826	11,409	15,730	3,270	17,173	8,868	116,370
Coleoptera (adults)	637	303	886	257	1,232	298	1,335	248	1,976	725	7,897
Hemiptera	1,123	413	880	365	1,276	462	728	228	1,228	550	7,253
Diptera (adults)	235	283	373	371	458	487	558	259	1,169	1,634	5,827
Formicidae	230	98	339	219	669	229	231	51	2,110	413	4,589
Hymenoptera (adults)	100	185	181	271	266	431	262	189	531	787	3,203
Diplopoda	178	198	60	92	122	140	214	135	874	700	2,713
Orthoptera	75	45	196	50	226	148	293	72	682	404	2,191
Lepidoptera (larvae)	59	37	105	39	163	58	137	57	416	127	1,198
Psocoptera	66	33	9	9	280	237	67	45	64	85	895
Microcoryphia	89	75	85	51	22	27	120	40	33	101	643
Homoptera	104	43	59	35	104	48	55	21	53	60	582
Lepidoptera (adults)	5	10	9	10	31	29	33	10	154	280	571
Neuroptera (larvae)	45	35	37	29	74	52	52	23	36	38	421
Coleoptera (larvae)	22	10	44	8	29	19	9	2	15	7	165
Other (non-arachnids)	15	7	16	37	5	18	5	4	11	13	131
Neuroptera (adults)	7	5	10	4	9	11	17	5	10	12	90
Hymenoptera (larvae)	7	1	1	1	11	5	8	1	3		38
Lepidoptera (pupae)							2				2
Total spiders (Araneae)	875	822	1,027	927	1,497	1,256	969	461	1,749	1,475	11,058
Gnaphosidae	204	178	433	359	635	438	375	157	594	402	3,775
Agelenidae	159	170	203	241	202	220	174	91	160	123	1,743
Amaurobiidae	250	262	175	155	192	143	102	84	108	79	1,550
Linyphiidae	122	78	50	43	92	189	65	31	64	282	1,016
Thomisidae	14	22	41	35	98	60	93	31	358	195	947
Anyphaenidae	27	13	27	13	78	69	75	10	124	84	520
Other	53	58	34	27	35	53	34	24	30	92	440
Philodromidae	11	11	24	15	50	26	18	10	92	43	300
Salticidae	5	8	14	8	41	17	12	4	71	87	267
Lycosidae	2	2	18	11	18	13	11	6	82	48	211
Theridiidae	5	3	2	4	43	19	7	7	54	22	166
Liocranidae	1	6	2	10	1	3		4	3	2	32
Dictynidae	3			1	4	3		1	4	11	27
Pholcidae	15	3		2	4			1	1		26
Araneidae	3	3	1	2	2	1	3		2	1	18
Hahniidae	1	4	3		1	1			1	1	12
Clubionidae		1		1						2	4
Oxyopidae									1	1	2
Antrodiaetidae						1					1
Segestriidae					1						1
Opiliones	37	10	38	17	34	34	73	9	93	52	397

Treatments are defined by retention level (%) and spatial pattern (A, aggregated; D, dispersed). Values are total numbers of individuals collected in 2003 and 2004 from all traps in the three replicates of each treatment. Numbers in parentheses are total numbers of traps; note that 15%A was sampled with ca. 50% fewer traps than other treatments; abundance values should be viewed accordingly.

Spiders accounted for >95% of arachnids (Table 1); 11,058 individuals represented at least 19 families (Table 1). One-third (33.1%) of these were Gnaphosidae (nocturnal running spiders), followed by Agelenidae (funnel-web builders, 15.2%), Amaurobiidae (hackled-band spiders, 13.5%), Linyphiidae (sheet-web builders, 8.9%), and Thomisidae (crab spiders, 8.3%). The most frequent taxa were *Sergiolus montanus* (Gnaphosidae, 20.5%), *Callobius* spp. (Amaurobiidae, 14.0%), *Novalena intermedia* (Agelenidae, 11.5%), *Orodassus assimilis* (Cnaphosidae, 7.3%), and *Xysticus locuples* (Thomisidae, 6.3%).

3.2. Arthropod responses to retention treatments

Retention treatments produced large and significant changes in the abundance of bark-dwelling arthropods and these effects were consistent over time (non-significant treatment \times year interactions; Table 2). The overall F-statistic screening for differences among treatments in the total abundance of insects (excluding Collembola) was highly significant (Table 2). In contrast, retention treatment had no discernable effect on the abundance of the most numerous group, Collembola.

All retention treatments supported significantly higher abundance of bark-dwelling insects than did controls (Fig. 2a). This increase was most dramatic at 15% retention where abundance was 1.8 times higher than at 40% retention and 2.6 times higher than in controls (Fig. 2a). Most groups of insects showed similar trends (Fig. 2b–f), including significantly greater abundance at 15% than at 40% retention.

On average, more insects were collected in dispersed than in aggregated treatments, but this trend was not statistically significant (dispersed vs. aggregated; $t_s = 1.58$; $P = 0.153$; Fig. 2a). Formicidae (primarily carpenter ants, *Camponotus* spp.) were an exception, with significantly higher abundance in dispersed than in aggregated treatments (Fig. 2f).

Spiders were ca. 40% more abundant in retention treatments than in controls (Table 2; Fig. 3a). Gnaphosidae and Thomisidae showed the strongest positive responses, exhibiting an average of 5.8 and 2.2 greater densities, respectively, in retention treatments than in controls (Fig. 3d, f). Thomisidae were more than an order of magnitude (12.2 times) more numerous in 15%D than in controls. In contrast, Amaurobiidae (primarily *Callobius* spp.) declined by as much as 54% in response to

Table 2

Results of split-split-plot ANOVAs testing effects of retention treatment, status (live tree or snag), and year on activity-density (individuals collected/trap/day) of bark-dwelling arthropods.

Arthropod taxa	Treatment ($F_{4,9}$)	Status ($F_{1,10}$)	Year ($F_{1,20}$)	Treatment \times Status ($F_{4,10}$)	Treatment \times Year ($F_{4,20}$)	Status \times Year ($F_{1,20}$)	Treatment \times Status \times Year ($F_{4,20}$)
Total insects	8.76 [*]	15.33 [*]	8.87 [*]	0.33	0.54	0.13	0.21
Collembola	1.17	21.76 [*]	97.11 [*]	0.43	1.24	1.03	0.18
Coleoptera (adults)	2.16	42.48 [*]	1.15	1.15	0.35	2.25	0.59
Hemiptera	1.36	12.07 [*]	6.12 [*]	0.31	1.16	0.08	0.10
Diptera (adults)	5.64 [*]	2.58	4.81 [*]	0.52	0.74	3.11	0.25
Formicidae	4.22 [*]	14.32 [*]	12.15 [*]	2.14	1.53	0.00	0.58
Hymenoptera (adults)	7.60 [*]	7.99 [*]	7.99 [*]	0.05	0.85	0.04	0.32
Diplopoda	0.97	0.22	1.66	0.48	0.27	2.62	0.04
Orthoptera	3.36	12.89 [*]	0.42	0.68	1.96	0.00	1.06
Total spiders (Araneae)	5.38 [*]	3.39	6.71 [*]	0.21	1.01	0.89	0.17
Gnaphosidae	2.78	4.60	10.16 [*]	0.83	0.11	0.01	0.38
Agelenidae	2.19	1.90	0.03	1.50	0.60	1.18	1.38
Amaurobiidae	7.90 [*]	0.29	0.45	0.58	0.13	0.01	0.51
Linyphiidae	1.97	4.59	0.08	4.22 [*]	0.70	0.85	0.76
Thomisidae	12.23 [*]	3.94	5.06 [*]	2.73	1.84	1.07	0.41

Asterisks (^{*}) denote significant ($P \leq 0.05$) and underlined values marginally significant ($0.05 < P < 0.10$) main effects or interactions. Analyses were limited to taxa comprising >5% of all individuals. Total insects do not include Collembola.

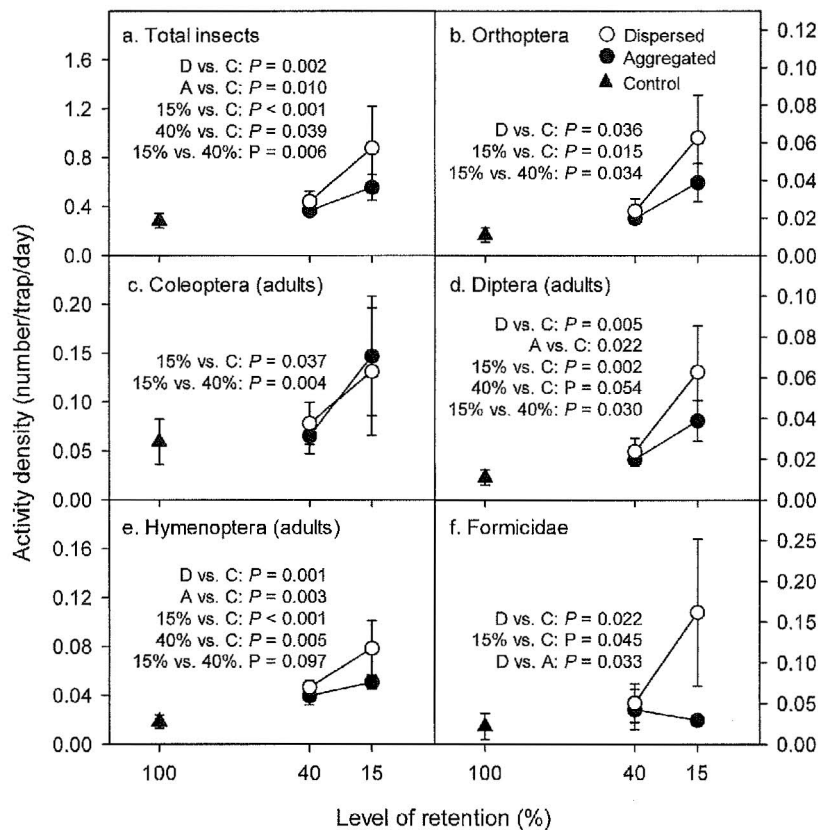


Fig. 2. Abundance (mean \pm 1 SE; $n = 3$) of major groups of bark-dwelling insects among treatments (see also Table 2). Means represent the average of live trees and snags for both sampling years. P values (reported if < 0.10) are from a priori contrasts (t -tests). Treatment codes: C, control; A, aggregated retention; D, dispersed retention; 15%, 15% retention; and 40%, 40% retention. Total insects do not include Collembola.

treatments (Fig. 3c). Unlike the insects, most groups of spiders showed significant responses to pattern of retention: Agelenidae and Amaurobiidae had greater (or marginally greater) densities in aggregated treatments (Fig. 3b, c), and Linyphiidae and Thomisidae, greater densities in dispersed treatments (Fig. 3e, f).

3.3. Effects of tree status

Total abundance of insects was significantly greater (2.2 times) on live trees than on snags (Tables 1 and 2). Live trees yielded significantly more Collembola (2.4 times), adult Coleoptera (3.3 times), Orthoptera (2.0 times), and Formicidae (3.5 times) than

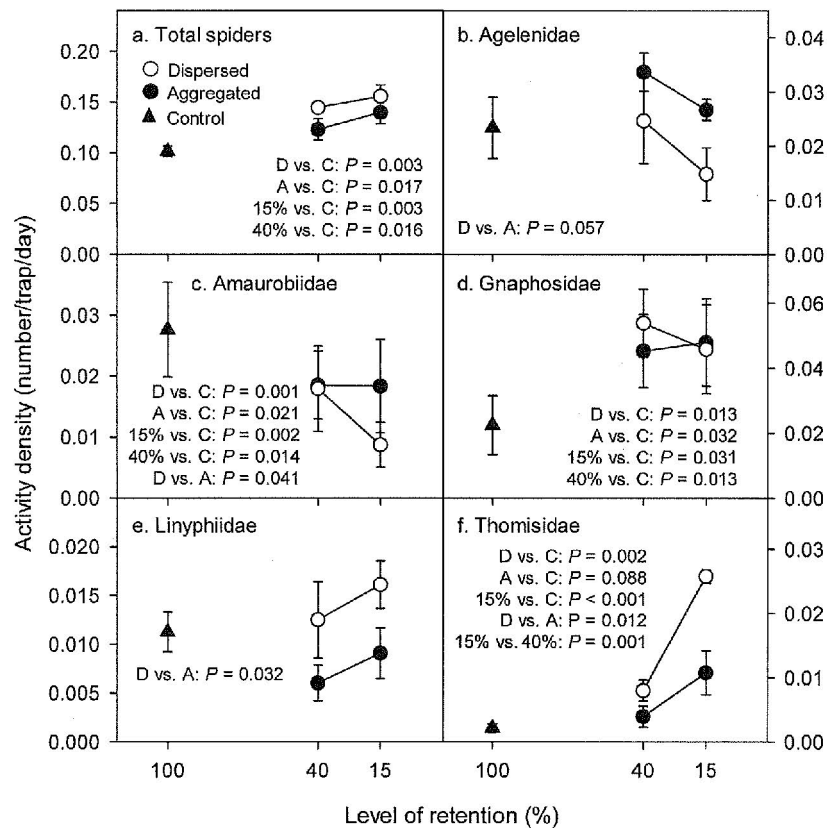


Fig. 3. Abundance (mean \pm 1 SE; $n = 3$) of bark-dwelling spiders among treatments (see also Table 2). See Fig. 2 for other details.

did snags (Tables 1 and 2). In contrast, adult Hymenoptera were 1.4 times more abundant on snags than on live trees. Tree status had no discernable effect on numbers of adult Diptera or Diplopoda.

In contrast to insects, spiders showed weaker responses to tree status (24% more abundant on live trees; Table 2). Among individual taxa, Gnaphosidae and Thomisidae showed marginally

greater abundance on live trees and Linyphiidae, marginally greater abundance on snags (Tables 1 and 2).

3.4. Correlations with local habitat structure

We detected many significant correlations between arthropod abundance and selected measures of habitat structure. Although

Table 3

Pearson correlation coefficients between activity-density (individuals collected/trap/day) and selected measures of habitat structure.

Arthropod taxa	DBH (cm)		Overstory density (stems/ha)		Overstory basal area (m ² /ha)		Herb cover (%)		Shrub cover (%)		Understory hardwood cover (%)		Understory conifer cover (%)	
	Live (280)	Snag (260)	Live (265)	Snag (214)	Live (265)	Snag (214)	Live (254)	Snag (188)	Live (254)	Snag (188)	Live (254)	Snag (188)	Live (254)	Snag (188)
Total insects	-0.05	0.02	-0.12*	0.01	-0.29*	-0.26*	0.04	0.01	-0.24*	-0.29*	-0.16*	-0.25*	0.15*	0.17*
Collembola	-0.07	0.04	0.04	-0.02	0.01	-0.02	-0.01	0.01	-0.18*	-0.08	-0.09	0.01	0.14*	0.14*
Diplopoda	-0.02	-0.10	-0.10	-0.08	-0.19*	-0.17*	0.02	-0.02	-0.19*	-0.30*	-0.14*	-0.21*	0.09	0.06
Orthoptera	0.20*	0.05	-0.17*	-0.14*	-0.23*	-0.32*	0.18*	0.18*	0.07	-0.08	0.04	-0.11	0.02	0.11
Hemiptera	0.09	0.01	0.06	0.05	0.04	0.17*	-0.19*	-0.27*	-0.27*	-0.33*	-0.18*	-0.28*	0.01	0.10
Coleoptera (adults)	0.01	-0.13*	-0.04	0.20*	-0.25*	-0.17*	0.19*	0.09	-0.07	-0.11	-0.08	-0.08	0.26*	0.21*
Diptera (adults)	0.06	0.02	-0.08	0.06	-0.24*	-0.17*	0.02	0.05	-0.09	0.03	-0.03	-0.04	0.12	0.12
Hymenoptera (adults)	0.10	-0.07	-0.13*	-0.12*	-0.30*	-0.26*	0.18*	0.13	-0.01	-0.09	-0.02	-0.09	0.07	0.07
Formicidae	-0.01	-0.03	-0.12*	0.08	-0.25*	-0.13	0.04	-0.09	-0.18*	-0.28*	-0.12	-0.16*	0.08	0.06
Total spiders (Araneae)	0.37*	0.08	-0.17*	-0.09	-0.26*	-0.18*	0.23*	0.09	0.14*	0.06	0.13*	-0.02	0.03	0.08
Agelenidae	0.09	0.13*	0.14*	0.07	0.15*	0.22*	-0.08	-0.23*	-0.19*	-0.08	-0.06	-0.01	-0.01	0.02
Amaurobiidae	0.14*	0.02	0.08	0.33*	-0.02	0.33*	0.16	-0.17	0.09	0.17	-0.06	-0.06	0.13	0.14
Gnaphosidae	0.33*	0.20*	-0.12	0.10	-0.29*	-0.10	0.33*	0.22*	0.26*	0.18*	0.22*	0.13	0.09	0.10
Linyphiidae	-0.02	-0.20*	0.02	-0.15*	0.09	-0.31*	-0.01	-0.04	0.01	-0.19*	-0.03	-0.16*	-0.01	0.03
Thomisidae	0.13*	-0.02	-0.30*	-0.23*	-0.38*	-0.23*	0.10	0.06	-0.01	0.05	-0.06	0.01	-0.01	0.01

Numbers in parentheses represent sample sizes for correlations (across all experimental units). Asterisks (*) denote significant ($P \leq 0.05$) and underlined values marginally significant ($0.05 < P < 0.10$) correlations. Arthropod abundances were averaged for 2003 and 2004 prior to analysis. Tests were limited to taxa comprising $>5\%$ of all individuals. Total insects exclude Collembola.

most variables explained a small percentage of the variation in arthropod abundance, 40% of tests (83 of 210) were significant (Table 3). Overall, the frequency of significant relationships was greater on live trees than on snags (43% vs. 36% of tests, respectively; Table 3). Significant responses to tree diameter were consistently positive on live trees, but less frequent and of mixed sign on snags. Most (78%) of the significant associations with tree diameter were found among spiders. More than 70% of arthropod groups on live trees and/or snags showed negative correlations with overstory basal area. Similar predominantly negative relationships were observed with tree density and cover of tall shrubs and understory hardwoods, although these were less frequent. Notable exceptions were Amaurobiidae and Agelenidae, whose abundance was positively correlated with tree density and basal area. Significant correlations with cover of herbs were mainly positive, occurring more frequently on live trees than on snags. Correlations with the cover of understory conifers were consistently positive, but infrequent, and none were found among spiders.

4. Discussion

4.1. Abundance and composition of corticolous arthropods

Live trees and snags of Douglas-fir supported rich and abundant communities of corticolous arthropods that share many similarities to communities in other forest ecosystems. For example, Coleoptera, Orthoptera and Hemiptera - groups common in our samples - also predominate on longleaf and loblolly pine (Hanula and Franzreb, 1998; Horn and Hanula, 2002). Weevils (Curculionidae), which accounted for as many as 68% of adult Coleoptera, often dominate communities on longleaf pine (Hanula and Franzreb, 1998) and contribute significantly to communities on a variety of other tree species (Moeed and Meads, 1983; Nicolai, 1986). Spiders and other arachnids are major components of the bark arthropod fauna on several species of pine (Hanula and New, 1996; Hanula and Franzreb, 1998; Hanula et al., 2000; Collins et al., 2002; Horn and Hanula, 2002), beech, maple (Peterson et al., 1989), and other North American and New Zealand tree species (Jackson, 1979; Moeed and Meads, 1983).

The most noticeable characteristic of the bark-arthropod community in our study is the numerical dominance of transient taxa, including most groups of detritivores (Collembola and Diplopoda) and herbivores (Curculionidae and Orthoptera). This suggests a strong ecological tie with arthropod communities in the understory vegetation and forest floor. Collembola, which are primarily fungal grazers and detritivores, often migrate from forest litter onto tree boles and into the canopy (Andre, 1983; Halaj et al., 1997, 2000) where they appear to feed on lichens and fungal hyphae (Stubbs, 1989; Pettersson et al., 1995). Adult weevils move from forest litter to feeding sites in the canopy, and are frequently collected in crawl traps (Hanula and New, 1996). The majority of Orthoptera in our study were hump-winged crickets, *Cyphoderris* spp. (Prophalangopsidae), which hide in bark fissures during the day and feed at night on understory vegetation. Suspected links between corticolous and understory/forest-floor communities have been documented elsewhere, as well. In a study of corticolous arthropods on longleaf pine, Hanula and Franzreb (1998) found that a large proportion of arthropods originated in the litter community whereas resident species contributed less to overall biomass. Collins et al. (2002) suggest that, although some corticolous arthropods may use bark for overwintering or egg laying, most activity occurs in the understory vegetation and forest floor. Hanula and Franzreb (1998) further speculate that some predators, such as spiders, are resident to bark where they feed on these more transient species. Previous research in Douglas-fir

forest of western Oregon and Washington shows that the vast majority of spider species collected from bark also frequent tree foliage and the forest floor (Halaj et al., 1997, 1998, 2000, 2008).

4.2. Arthropod responses to green-tree retention treatments

With the exception of Collembola, retention treatments had significant and mostly positive effects on the abundance of bark-dwelling arthropods. This result is consistent with other studies reporting positive effects of open habitats on bark arthropods (Hanula et al., 2000) including significantly higher densities in open pine stands than in those with a denser midstory (Collins et al., 2002). Collins et al. (2002) speculate that most bark-dwelling arthropods are colonizers, originating from a rich herbaceous vegetation that can develop in more open forest stands. Indeed, in our study system, richness and cover of herbaceous species were greater at 15 than at 40% retention (C.B. Halpern, unpublished data).

Interestingly, pattern of retention was not a significant factor for most insect groups although some showed slightly elevated densities in dispersed treatments. This general lack of response to the spatial distribution of trees parallels our finding for litter arthropods in the same study system (Halaj et al., 2008). This result may reflect the similarity of microclimatic conditions and understory vegetation in dispersed treatments and the cut portions of aggregated treatments (Halpern et al., 2005; Heithecker and Halpern, 2006)-conditions fostering development of similar arthropod communities that colonize remnant trees in both settings.

A notable exception was ants (Formicidae) whose densities were significantly higher in dispersed than aggregated treatments, particularly at 15% retention. Ant abundance also showed significant negative correlations with habitat variables associated with older closed-canopy forests (i.e., overstory basal area and tree density, cover of shrubs and understory hardwoods). The affinity of ants for open habitats may reflect greater availability of prey and/or nesting sites in post-harvest woody debris.

Spiders, as a group, increased significantly in retention treatments, reflecting increasing abundance of several species of Gnaphosidae (*G. montanus* and *G. assimilis*) and Thomisidae (*X. locuples*). The latter were also significantly more abundant in dispersed treatments. Because none of these are known habitat specialists, their preference for more open treatments may reflect the increased availability of arthropod prey. These responses parallel those observed for litter spiders in the same sites (Halaj et al., 2008). Interestingly, Linyphiidae were more abundant in dispersed than in aggregated treatments and tended to decrease with overstory density and basal area. This contrasts to their responses in the litter community where they were comprised of taxa predominantly associated with old-growth habitats (Halaj et al., 2008). Amaurobiidae (*Callobius* spp.) were the only group of spiders to show a dear decline after harvest and positive responses to overstory density and basal area, suggesting a preference for undisturbed forest. Agelenidae showed similar habitat preferences with abundance decreasing in dispersed treatments and increasing with overstory density and basal area, similar to responses of litter-dwelling Agelenidae (Halaj et al., 2008).

4.3. Effects of tree status

Live trees hosted more than twice as many arthropods as did snags. This trend was consistent for most major groups of insects (Collembola, Orthoptera, Hemiptera, Coleoptera, and Formicidae), suggesting that snags provide poorer quality habitat. Similarly, Peck and Niwa (unpublished data) found significantly more individuals of herbivorous Coleoptera (58%) and ants (*Camponotus*

and *Formica* species) on boles of live trees than on snags in thinned and control stands of *Abies* in southwestern Oregon. Live trees may offer more food resources, including foliage and arboreal epiphytes for herbivores, and in turn, greater abundance of arthropod prey for predatory species. Differences in the physical and chemical properties of bark on live and dead trees may also affect habitat quality.

Interestingly, although Collembola (the most numerous arthropods in this study) were not sensitive to habitat differences at the treatment level, their abundance was 50% lower on snags than on live trees; Hemiptera showed a similar pattern. This suggests that microhabitat conditions on live trees may be more important for these groups than larger scale changes in forest structure. These moisture-sensitive arthropods may respond positively to local increases in humidity or food supply on live trees supporting canopy foliage. Previous experimental work is consistent with this hypothesis: Collembola on Douglas-fir were highly sensitive to changes in arboreal microhabitats induced by removing needles and thinning branches (Halaj et al., 2000). Similar changes occur during the transition from live tree to snag.

The greater abundance on live trees of arthropods that serve as prey may explain the corresponding increase of predators such as ants and spiders. In addition, ants often engage in aphid-tending activities (Bristow, 1984; Bach, 1991; Halaj et al., 1997) and their preference for live trees may reflect the presence of canopy foliage necessary to sustain colonies of sap-feeding aphids. Spiders were more numerous on live trees than on snags, but this increase was only marginally significant. Many species of spiders are limited by availability of suitable foraging sites, a factor closely linked to habitat heterogeneity (Gunnarsson, 1990, 1996; Halaj et al., 1998, 2000). Snags can provide more structurally diverse habitat due to mechanical injuries, sloughing of bark, and woodpecker activity (Jackson, 1979). Thus, it is possible that greater prey availability on live trees was offset by greater habitat suitability on snags.

4.4. Effects of local habitat structure

We detected many significant associations between the activity-density of bark arthropods and local habitat structure—associations that may underlie the larger scale patterns observed among treatments. It has been suggested that variation in the composition of bark-arthropod communities among tree species reflects a variety of ecological factors, including bark rugosity and thermal properties (Jackson, 1979; Nicolai, 1986; Mariani and Manuwal, 1990; Horn and Hauula, 2002), presence of epiphytes on tree boles (Nicolai, 1986; Stubbs, 1989; Pettersson et al., 1995), and characteristics of the understory vegetation and forest floor (strata that may serve as sources for colonization of tree boles; Hauula and Franzreb, 1998; Duguay et al., 2000; Collins et al., 2002).

Several groups of arthropods, primarily spiders, showed significant positive associations with tree diameter in our study. Moeed and Meads (1983) also reported positive relationships between spider density and tree diameter in four Australian tree species. The mechanism for this relationship may be an indirect one: Mariani and Manuwal (1990) found strong positive correlations between depth of bark furrows (rugosity) in Douglas-fir and the abundance of spiders and other soft-bodied arthropods; bark rugosity, in turn, showed a strong positive correlation with tree diameter.

Spiders respond strongly to the structural complexity of their habitats. For example, as much as 60–70% of the variation in abundance of arboreal spiders in forests of western Oregon can be explained by the physical structure of host species (Halaj et al., 1998). Greater depth of bark fissures may provide greater microclimatic stability and protection from bird predation (Jackson, 1979; Nicolai, 1986). Yet, these relationships may not

apply to all systems. Peterson et al. (1989) found no relationship between tree diameter, bark texture, and abundance of bark-dwelling arthropods on American beech or sugar maple. The strength of these relationships may vary with species-specific differences in the depth and complexity of bark habitats.

In forests of loblolly and shortleaf pine, Collins et al. (2002) speculated that the herbaceous understory functions as a dispersal source for colonization of tree boles and thus, may exert stronger controls on arthropod composition than does bark texture. In contrast, in forests of longleaf pine, Hanula et al. (2000) found no association between attributes of the herb layer and the diversity, abundance, or biomass of bark-dwelling arthropods. In the current study, several lines of evidence support the hypothesis that harvest treatments influence the composition and abundance of arthropod communities indirectly through effects on understory vegetation. First, herbivorous groups dependent on herbaceous vegetation—plant bugs (Hemiptera), Orthoptera, and Coleoptera (mostly weevils)—were abundant in our samples. Second, at the treatment level, abundance of most arthropod taxa was highest in the 15% retention treatments which supported the greatest cover of herbaceous plants (CB, Halpern, unpublished data). Finally, at a local scale (individual plots), many arthropod groups showed negative correlations with overstory basal area and density and positive correlations with herb cover, paralleling relationships at larger scales (treatment units). At the same time, individual correlations explained only a small portion of the variation in arthropod abundance suggesting that many factors, including those not measured, may contribute to the observed patterns of abundance.

4.5. Management implications

From a management perspective, retention treatments that produce stand conditions or tree characteristics that increase prey availability should also benefit higher trophic levels, such as avian predators. Our results indicate that timber harvests with low to moderate levels of green-tree retention create conditions that are conducive to most groups of bark-dwelling arthropods. Among the many taxa considered, only the spider family Amaurobiidae was adversely affected by harvest (suggesting a preference for undisturbed or interior-forest conditions). However, a potential limitation of our analysis is that we express arthropod abundance on an individual-tree basis. Although retention treatments had higher concentrations of arthropods per tree bole they had fewer trees than did controls and hence, lower prey availability at the stand level. On the other hand, optimal foraging theory predicts that a higher concentration of prey on residual trees should make retention treatments more attractive to predators: energetically, it is more efficient to forage in these habitat patches. Arthropod populations that benefit from the development of herbaceous vegetation in the post-harvest environment may also function as reservoirs of insect prey in the local landscape. For example, in our experimental treatments, forest aggregates harbored significantly greater concentrations of bark-dwelling arthropods than did uncut forests, suggesting influx from the post-harvest matrix. Although open habitats are generally not favored by cavity-nesting species such as the brown creeper (Hutto, 2000; Lundquist and Manuwal, 1990), Mayrhofer (2006) documented their preferential use of forest aggregates and treatment unit edges (rather than undisturbed forest) in a companion study, supporting our conclusion. Standards and guidelines in the Northwest Forest Plan stipulate retention of large-diameter trees and snags as critical elements of wildlife habitat (USDA and USDI, 1994). Our findings provide an additional example of the ecological importance of retaining large, live trees in managed forests—as habitats for arthropod prey and as foraging substrates for bark-gleaning birds.

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