

CANOPY ARTHROPOD RESPONSE TO DENSITY AND DISTRIBUTION OF GREEN TREES RETAINED AFTER PARTIAL HARVEST

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Abstract. We measured canopy arthropod responses to six contrasting green-tree retention treatments at six locations (blocks) in western Oregon and Washington as part of the Demonstration of Ecosystem Management Options (DEMO) study. Treatments were 100% retention (uncut), 75% retention with three 1-ha harvested gaps, 40% dispersed retention, 40% aggregated retention with five 1-ha uncut aggregates, 15% dispersed retention, and 15% aggregated retention with two 1-ha uncut aggregates. Arthropods were sampled from upper, mid-, and lower crown levels of one overstory Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and from three understory vine maple (*Acer circinatum* Pursh) in each treatment unit during June and August each year to assess seasonal variation in abundances. Pretreatment data were collected in 1996 and posttreatment data in 1999–2000. Arthropods showed little evidence of response to treatments, but the abundance of arthropods on both plant species showed significant variation among blocks, reflecting responses to environmental gradients at a regional scale. Arthropod abundance also varied significantly over time in unmanipulated (control) treatments, suggesting sensitivity to annual changes in weather. Our results suggest that disturbance at this intensity or scale has little influence on canopy arthropods in the short term. Future sampling will be necessary to evaluate the extent to which arthropods respond to changes in environmental conditions created by these treatments over longer time periods.

Key words: *Acer circinatum*; disturbance; Douglas-fir; green-tree retention; insect; mite; *Pseudotsuga menziesii*; spider; vine maple.

INTRODUCTION

Clearcut harvesting in the montane coniferous forests of the Pacific Northwest has greatly altered ecosystem structure and function. Clearcutting has reduced the diversity and patch size of forested habitats, and fragmentation of old growth has led to declines in the abundance and viability of many forest species. The resulting network of disturbed habitats and roads has facilitated colonization and spread of invasive species, and increased erosion has caused sedimentation of fish-bearing streams. These changes threaten the integrity of ecological processes that maintain forest ecosystems and the sustainability of forest resources (Kohm and Franklin 1997, Christensen et al. 2000, Sullivan and Sullivan 2001).

Alternative approaches to managing forest ecosystems for sustainable yields of wood and fiber resources have focused on more selective methods of harvest to reduce the extent of canopy-opening and soil distur-

bance (Carey et al. 1996, Aubry et al. 1999, Franklin et al. 1999, Christensen et al. 2000, Gram et al. 2001). These approaches generally retain structural elements (including live trees) of the forest following partial harvest. Live (green) trees can be retained at different densities and/or distributions (e.g., evenly dispersed or in aggregates). Density of retained trees influences canopy cover and the penetration of light, water, and airflow, affecting vertical and horizontal gradients in temperature and relative humidity (Parker 1995). The pattern in which trees are retained can also affect environmental conditions. Clearcutting creates distinct edges and sharp gradients in environmental conditions from exposed open areas to more protected habitat at the center of fragments, whereas selective cutting reduces the contrast between harvested and unharvested patches. However, the effects of these changes in forest structure on various plant and animal species are largely unknown.

Forest canopies represent major ecological functions (e.g., photosynthesis; evapotranspiration; and interception of light, water, wind, and nutrients) that control biomass accumulation and environmental conditions (Ruangpanit 1985, Chen et al. 1995, Lewis 1998). Arthropods can dramatically alter canopy structure and function in ways that can stabilize primary production or interfere with management goals (e.g., Mattson and Addy 1975, Romme et al. 1986, Schowalter 2000). For example, low-intensity foliage feeding by insects can

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stimulate nutrient turnover and increase tree growth (Alfaro and Shepherd 1991), whereas high-intensity feeding can reduce tree growth and ultimately lead to tree mortality and opening of the canopy (Schowalter et al. 1986).

Effects of changes in tree density and distribution on arthropod abundances and community structure are not well understood (Barker and Pinard 2001, Foggo et al. 2001). Some arthropod species respond positively, others negatively, and some show no response to canopy-opening disturbances or to forest edges, depending on their adaptations to temperature, relative humidity, changes in plant growth, foliage chemistry, exposure to predators, and other factors (Schowalter et al. 1981, Schowalter 1985, 1995, Shure and Phillips 1991, Schowalter and Turchin 1993, Shure and Wilson 1993, Dudt and Shure 1994, Ozanne et al. 1997, Roland and Taylor 1997, Schowalter and Ganio 1999). Tree spacing also affects the ability of host-seeking insects to find or reach suitable resources. Insects have limited energy reserves and may be unable to travel between widely spaced hosts. Furthermore, many insects rely on detection of volatile chemicals to locate mates or suitable resources (Amman et al. 1988, Harborne 1994, Roelofs 1995, Cardé 1996). Canopy opening creates convection zones that carry these chemicals above the canopy, impeding detection and colonization of resources by insects (Fares et al. 1980). Few arthropod species have been studied sufficiently to predict responses to changes in tree spacing.

Because insects are small and reproduce rapidly, population sizes can change quickly in response to changes in environmental conditions, such as those resulting from timber harvest (Schowalter 1985). Canopy opening generally increases the abundance of sap-sucking herbivores (such as aphids and scale insects) and stump-feeding insects, and reduces the abundance of folivores (foliage-chewing herbivores such as caterpillars and beetles), bark beetles, predators, and detritivores (Schowalter et al. 1981, Witcosky et al. 1986, Shure and Phillips 1991, Schowalter and Turchin 1993, Schowalter 1995, Roland and Taylor 1997, Schowalter and Ganio 1999, Work 2000). Therefore, we would expect varying amounts and distributions of green trees retained after partial harvest to affect arthropod species and functional groups in different ways over short time periods.

We compared changes in canopy arthropod abundances on overstory Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and understory vine maple (*Acer circinatum* Pursh) among six green-tree retention treatments as part of the Demonstration of Ecosystem Management Options (DEMO) study in western Oregon and Washington (Aubry et al. 1999, Progar et al. 1999). We expected that abundances of sap-sucking species would increase, and abundances of folivores, detritivores, and predators would decrease, at lower levels of overstory retention, as a result of their differential re-

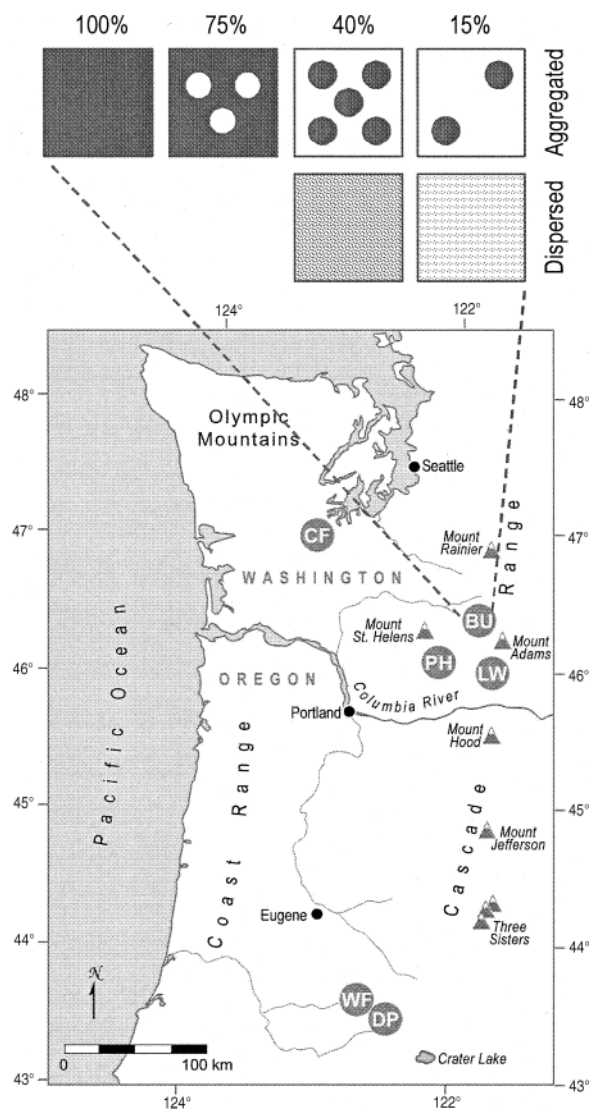


FIG. 1. Experimental design for retention treatments in the Demonstration of Ecosystem Management Options (DEMO) study. In aggregated treatments, dark gray represents intact forest, and white represents adjacent harvest areas. Each experimental unit is 13 ha. Treatments were replicated in each of six blocks in western Oregon and Washington. The figure is reprinted from Halpern and McKenzie (2001) with permission from Elsevier Science.

sponses to changes in temperature, relative humidity, and plant growth rate (Shure and Phillips 1991, Schowalter 1995). Furthermore, we expected that responses to harvest would be more pronounced at the edges of forest aggregates (or forest gaps) than in more interior locations, given the greater degree of exposure to solar radiation at edges (Roland and Taylor 1997, Work 2000, Foggo et al. 2001).

METHODS

The DEMO study was established at six locations (blocks) dominated by 65- to 170-yr-old Douglas-fir

TABLE 1. Posttreatment (1999–2000) abundances, mean (and SE), of arthropod functional groups on Douglas-fir, in each of the six green-tree retention treatments.

Taxon or measure	Posttreatment abundance (no. arthropods/kg plant material)			
	100%	75%A	40%D	40%A
Folivores	9.7 (7.9)	4.7 (1.7)	38.3 (33.2)	10.3 (7.0)
Sap-suckers	22.0 (5.8)	30.3 (16.4)	22.6 (5.6)	19.0 (4.3)
Gallformers	0.7 (0.5)	0.8 (0.4)	7.0 (6.1)	1.9 (0.9)
Predators	33.8 (7.9)	24.8 (5.2)	33.4 (11.7)	35.5 (8.9)
Detritivores	79.3 (19.0)	52.9 (12.0)	92.1 (57.2)	57.9 (19.7)
Total abundance	191.1 ^{ab} (28.3)	136.1 ^b (23.7)	268.4 ^{ab} (70.5)	284.1 ^{ab} (87.5)
Shannon-Weiner index	2.1 (0.2)	2.4 (0.1)	1.9 (0.2)	2.0 (0.3)
Predator-prey ratio	0.4 (0.1)	0.2 (0.1)	0.1 (0.1)	0.4 (0.2)

Notes: Data represent the pooled abundance of June and August samples ($n = 6$ replicates). Treatment codes: 100%, control; 75%A, 75% aggregated retention; 40%D, 40% dispersed retention; 40%A, 40% aggregated retention; 15%D, 15% dispersed retention; 15%A, 15% aggregated retention. Treatment means followed by different letters were significantly different based on Tukey's multiple comparison test.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

forests in western Oregon and Washington: Dog Prairie (DP) and Watson Falls (WF) in the Umpqua National Forest in southwestern Oregon; Capitol State Forest (CF) southwest of Olympia, Washington; and Butte (BU; see Plate 1), Paradise Hills (PH), and Little White Salmon (LW) in the Gifford Pinchot National Forest in southwestern Washington (Aubry et al. 1999). Six treatments were randomly assigned to six, 13-ha treatment units in each block (Fig. 1): (1) 100% retention (100%); (2) 75% aggregated retention, with three 1-ha harvested gaps (75%A); (3) 40% dispersed retention (40%D); (4) 40% aggregated retention, with five 1-ha uncut aggregates (40%A); (5) 15% dispersed retention (15%D); and (6) 15% aggregated retention, with two 1-ha uncut aggregates (15%A). Treatment plots were surrounded by a 40-m buffer of the same forest type; plots within blocks generally were separated by 1–10 km.

Canopy arthropods were sampled in 1996 (pretreatment) and in both 1999 and 2000 (posttreatment). Harvests were completed at BU and PH during summer/fall 1997; at CF during winter/spring 1998; and at DP, LW, and WF during summer/fall 1998. One dominant Douglas-fir in each treatment unit was rigged for canopy access in 1996 (i.e., six replicate trees per treatment). In aggregated retention units, the sample tree was near the center of a planned aggregate. Following treatment, an additional Douglas-fir at the edge of the aggregate was rigged for canopy access. The same tree(s) in each treatment unit were sampled each year. This design precluded assessment of within-plot variation of arthropod abundance but was sufficient for statistical analysis of treatment effects, since samples from multiple trees within plots would be pooled by plot (the independent unit of replication) for statistical analysis (Hurlbert 1984). Previous studies have indicated that this experimental design is adequate to detect significant differences in canopy arthropod abundances among stands with contrasting canopy structures. For example, 12 of 45 taxa and functional groups evaluated

by Schowalter (1995) and 16 of 57 taxa and functional groups evaluated by Schowalter and Ganio (1999) showed significant differences in abundance among plots, of different age or intensity of canopy-opening disturbance, where a single tree of each species was sampled in each plot.

In addition, three understory vine maples were sampled in each treatment unit in the three blocks in which it was common (BU, CF, and LW). Vine maple is a widespread, and often dominant, component of the understory in these coniferous forests (Franklin and Dyr-

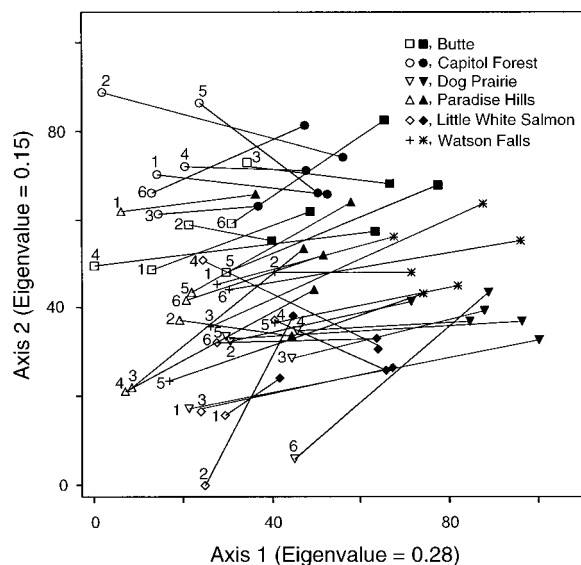


FIG. 2. Detrended correspondence analysis (DCA) of arthropod abundances (taxa in >5% of samples) on Douglas-fir before (1996, open symbols) and after (mean of 1999 and 2000, closed symbols) each of six green-tree retention treatments in six blocks in western Oregon and Washington. Numbers represent treatments: 1, 100%; 2, 75%A; 3, 40%D; 4, 40%A; 5, 15%D; 6, 15%A (see Methods and Fig. 1 for description of treatments). Lines connect pretreatment and posttreatment data for each treatment unit. Data represent pooled abundances from June and August for each sample.

TABLE 1. Extended.

Posttreatment abundance (no. arthropods/kg plant material)		MSE	<i>F</i>	Treatment	Block
15%D	15%A			<i>F</i> _{5,25}	<i>F</i> _{5,25}
7.2 (5.3)	6.0 (1.9)	1.3	0.9	0.5	1.3
21.1 (10.7)	24.2 (5.0)	0.4	1.9	0.4	3.4*
6.4 (6.3)	43.3 (41.7)	0.9	3.8	0.9	6.7***
23.5 (7.9)	47.4 (14.5)	0.2	3.4	1.7	5.1***
48.1 (17.3)	77.5 (17.4)	0.4	5.8	1.3	10.3***
178.3 ^{ab} (51.6)	308.3 ^a (54.8)	0.2	3.2	2.8*	3.7**
1.8 (0.4)	1.9 (0.3)	0.0	4.6	1.3	7.9***
0.2 (0.1)	0.4 (0.2)	0.0	2.6	0.9	4.3**

ness 1988). In aggregated treatment units, vine maples were sampled near the center of the same aggregate used for sampling Douglas-fir. Following treatment, three additional vine maples were selected at the edge of the chosen aggregate.

Samples from Douglas-fir were collected by climbing each tree using the single-rope technique, quickly slipping a plastic bag over a foliated branch (0.5 m, 30–50 g dry mass), clipping the branch, and sealing the bag. Each tree was sampled at three canopy levels, upper (within 5 m of top), mid, and lower (within 5 m of lowest foliated branches), without regard to aspect, in June and August each year to capture variation in arthropod abundance resulting from seasonal changes in climate and foliage development (Schowalter 1995, Schowalter and Ganio 1998). Samples from vine maple were collected at the same time from the ground by quickly slipping a plastic bag over a foliated branch (as above). This sampling technique emphasizes the sedentary fauna that is present on foliage and twig surfaces at any given sampling time (e.g., aphids, caterpillars, spiders, mites), but tends to underrepresent highly mobile species that could be alarmed and escape (Schowalter 1995, Schowalter and Ganio 1999). Other sampling techniques have different biases. For example, interception traps emphasize flying adult insects which may or may not be associated with a particular plant or even a particular treatment unit, whereas can-

opy foggers emphasize unattached arthropods that reach collectors on the ground, but exclude many small arthropods that are intercepted by vegetation (e.g., Majer and Recher 1988, Blanton 1990).

Samples were sorted in the laboratory by inspecting bags for mobile arthropods, then scanning samples under a dissecting microscope (10×) and collecting, identifying, and tabulating all arthropods. Plant material was dried at 50°C to constant mass. Arthropod abundances were standardized as number per kilogram of plant sample (including woody material).

DATA ANALYSES

Arthropod taxa often are categorized by functional group to focus on similar resource utilization strategies (Romoser and Stoffolano 1998). For comparative purposes, we followed previous functional group designations (see Schowalter et al. 1981, Schowalter 1995, Schowalter and Ganio 1999), including folivores (all foliage chewing caterpillars, sawflies, beetles), sap-suckers (primarily aphids, scale insects, and leafhoppers), gall-formers (primarily gall midges), predators (especially spiders, mites, beetles, snakeflies, and true bugs), and detritivores (primarily bark lice, springtails, oribatid mites, and fungus gnats). However, species within functional groups may respond to environmental changes in different ways (Schowalter et al. 1999). Therefore, we analyzed data for individual species that

TABLE 2. Posttreatment (1999–2000) abundances, mean (and SE), of arthropod functional groups on Douglas-fir, on edge and interior trees in aggregated retention treatments (15%A, 40%A, and 75%A).

Taxon or measure	No. arthropods/kg plant material		MSE		Treatment <i>F</i> _{2,25}	Position <i>F</i> _{1,25}	Treatment × position
	Edge	Interior	Whole plot (treatment)	Split plot (position)			<i>F</i> _{2,25}
Folivores	12.0 (4.4)	7.0 (2.4)	1.3	0.4	0.9	1.4	0.8
Sap-suckers	48.8 (17.5)	24.6 (5.6)	0.8	0.8	1.9	1.0	0.8
Gallformers	3.5 (3.2)	15.3 (13.9)	1.5	1.0	0.1	2.0	2.5
Predators	31.4 (5.4)	35.9 (6.0)	0.4	0.2	1.5	1.1	1.4
Detritivores	54.4 (9.8)	62.8 (9.4)	0.8	0.2	1.0	1.2	1.6
Total abundance	191.9 (25.0)	242.9 (37.9)	0.2	0.3	3.6	1.5	1.0
Shannon-Weiner index	2.3 (0.2)	2.1 (0.2)	0.1	0.0	1.6	1.9	1.1

Notes: Data represent the pooled abundance of June and August samples (*n* = 6 replicates). See Table 1 for treatment definitions.

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

TABLE 3. Posttreatment (1999–2000) abundances, mean (and SE), of arthropod functional groups on vine maple, in each of the six green-tree retention treatments.

Taxon or measure	Abundance (no. arthropods/kg plant material)			
	100%	75%A	40%D	40%A
Folivores	52.4 (32.8)	18.4 (7.9)	7.5 (3.7)	5.8 (5.8)
Sap-suckers	405.4 (197.0)	115.3 (102.0)	124.9 (34.2)	158.4 (92.9)
Gallformers	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Predators	236.9 (180.4)	39.5 (20.6)	69.7 (35.9)	134.4 (50.5)
Detritivores	57.0 (57.0)	58.3 (29.3)	491.7 (451.1)	100.7 (45.1)
Miscellaneous	20.6 (18.4)	24.0 (11.9)	73.5 (31.2)	112.8 (75.9)
Total abundance	772.3 (356.0)	255.5 (150.0)	767.2 (443.0)	512.0 (148.1)
Shannon-Weiner index	1.5 (0.3)	1.8 (0.2)	1.3 (0.4)	1.9 (0.3)
Predator-prey ratio	0.3 (0.2)	0.3 (0.1)	0.6 (0.4)	0.4 (0.3)

Notes: Data represent the pooled abundance of June and August samples ($n = 3$ replicates). See Table 1 for other details.

were sufficiently abundant. We also calculated total abundance of arthropods, predator-prey ratio, and the Shannon-Wiener diversity index (Magurran 1988) for each sample.

Data were pooled for the three canopy levels sampled (upper, mid-, and lower) on each host tree to represent the total arthropod community present, and to ensure sufficient data for analyses. In aggregated retention treatments, only interior trees were used in analyses of treatment effects. Residuals from untransformed data for the 20 most abundant taxa (for the combined 3-yr data set) and for functional groups were assessed for normality and equal variances. Results indicated a failure to meet either assumption. Therefore, data were transformed to their natural logarithms ($y + 1$), achieving homogeneity of variances and normality for most taxa and groups (Christensen 1996). However, pooling and transformation did not normalize data for several taxa due to insufficient abundance in some treatment units, but were an improvement over untransformed data.

We tested the null hypotheses that arthropod abundances on Douglas-fir and vine maple did not differ among treatments using ANOVA on transformed data for a randomized complete block design. For each tree species sampled, we conducted tests on the mean of the posttreatment samples (1999 and 2000), and on the difference between the mean pre- and posttreatment abundances for each arthropod species or functional group (Gram et al. 2001). We also analyzed June and August samples separately to test whether treatment effects differed with season. All ANOVAs were conducted using the PROC GLM procedure in SAS version 8.2 (SAS Institute 2001). Tukey's multiple comparison test was used to compare means for taxa showing significant treatment effects.

The large number of taxa analyzed in this study increases the probability of Type I error, i.e., we expect one taxon per 20 analyzed to show significant responses erroneously ($P = 0.05$). However, we expect the same error rate if these species were studied and reported individually. Evaluation of multiple taxa in this study has the advantage of indicating the degree of consis-

tency of responses to treatments among taxa (e.g., Moran 2003). Furthermore, analyzing multiple taxa should reduce the probability of Type II error, i.e., some taxa should show nonsignificant responses erroneously, but if treatments have general effects among taxa or functional groups, then some should show significant responses.

We further investigated the effects of level and pattern of green-tree retention on arthropod community composition with detrended correspondence analysis (DCA). DCA is an ordination technique that is particularly useful for analyses of ecological data sets based on samples and species (Hill and Gauch 1980). For each arthropod community sampled (Douglas-fir and vine maple), separate analyses were conducted on post-harvest data (mean of 1999 and 2000 samples), and on pre- and postharvest data sets. Data transformation ($\log_{10}(y + 1)$) was performed to reduce beta diversity, sampling unit and taxa skewness, and the coefficient of variation among taxa and functional groups (Christensen 1996). Taxa occurring in <5% of the units sampled were excluded and rare species downweighted. Blocked multiple response permutation procedure (MRPP, based on Euclidean distance) was then used to test for compositional differences among treatments based on postharvest data. MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups of entities. MRPP has the advantage of not requiring assumptions of distribution (such as normality and homogeneity of variances) that are seldom met in ecological community data (Biondini et al. 1985, Mielke and Berry 2001). We used PC-ORD (version 4) for both DCA and MRPP (McCune and Mefford 1995).

In addition, we tested whether arthropod responses differed between trees located at the edge and interior of the aggregated retention treatments for both Douglas-fir and vine maple. Split-plot ANOVAs were used to test for effects of position within treatments (edge vs. interior) and its potential interaction with level of retention (15%A, 40%A, and 75%A). Where significant interactions were observed, paired t tests were used to compare the means of positions within treatments.

TABLE 3. Extended.

Abundance (no. arthropods/kg plant material)		MSE	F	Treatment	Block
15%D	15%A			$F_{5,10}$	$F_{2,10}$
29.5 (14.1)	41.0 (37.4)	3.4	0.6	0.6	0.6
55.9 (13.2)	226.7 (43.2)	0.9	2.5	1.6	4.6*
17.4 (17.4)	0.0 (0.0)	0.9	1.0	1.0	1.0
194.0 (116.4)	81.8 (14.7)	1.9	1.1	0.9	1.6
33.7 (18.3)	21.0 (9.9)	2.4	1.7	1.7	1.8
241.2 (124.5)	54.5 (27.3)	1.9	3.3	1.2	8.5**
571.7 (136.1)	425.0 (25.2)	0.6	0.9	1.0	0.5
1.8 (0.4)	1.5 (0.2)	0.0	1.9	1.1	3.9
0.4 (0.3)	0.2 (0.0)	0.1	0.2	0.3	0.1

RESULTS

Over 200 arthropod taxa were collected during this study; 158 taxa were collected on Douglas-fir, of which 77 occurred in at least 5% of samples, and 90 taxa on vine maple, of which 57 occurred in at least 5% of samples. Most taxa occurred too infrequently for statistical analyses, but all were included in abundances used in analyses of functional groups and taxonomic diversity. The arthropod community on Douglas-fir was dominated by several species of aphids (*Cinara* spp. and *Elatobium abietinum* (Walker)), adelgids (*Adelges cooleyi* (Gillette), an exotic species), and thrips. The community on vine maple was dominated by the California maple aphid (*Periphyllus californiensis* (Shinji), an exotic species).

Douglas-fir

We were unable to detect significant treatment effects for most taxa, whether analyses were based on post-treatment data or on differences between pre- and post-treatment means. Of 26 tests on postharvest abundance, only two taxa showed a significant response to treatment (Table 1; Appendix: Table A1): Psocoptera (15%A > 15%D) and total arthropods (15%A > 75%A). When analyzed seasonally, however, Psocoptera responses were significant in August (15%A > 15%D, 40%D, and 40%A), but not in June. In contrast, 17 of 25 taxa and functional groups showed significant variation in abundance among blocks, as did predator-prey ratio and arthropod diversity (Table 1; Appendix: Table A1).

Detrended correspondence analysis (DCA) of both pre- and postharvest samples confirmed the results of univariate analyses in showing distinct clustering of treatment units by block (Fig. 2). DCA separated pre- and postharvest samples (low and high scores on Axis 1, respectively), but there was no evidence that the magnitude or direction of change was related to treatment. Results of blocked MRPP based on postharvest data were consistent with this result; treatments did not differ in species composition (A statistic = 0.0078, P = 0.14).

Few taxa showed evidence of position effects (edge vs. interior trees) in aggregated treatments. Miridae and Psocoptera were significantly more abundant on interior than on edge trees (Table 2; Appendix: Table A2). For Psocoptera, however, this effect was apparent in August, but not in June (data not shown). Three taxa (Syrphidae, *Scapheremaeus*, and Acaridae) showed a significant treatment-by-position interaction ($P \leq 0.03$). For these taxa, subsequent t tests revealed significant effects of position primarily at lower levels of retention: Acaridae were more abundant on interior trees in 15%A (but the opposite was true in 75%A), and *Scapheremaeus* and Syrphidae were more abundant on edge trees in 15%A and 40%A, respectively. Arthropod diversity did not differ between edge and interior positions (Table 2).

Vine maple

Patterns for arthropods on vine maple were generally similar to those on Douglas-fir. Only a single taxon, *Camisia carrolli* (Andre), showed a significant response to treatment (postharvest means for 40%A > 75%A, 40%D, and 15%D; Table 3; Appendix: Table A3). Geometrid larvae showed a significant response to treatment in August (P = 0.04), but not in June. Several taxa common in pretreatment samples were absent after treatment (Gallformers, Formicidae, Hypogasturidae, and Acaridae). Detrended correspondence analysis suggested a convergence (toward the mid-left of the ordination) in species composition among treatment units after harvest (Fig. 3). Blocked MRPP indicated no significant differences in postharvest species composition among treatments (A statistic = -0.0005, P = 0.49).

As with Douglas-fir, few taxa on vine maple showed a response to position (edge vs. interior) within aggregated treatments. Cantharid beetles were significantly more abundant on edge maples and linyphiid spiders on interior maples (Table 4; Appendix: Table A4). Chironomid flies and thrips sp. 2 showed significant treatment-by-position interactions. Both showed significantly greater abundance at forest edges at 15% reten-

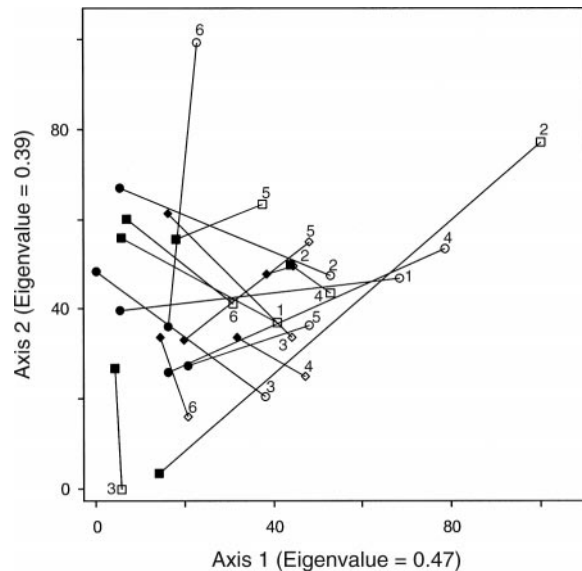


FIG. 3. Detrended correspondence analysis (DCA) of arthropod abundances (taxa in >5% of samples) on vine maple before (1996) and after (mean of 1999 and 2000) treatment in each of six green-tree retention treatments in three blocks in western Washington. Lines connect pre- and post-treatment data for each treatment unit. See Fig. 2 for other details.

tion, but no differences in abundance at higher levels of retention. Arthropod diversity did not differ between edge and interior positions on vine maple (Table 4).

DISCUSSION

This study was designed to evaluate arthropod responses to strongly contrasting densities and distributions of live trees retained during partial harvest of mature coniferous forests in the Pacific Northwest. Few taxa showed significant responses to treatment or to position within aggregated treatments, but many taxa varied significantly in abundance among blocks. This latter variation is not surprising given the latitudinal gradient (270 km) encompassed by sample locations (Progar and Schowalter 2002).

There are several possible explanations for the apparent absence of significant treatment effects in this

study. First, we observed marked changes in abundance and species composition in control treatments over time (1996 vs. 1999 and 2000), suggesting that effects of harvest treatments may simply have been masked by annual fluctuations in weather. Second, sampling intensity within treatment units (one Douglas-fir) may have been insufficient to capture true treatment means. However, we found virtually identical results for vine maple, for which we sampled three individuals per unit. Finally, responses to treatments may have varied among blocks, but assessment of treatment $\times$ block interactions would have required within-block replication of treatments. Schowalter et al. (2003) found that forest-floor arthropod assemblages responded differently among blocks to variable-density retention treatments, reflecting distinct initial conditions resulting from different management histories. We also note that our data are based on abundance per kilogram of plant sample. If arthropod intensity (number per kilogram) does not differ significantly among treatments, then abundance per hectare should be proportional to the density of retained trees, i.e., arthropod density (number per hectare) would decline along with the density of trees.

In previous studies, abundances of 25–30% of canopy arthropod taxa varied significantly among Douglas-fir age classes (Schowalter 1995, Progar and Schowalter 2002), but not between undisturbed and green-tree retention stands (Schowalter 1995). Generally, sap-sucking taxa, such as aphids and scale insects, respond positively and dramatically, whereas folivores, predators, and detritivores respond negatively, to canopy-opening disturbances (Schowalter and Ganio 2003). In eastern deciduous forests, many arthropod taxa responded significantly to changes in abiotic or plant conditions following canopy-opening disturbance (Schowalter et al. 1981, Shure and Phillips 1991, Schowalter and Ganio 1999). For example, Shure and Phillips (1991) found that arthropod abundance was significantly affected by gap size, with interior forest species declining, and species characteristic of open habitats increasing, with gap size. Ozanne et al. (1997) and Roland and Taylor (1997) reported reduced abun-

TABLE 4. Posttreatment (1999–2000) abundances, mean (and SE), of arthropod functional groups on vine maple, on edge and interior trees in aggregated retention treatments (15%A, 40%A, and 75%A).

Taxon or measure	No. arthropods/kg plant material		MSE			Position $F_{1,10}$	Treatment $\times$ position $F_{2,10}$
	Edge	Interior	Whole plot (treatment)	Split plot (position)	Treatment $F_{2,10}$		
Folivores	21.9 (5.2)	21.7 (12.3)	2.1	2.1	0.6	1.2	0.8
Sap-suckers	716.2 (348.6)	166.8 (44.8)	5.3	2.2	1.6	0.0	0.5
Gallformers	19.3 (19.3)	0.0 (0.0)	1.0	1.5	1.0	1.0	1.0
Predators	94.8 (23.0)	85.2 (21.3)	1.6	1.0	3.1	0.2	0.1
Detritivores	54.0 (18.4)	60.0 (19.5)	2.3	1.3	0.0	1.1	2.7
Miscellaneous	85.4 (25.1)	63.8 (26.9)	1.6	1.3	1.3	1.8	0.8
Total abundance	991.6 (366.3)	397.5 (71.9)	1.2	0.3	2.5	2.4	0.1
Shannon-Weiner index	1.5 (0.2)	1.7 (0.1)	0.1	0.0	0.0	2.7	0.9

Note: See Table 2 for other details.

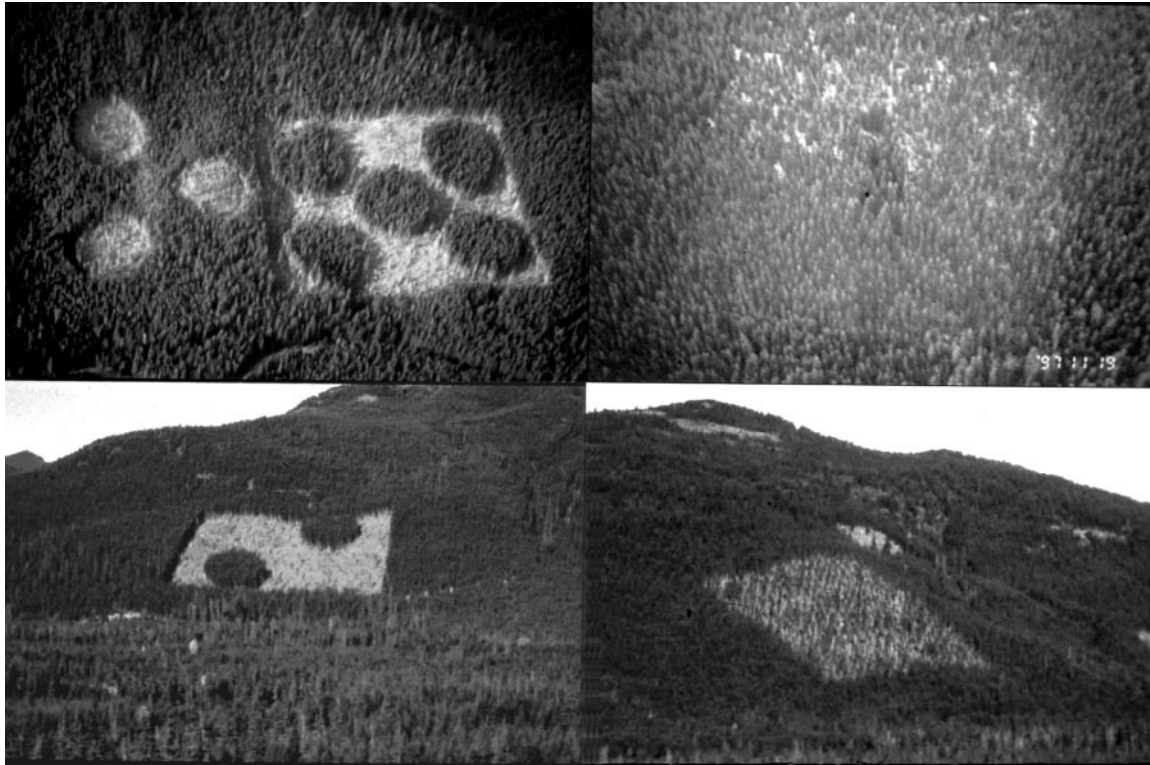


PLATE 1. Demonstration of Ecosystem Management Options plots at the Butte (BU) block near Randall, WA. Treatments (clockwise from upper left) are 75% aggregated (75%A) and 40% aggregated (40%A) retention; 40% dispersed (40%D) retention; 15% dispersed (15%D) retention; and 15% aggregated (15%A) retention. Plots are 13 ha; circular gaps or aggregates are 1 ha each. The 100% retention (untreated) plot is similar to the matrix surrounding the treated plots. Photos courtesy of the U.S. Forest Service (top two photos by Jon Nakae and Jim White; bottom two by Tom Savage).

dances of predaceous arthropods at forest edges. However, Gram et al. (2001) reported results similar to ours for folivorous caterpillars (although their canopy-opening treatments removed only 10% of the canopy), with responses within the range of background variation. They found that the number of significant responses increased from the first to the second year after treatment, suggesting that treatment effects could become more apparent over longer time periods, or if a larger proportion of the landscape were affected.

Arthropods in the upper canopy of forests may be relatively resistant to increased exposure resulting from canopy opening. By contrast, forest-floor arthropods may be more sensitive to altered microclimate, especially to desiccation resulting from increased solar exposure of the forest floor following canopy opening disturbance (Niemela et al. 1992, Niemela and Spence 1994, Work 2000, Schowalter et al. 2003). Our sampling method emphasized arthropods from the relatively sheltered interior of tree crowns of overstory dominants. However, arthropods on vine maple, generally shaded prior to treatment, also showed little response to canopy opening and increased solar exposure.

Although arthropod responses to green-tree retention treatments in this study generally were not significant, these data are important for management decisions. Ar-

thropods represent 80–90% of the diversity of plant and animal species in forests (Schowalter 2000) and can dramatically affect forest structure and function in ways that can stabilize primary production or interfere with management goals (Mattson and Addy 1975, Schowalter 2000).

Management for arthropod diversity and abundance may require greater attention to responses at larger spatial scales and over longer time periods. Changes in forest structure are known to increase the likelihood of outbreaks of some insect populations (Witcosky et al. 1986, Amman et al. 1988, Schowalter and Turchin 1993). Changes in plant species composition or growth patterns resulting from changes in harvest practices also affect arthropod diversity and abundance (e.g., Schowalter and Ganio 1998). The results of this study suggest that arthropods are more sensitive to large-scale gradients in environmental conditions or annual fluctuations in weather, than they are to local changes in canopy structure. However, further study will be necessary to determine whether, in the long term, persistent differences in canopy environment or host condition lead to differential reproduction or survival of arthropods.

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LITERATURE CITED

- Alfaro, R. I., and R. F. Shepherd. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by the Douglas-fir tussock moth. *Forest Science* 37:959–964.
- Amman, G. D., M. D. McGregor, R. F. Schmitz, and R. D. Oakes. 1988. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Canadian Journal of Forest Research* 18:688–695.
- Aubry, K. B., M. P. Amaranthus, C. B. Halpern, J. D. White, B. L. Woodard, C. E. Peterson, C. A. Lagoudakis, and A. J. Horton. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. *Northwest Science* 73(Special Issue): 12–26.
- Barker, M. G., and M. A. Pinard. 2001. Forest canopy research: sampling problems and some solutions. *Plant Ecology* 153:23–38.
- Biondini, M. E., C. D. Bonham, and E. F. Redente. 1985. Secondary successional patterns in a sagebrush community as they relate to soil disturbance and soil biological activity. *Vegetatio* 60:25–36.
- Blanton, C. M. 1990. Canopy arthropod sampling: a comparison of collapsible bag and fogging methods. *Journal of Agricultural Entomology* 7:41–50.
- Cardé, R. T. 1996. Odour plumes and odour-mediated flight in insects. Pages 54–70 in *Olfaction in mosquito–host interactions* (Ciba Foundation Symposium 200). John Wiley and Sons, Chichester, UK.
- Carey, A. B., D. R. Thysell, L. J. Villa, T. M. Wilson, S. M. Wilson, J. M. Trappe, W. Colgan, E. R. Ingham, and M. Holmes. 1996. Foundations of biodiversity in managed Douglas-fir forests. Pages 68–82 in D. L. Peterson and C. V. Klimas, editors. *The role of restoration in ecosystem management*. Society for Ecological Restoration, Madison, Wisconsin, USA.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74–86.
- Christensen, N. L., Jr., S. V. Gregory, P. R. Hagenstein, T. A. Heberlein, J. C. Hendee, J. T. Olson, J. M. Peek, D. A. Perry, T. D. Schowalter, K. Sullivan, G. D. Tilman, and K. A. Vogt. 2000. *Environmental issues in Pacific Northwest forest management*. National Academy Press, Washington, D.C., USA.
- Christensen, R. 1996. *Analysis of variance, design and regression*. Chapman and Hall, London, UK.
- Dudt, J. F., and D. J. Shure. 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology* 75:86–98.
- Fares, Y., P. J. H. Sharpe, and C. E. Magnusen. 1980. Pheromone dispersion in forests. *Journal of Theoretical Biology* 84:335–359.
- Foggo, A., C. M. P. Ozanne, M. R. Speight, and C. Hambler. 2001. Edge effects and tropical forest canopy invertebrates. *Plant Ecology* 153:347–359.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Franklin, J. F., L. A. Norris, D. R. Berg, and G. R. Smith. 1999. The history of DEMO: an experiment in regeneration harvest of northwestern forest ecosystems. *Northwest Science* 73(Special Issue):3–11.
- Gram, W. K., V. L. Sork, R. J. Marquis, R. B. Renken, R. L. Clawson, J. Faaborg, D. A. Fantz, J. Le Corff, J. Lill, and P. A. Porneluzi. 2001. Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest. *Ecological Applications* 11:1667–1679.
- Halpern, C. B., and D. McKenzie. 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. *Forest Ecology and Management* 154:215–225.
- Harborne, J. B. 1994. *Introduction to ecological biochemistry*. Fourth edition. Academic Press, London, UK.
- Hill, M. O., and H. G. Gauch. 1980. Detrended ordination analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Kohm, K. A., and J. F. Franklin, editors. 1997. *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, D.C., USA.
- Lewis, T. 1998. The effect of deforestation on ground surface temperatures. *Global and Planetary Change* 18:1–13.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey, USA.
- Majer, J. D., and H. F. Recher. 1988. Invertebrate communities on Western Australian eucalypts—a comparison of branch clipping and chemical knockdown procedures. *Australian Journal of Ecology* 13:269–278.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–522.
- McCune, B., and M. J. Mefford. 1995. *PC-Ord. Multivariate analysis of ecological data, version 4*. MjM Software Design, Gleneden Beach, Oregon, USA.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- Niemela, J., D. Langor, and J. R. Spence. 1992. Effects of clear-cut harvesting on boreal ground beetle assemblages in western Canada. *Conservation Biology* 7:551–561.
- Niemela, J., and J. R. Spence. 1994. Distribution of forest dwelling carabids: spatial scale and concept of communities. *Ecography* 17:166–175.
- Ozanne, C. M. P., C. Hambler, A. Foggo, and M. R. Speight. 1997. The significance of edge effects in the management of forests for invertebrate diversity. Pages 534–550 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy arthropods*. Chapman and Hall, London, UK.
- Parker, G. G. 1995. Structure and microclimate of forest canopies. Pages 73–106 in M. D. Lowman and N. M. Nadkarni, editors. *Forest canopies*. Academic Press, San Diego, California, USA.
- Progar, R. A., and T. D. Schowalter. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas-fir *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. *Ecography* 25:129–138.
- Progar, R. A., T. D. Schowalter, and T. Work. 1999. Arboreal invertebrate responses to varying levels and patterns of green-tree retention in northwestern forests. *Northwest Science* 73(Special Issue):77–86.
- Roelofs, W. L. 1995. Chemistry of sex attraction. *Proceedings of the National Academy of Sciences (USA)* 92:44–49.

- Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710–713.
- Romme, W. H., D. H. Knight, and J. B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *American Naturalist* **127**: 484–494.
- Romoser, W. S., and J. G. Stoffolano, Jr. 1998. The science of entomology. Fourth edition. McGraw-Hill, Boston, Massachusetts, USA.
- Ruangpanit, N. 1985. Percent crown cover related to water and soil losses in mountainous forest in Thailand. Pages 462–471 in S. A. El-Swaify, W. C. Moldenhauer, and A. Lo, editors. Soil erosion and conservation. Soil Conservation Society of America, Ankeny, Iowa, USA.
- SAS Institute. 2001. SAS user's guide. SAS Institute, Cary, North Carolina, USA.
- Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pages 235–252 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.
- Schowalter, T. D. 1995. Canopy arthropod community responses to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* **78**:115–125.
- Schowalter, T. D. 2000. Insect ecology: an ecosystem approach. Academic Press, San Diego, California, USA.
- Schowalter, T. D., and L. M. Ganio. 1998. Vertical and seasonal variation in canopy arthropod abundances in an old-growth conifer forest in southwestern Washington. *Bulletin of Entomological Research* **88**:633–640.
- Schowalter, T. D., and L. M. Ganio. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* **24**: 191–201.
- Schowalter, T. D., and L. M. Ganio. 2003. Diel, seasonal and disturbance-induced variation in invertebrate assemblages. Pages 315–328 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. Arthropods of tropical forests. Cambridge University Press, Cambridge, UK.
- Schowalter, T. D., W. W. Hargrove, and D. A. Crossley, Jr. 1986. Herbivory in forested ecosystems. *Annual Review of Entomology* **31**:177–196.
- Schowalter, T. D., D. C. Lightfoot, and W. G. Whitford. 1999. Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *American Midland Naturalist* **142**:281–290.
- Schowalter, T. D., and P. Turchin. 1993. Southern pine beetle infestation development: interaction between pine and hardwood basal areas. *Forest Science* **39**:201–210.
- Schowalter, T. D., J. W. Webb, and D. A. Crossley, Jr. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* **62**:1010–1019.
- Schowalter, T. D., Y. L. Zhang, and J. J. Rykken. 2003. Litter invertebrate responses to variable density thinning in western Washington forest. *Ecological Applications* **13**:1204–1211.
- Shure, D. J., and D. L. Phillips. 1991. Patch size of forest openings and arthropod populations. *Oecologia* **86**:325–334.
- Shure, D. J., and L. A. Wilson. 1993. Patch-size effects on plant phenolics in successional openings of the southern Appalachians. *Ecology* **74**:55–67.
- Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *Journal of Applied Ecology* **38**:1234–1252.
- Witcosky, J. J., T. D. Schowalter, and E. M. Hansen. 1986. The influence of time of precommercial thinning on the colonization of Douglas-fir by three species of root-colonizing insects. *Canadian Journal of Forest Research* **16**: 745–749.
- Work, T. T. 2000. Edge effects of clearcut harvesting on ground arthropod composition and predator community structure in old-growth Douglas-fir forests. Dissertation. Oregon State University, Corvallis, Oregon, USA.

APPENDIX

Tables showing mean posttreatment abundances of the 20 most abundant arthropod taxa on Douglas-fir by functional group in each of the six green-tree retention treatments, on Douglas-fir by functional group on edge and interior trees in aggregated retention treatments, on vine maple by functional group in each of the six green-tree retention treatments, and on vine maple by functional group on edge and interior trees in aggregated retention treatments are available in ESA's Electronic Data Archive: *Ecological Archives* A015-047-A1.