

Effect of Thinning on Flying Insect Communities Using Window Traps in Young Douglas-Fir (*Pseudotsuga menziesii* (Mirb.) Franco) Forests in the Pacific Northwestern America

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The response of insects to four thinning intensities (control, light-thin, heavy-thin, or light-thin with gaps) was examined in 40- to 60-year-old Douglas-fir stands on the Willamette National Forest in Oregon, USA. In both 2000 and 2001, flying insect assemblages were collected from window traps placed over the forest floor in the center of each treatment block during two annual intervals: 1) June through August (early-season) and 2) August through October (late-season). The seasonal responses by these insects showed statistically significant differences in species richness ($F=22.21$, $P < 0.001$) and mean abundance ($F=34.87$, $P < 0.001$). The greatest numbers of taxa generated via indicator species analysis were in the early season and within the treatment of light-thin with gap (L/G). In particular, the woodborer beetle, *Buprestis* (Buprestidae), was strongly associated with L/G (Indicator Value = 52.4, $P \leq 0.001$). Two beetle taxa, *Ampedus* (Elateridae, $IV=84.7$, $P \leq 0.001$) and members of Cermabycidae ($IV=58.4$, $P \leq 0.001$), were correlated significantly with early-season, whereas *Melanoplus* (Acrididae) was associated with late-season ($IV=21.3$, $P > 0.05$) and L/G ($IV=29.2$, $P \leq 0.05$). For all thinning treatments, the numbers of species and individuals were higher in the early season than the late season. Non-metric multidimensional scaling showed that Axis 1 (65%) and Axis 2 (27%) explained 92% of the variance. The former was strongly associated with thinning intensity, having higher coefficients of species richness ($r=0.645$) and species diversity ($r=0.583$). The multi-response permutation procedures showed a statistically significant difference for thinning intensity (T -statistics = -4.6322, A -statistics = 0.0479, $P < 0.0001$). These results suggest that heavier thinning can result in more diverse populations of flying insects, including herbivores and predators.

Keywords: biodiversity, Douglas-fir, flying insects, NMS, thinning, window trap

Since the 1930s and 1940s, the number of older forests has been steadily reduced in the landscape through selective cutting or clearcut patches of various sizes, while the amount of young, managed stands has vastly increased in the Pacific Northwest region of the United States (Hunter, 1993). Although silvicultural knowledge pertinent to the management of young ecosystems has become significant in that region, the public is voicing concern over the dramatic changes to those structures. This project is part of a multidisciplinary research effort by the U.S. Forest Service and it is called Young Stand Thinning and Diversity Study. Its silvicultural design is predicted to provide a sustainable rate of timber harvesting and maintain an array of late-successional characteristics, which is a primary requirement of the Pacific Northwest Forest Plan (Hunter, 1993; Ribe, 1999). The goal of that study is to determine to what extent these management strategies will accelerate the return of old-growth attributes and promote more diverse stands.

Forest insects are an important component that depends upon the complexity of a particular ecosystem (Schowalter et al., 1986; Stork et al., 1997; Schowalter and Ganio, 1998; Hunter, 2001, 2002). Their role during changing environmental conditions can significantly affect forest productivity and nutrient cycling (Schowalter et al., 1986; Hunter, 2002; Williams and Liebhold, 2002; Reynolds and Hunter, 2004). Nevertheless, studies of insects are difficult to conduct because of their taxonomic complexity and the generally un-replicated nature of forest treatments. In addition,

it is challenging to determine how insects respond to altered forest habitats and management practices. In some examinations, true tree-canopy arthropod communities have been compared between stands of different ages or as part of a tally of disturbance histories at the ecosystem level (Schowalter and Crossley, 1988; Schowalter, 1995, 2000; Lowman and Rinker, 2004). Current questions about the protection of biological diversity and forest health under alternative management scenarios require that quantitative data from replicated plots be available to assess insect responses to modifications in environmental conditions (Schowalter, 1995, 2000; McIntosh et al., 2001).

Taxa from all functional groups have shown significant reactions to silvicultural treatments, especially through an increase in the abundance of some herbivorous arthropods in relatively homogeneous stands or a decline in populations of detritivores and some predators in harvested stands (Progar et al., 1999). Reducing host-tree density should have a strong impact on herbivore populations because of changes in the microclimate, host-plant conditions, and the proximity of new hosts (Lorio, 1980; Schowalter et al., 1986; Amman et al., 1988; McMillin and Wagner, 1993; Muzika and Liebhold, 2000; Harrington et al., 2001). Although many predators and detritivores, as well as some herbivores, are less abundant or absent in disturbed stands (Kruess and Tschamtkke, 1994; Schowalter, 1994, 1995) and some defoliators are sensitive to tree spacing and, so, decrease in numbers in thinned stands (Batzler, 1976; Lance, 1983; Schowalter, 1995; Muzika and Liebhold, 2000), it is still critical that researchers know the scientific capacity for utilizing intercept traps, e.g., window traps. Evaluating trends in groups

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of flying insects that are associated with forest species and management regimes is important to our understanding of changes in the diversity and dynamics of populations or communities (Progar et al., 1999; Cronin et al., 2000; McIntosh et al., 2001). For example, the distribution and physical structure of forests can influence the spatial patterns of insect herbivore populations. Enhanced vegetative diversity may encourage predators by providing shelter or increasing the quantity of prey, which then helps maintain a high predator density. The largest role for herbivorous insects is to suppress the productivity of primary producers (Hodkinson and Hughes, 1982; Muzika and Liebhold, 2000).

The purpose of this current project was to assess the

responses of flying insects when different thinning treatments were applied within young, managed forest ecosystems in western Oregon. It was hypothesized that, as the level of thinning increased and tree spacings widened, the abundance of plant feeders (i.e., defoliators and bark beetles) and the predacious insects that preyed upon these herbivores would also grow.

MATERIALS AND METHODS

Study Sites

Study sites were located in the Willamette National For-

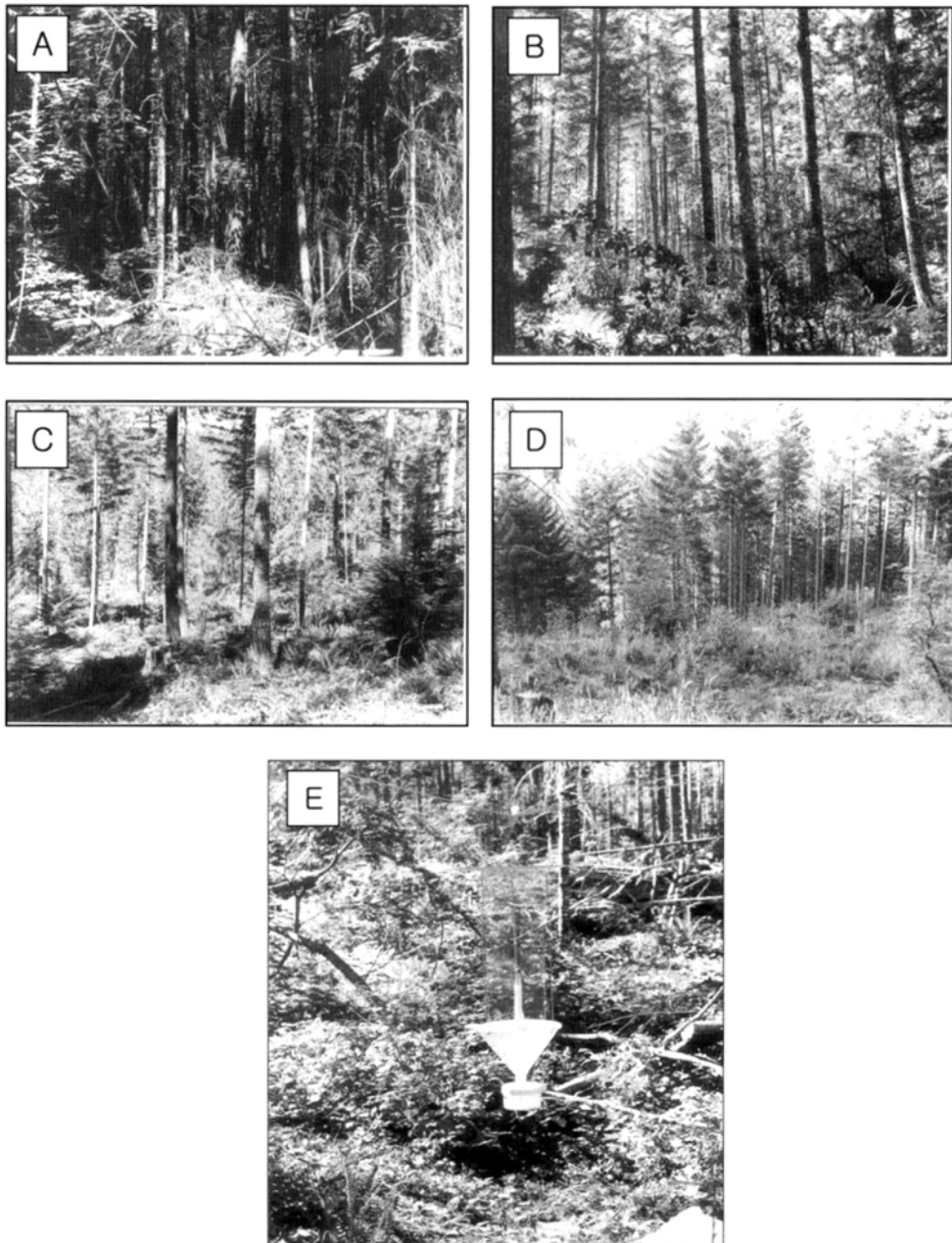


Figure 1. Four thinning treatments and a window trap on FLAT site in study areas within Willamette National Forest, Blue River District, in Oregon. (A) Control (CN: no treatment, usually 615 trees per hectare (tph)). (B) Light-thin (LT: 270 tph). (C) Heavy-thin (HT: 125 tph). (D) Light-thin with gaps (L/G: 270 tph). (E) A window trap (30 x 100 cm).

est (44° 07'30"N, 122° 15'00"W) on the western slopes of the Cascade Mountain Range, in Oregon, USA. These sites were thinned under one of four schemes: unthinned control (CN; no treatment, usually 615 residual trees per hectare [tph]), light-thin (LT; 270 tph), heavy-thin (HT; 125 tph), or light-thin with gaps (L/G; 270 tph) (Fig. 1). In each of four blocks, the areas to be thinned (~3 ha in size) were selected based on their homogeneity of stand age, soil class, size of thinning treatment, dominant tree species, slope, and elevation (Han and Kellogg, 2000). Each of these four treatments was in close proximity to each other in the four blocks, all of which were located in the TAP, MILL, FLAT, and WALK thinning areas on the Willamette National Forest (Hunter, 1993). This region receives approximately 4,000 mm of rainfall annually, with only 5% falling between July and August. The average yearly temperature is 10.1°C (ranging from 1.6°C in January to 18.9°C in July). Soils are generally well-developed on a tertiary volcanic substrate (Zobel et al., 1976). The dominant forest overstory comprises two conifer species, *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* [Raf.] Sarg. The climate of a typical Northwestern boreal forest zone encompasses a dry, hot summer and a wet and relatively warm winter. The dominant conifer trees were 40 to 60 years old, with heights from 18 to 27 m. Stands of >10 cm in diameter at breast height averaged approximately 615 tph.

Vegetation Analysis

Canopy covers were assessed with the moosehorn, a densitometer device, with the following values calculated after thinning: CN = 82% (\pm 10%), LT = 57% (\pm 18%), HT = 34% (\pm 20%), and L/G = 31% (\pm 24%). The greatest change observed in vegetative cover was a significant decrease in understory trees/tall shrubs (*Acer*, *Rhododendron*, *Vaccinium*) in all thinning treatments, relative to CN (Bohac et al., 1997). However, no plant species were lost completely during thinning, and species richness actually increased, mostly because of additional pioneering herbaceous species, e.g., *Epilobium* spp., *Senecio sylvaticus*, *Collomia heterophylla*, and *Cirsium* spp., that, although rarely encountered in the control plots, formed a significant presence on thinned sites. The more heavily thinned treatments, HT and L/G, consistently had higher frequency values for these species than did LT. Several other important species within the *Tsuga heterophylla* vegetation zone classification decreased in their percent coverage in thinned areas compared with CN. These included *Berberis nervosa*, *Acer circinatum*, *Polystichum munitum*, *Chimaphila menziesii*, *Achlys triphylla*, *Adenocaulon bicolor*, and *Viola sempervirens*. However, *Vancouveria hexandra*, *Trillium ovatum*, *Rubus ursinus*, and *Whipplea modesta* showed no significant changes in their cover or herb layers between thinned and CN plots. Although an increase in understory growth following thinning is generally expected for understory trees, shrubs, and herbs, insufficient time had elapsed in order to evaluate this parameter in the first year post-thin (Bohac et al., 1997). However, at five years post-treatment, data from understory tree/tall shrub tallies are starting to reveal expected treatment effects, although those results are not yet significant (Puettmann,

Prof. in Dept. Forest Science, Oregon State University, personal communication).

A Window Trap for the Flying Insects

A window trap is used to collect highly mobile or nocturnal insects. This method avoids the deficiencies of other insect-sampling techniques, such as shrub-bagging or beating sheets, which are not always as efficient when catching those more elusive types of invertebrates (Southwood, 1978; Schowalter, 1995; Schowalter and Canio, 1998; Yi, 2003; Yi et al., unpublished data). In the current study, one window trap, placed at the center of each thinning block, was employed over the entire collection period (Fig. 1). These traps were operated at all sites during 2000 (16 June through 14 October) and 2001 (18 June through 25 October). To account for the possibility of distinct seasonal changes in these arthropod communities, samples were gathered in the middle and at the end of each season: 11 August and 14 October in 2000, and 18 August and 25 October in 2001. Collections were made at the edges of the gaps in the L/G treatment to represent their highest impacts. For the other thinning treatments, samples were collected at the centers of the blocks to avoid special microhabitats (e.g., fallen logs, tree stumps, shrub thickets). Flying insects were identified to the finest possible taxonomic level of resolution, and samples also were examined microscopically and tabulated by taxon. A voucher of those arthropods was deposited at the Oregon State University Arthropod Collection in Corvallis, Oregon.

Statistical Analyses

Thinning treatments were assigned to stands in a randomized block design. Each of the four study areas was considered a regional replicate (block). Given this randomization, responses of individual taxa and groups to site (block) and thinning treatments were assessed by using a split-plot-in-time approach and analyses of variance (ANOVAs), with 3 df for block, 3 df for thinning treatment, and 1 df for season (Sokal and Rohlf, 1995). Three-way ANOVAs were used to test for differences in mean abundance and species richness in the insect communities (SAS Institute, 2001). Because these taxa occurred in insufficient numbers, this warranted a separate statistical evaluation of responses to sites, thinning treatments, seasons, and their interactions among these variables. All taxa of insects were averaged at the family level for statistical analyses of abundance patterns. *F*-statistics were calculated for site, thinning treatments, season, and interactions. The Tukey-Kramer procedure was used to compare treatment differences. In all analyses, the level of significance was at least $P = 0.05$ (SAS Institute, 2001). Species diversity was examined by alpha (α), beta (β), and gamma (γ) diversity. In general, α diversity is a measure of microhabitat diversity, β diversity indicates the change between communities or between microhabitats within homogeneous communities, and γ diversity is the total diversity of all sampled communities within a geographic area (Cody, 1986; McCune and Grace, 2002; Yi and Moldenke, 2005). These averaged data were analyzed via PC-ORD version 4.28 for multivariate analyses (McCune and Mefford, 1999; McCune and Grace,

2002). For each insect sample, the averaged main matrix had high beta diversity, moderate to extreme row and column skewness, and a high coefficient of variation among the sums of the columns (species) in the matrix. Thus, rare species that occurred in <5% of the samples were deleted, and the data were transformed by taking logarithms. Because Beals-smoothing is appropriate for heterogeneous community data sets with a large number of zeros in the data matrix, it was implemented to equalize the weights of abundant and less abundant species (Beals, 1984; McCune, 1994). Sørensen distance measures and data transformations were used for all analyses. Non-metric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976; Clarke, 1993) is an iterative method based on rank distances between sample units. It is particularly useful for ecological

gradient studies because of its lack of assumptions about the distribution or type of data and its general robustness. With NMS, the number of factors structuring a complex arthropod community can be determined so that the overall distribution of species assemblages may be qualitatively summarized across the gradients of different thinning levels. Likewise, Sørensen distance measures were applied here to calculate and ordinate the distances among site, tree species, and treatments in species space with species abundance. NMS was used in lieu of other ordination methods because it avoids the zero-truncation problems of Beals-smoothing. Multi-response permutation procedures (MRPP) were conducted with the software PC-ORD, a nonparametric protocol for testing the null hypothesis of no differences among groups of thinning treatments in the data matrix.

Table 1. Overall mean (standard errors in parentheses) abundances (number/a window trap) over two seasons (Early, June through August; Late, August through October) and for four thinning treatments (CN, control; LT, light-thin; HT, heavy-thin; L/G, light-thin with gaps) in young Douglas-fir stands on the Willamette National Forest in Oregon during 2000 and 2001.

Taxa	Early				Late			
	CN	LT	HT	L/G	CN	LT	HT	L/G
Herbivores	6.25 (1.80)	14.50 (7.14)	19.63 (7.25)	39.00 (10.07)	0.43 (0.30)	1.00 (0.38)	3.38 (1.19)	9.13 (2.98)
Buprestidae	-	0.13 (0.13)	0.50 (0.27)	1.88 (0.48)	-	-	-	1.63 (0.96)
Cerambycidae	0.38 (0.26)	1.00 (0.19)	2.50 (1.22)	2.38 (0.82)	0.14 (0.14)	-	-	0.25 (0.16)
Elateridae	4.00 (1.22)	9.88 (5.49)	4.50 (2.15)	13.38 (6.73)	0.14 (0.14)	0.71 (0.36)	0.38 (0.26)	0.75 (0.41)
Meloidea	0.25 (0.16)	-	0.25 (0.16)	3.88 (2.50)	-	-	-	0.13 (0.13)
Mordellidae	-	0.25 (0.25)	3.63 (1.84)	5.13 (1.86)	-	-	1.13 (0.88)	0.50 (0.33)
Scolytidae	0.13 (0.13)	1.25 (1.11)	0.63 (0.38)	0.38 (0.26)	-	-	-	0.25 (0.25)
Other beetles	0.13 (0.13)	0.25 (0.16)	0.25 (0.16)	0.50 (0.38)	-	-	-	0.25 (0.16)
Acroceridae	0.38 (0.26)	0.38 (0.38)	0.63 (0.32)	1.25 (0.53)	-	-	-	0.13 (0.13)
Other Diptera	0.38 (0.26)	-	-	0.25 (0.16)	0.14 (0.14)	0.14 (0.14)	0.13 (0.13)	0.50 (0.50)
Pentatomidae	-	0.13 (0.13)	2.50 (1.05)	0.75 (0.16)	-	0.14 (0.14)	0.75 (0.37)	1.25 (0.65)
Other Heteroptera	0.13 (0.13)	0.50 (0.27)	0.75 (0.37)	2.75 (0.70)	-	-	0.13 (0.13)	1.00 (0.50)
Homoptera	0.25 (0.25)	0.13 (0.13)	0.25 (0.16)	1.38 (0.73)	-	-	0.13 (0.13)	0.50 (0.27)
Hymenoptera	-	0.50 (0.38)	2.75 (1.69)	4.63 (2.48)	-	-	0.25 (0.16)	0.50 (0.33)
Lepidoptera	0.13 (0.13)	0.13 (0.13)	-	0.13 (0.13)	-	-	0.13 (0.13)	-
Acrididae	-	-	0.50 (0.33)	0.38 (0.26)	-	-	0.38 (0.18)	1.50 (0.60)
Plecoptera	0.13 (0.13)	-	-	-	-	-	0.00	-
Predator	3.50 (0.82)	7.88 (3.66)	9.38 (3.09)	13.75 (4.31)	0.43 (0.30)	1.43 (0.69)	2.13 (1.06)	8.50 (2.91)
Coleoptera	1.38 (0.63)	2.13 (0.93)	3.88 (2.26)	7.25 (3.13)	0.29 (0.29)	0.43 (0.30)	0.38 (0.26)	4.00 (2.03)
Asilidae	0.63 (0.32)	4.75 (3.77)	1.50 (0.71)	3.50 (1.50)	-	-	0.38 (0.26)	1.38 (0.50)
Other Diptera	0.88 (0.40)	0.75 (0.53)	2.25 (1.52)	0.75 (0.25)	0.14 (0.14)	0.71 (0.57)	0.50 (0.33)	1.13 (0.58)
Heteroptera	-	0.13 (0.13)	0.75 (0.41)	0.75 (0.41)	-	-	0.13 (0.13)	0.88 (0.44)
Hymenoptera	0.50 (0.19)	0.75 (0.37)	0.13 (0.13)	1.00 (0.60)	-	0.75 (0.75)	0.29 (0.18)	1.00 (0.27)
Mecoptera	-	-	0.13 (0.13)	0.25 (0.16)	-	-	-	-
Neuroptera	0.13 (0.13)	-	-	0.25 (0.16)	-	-	-	0.13 (0.13)
Raphidioptera	-	-	0.13 (0.13)	-	-	-	-	-
Detritivores	3.38 (1.08)	5.88 (1.01)	3.88 (0.64)	2.88 (0.67)	1.57 (0.53)	3.00 (1.02)	2.63 (0.98)	3.25 (0.84)
Coleoptera	1.13 (0.88)	1.13 (0.48)	0.50 (0.33)	0.75 (0.37)	-	0.29 (0.18)	-	0.38 (0.26)
Aradidae	0.50 (0.19)	0.13 (0.13)	-	-	-	-	-	0.13 (0.13)
Hodotermitidae	0.75 (0.25)	3.13 (1.22)	2.63 (0.68)	1.63 (0.38)	1.00 (0.53)	1.71 (0.64)	1.63 (1.08)	1.75 (0.88)
Psocoptera	1.00 (0.57)	1.50 (0.80)	0.75 (0.31)	0.50 (0.38)	0.57 (0.30)	1.00 (0.44)	1.00 (0.38)	1.00 (0.63)
Mean Species Richness	6.88 (0.93)	7.88 (1.16)	11.63 (1.71)	15.63 (2.58)	1.83 (0.31)	3.67 (0.71)	5.14 (1.20)	9.38 (1.95)
Shannon-Wiener diversity (H')	1.65 (0.14)	1.44 (0.17)	2.11 (0.13)	2.18 (0.15)	0.52 (0.18)	1.07 (0.25)	1.26 (0.29)	1.82 (0.27)

-, indicates data not available.

MRPP is useful when analyzing ecological data because it does not require assumptions of normality and constant variance (Biondini et al., 1988; McCune and Mefford, 1999; McCune and Grace, 2002; Schowalter et al., 2003). Values for indicator species were calculated according to the method of Dufrêne and Legendre (1997) – this is a simple, intuitive solution for identifying which species may serve as an indicator(s) of a particular environmental condition. This method combines a species' relative abundance with its relative frequency of occurrence in various groups of sites. The resultant values describe a taxon's reliability for indicating a grouping parameter, such as thinning and season. Data represent the percentile with p-values ($P < 0.05$), based on the proportion of 1000 randomized re-grouping trials that equal or exceed the maximum indicator value observed (i.e., a Monte Carlo test).

RESULTS

In all, 1331 individual flying insects were collected (486 individuals in 2000 and 845 individuals in 2001), which comprised 12 orders and 73 family groups. When the early- and late-season components were accounted for in each year, these data could be divided into sampling groups of 12

orders, 60 families, and 1043 individuals (early) and 9 orders, 44 families, and 287 individuals (late). Table 1 shows the overall mean abundance by season and thinning treatment. Only three taxa – *Ampedus* (Elateridae), *Acrocera* (Acroceridae) in herbivores, and *Asilus* (Assilidae) in predators – were found in both seasons. Generally speaking, as thinning intensity increased, the overall mean abundance of herbivores, including predators, rose both early and late in the collecting period. Table 1 presents those clear seasonal and thinning differences and demonstrates that the mean abundance ($F=22.21$, $P < 0.0001$) and mean species richness ($F=34.87$, $P < 0.0001$) of early-season are higher than late-season (Fig. 2).

Both the species richness and mean abundance were significantly different for thinning intensities: between CN and HT or L/G, and between HT and L/G in early-season; and between CN and HT or L/G in late-season (Tukey-Kramer procedure, $P < 0.05$; Fig. 2A, B). Seasonal effects showed

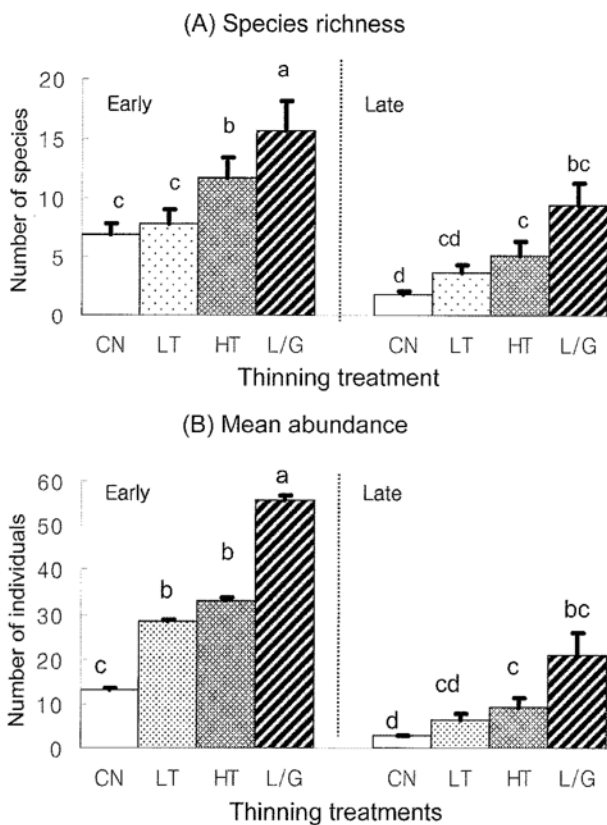


Figure 2. Species richness (A) and mean abundance (B) with standard error for flying insects in each treatment (CN, control; LT, light-thin; HT, heavy-thin; L/G, light-thin with gaps) and each season (Early, June to August; Late, August to October) in 2000 and 2001. Bars labeled with the different letters mean statistically significant difference ($P < 0.05$) and bars with bc or cd mean no statistically significant difference only between b and cor c and d, respectively ($P > 0.05$, by Tukey-Kramer procedure).

Table 2. Results of three-way ANOVA for the response of flying insect communities based on species richness and mean abundance.

Effects	DF	Species richness		Mean abundance	
		F Value	Pr > F	F Value	Pr > F
Block	3	5.93	0.003	5.49	0.004
Season	1	34.87	<.0001	22.21	<.0001
Block*Season	3	0.13	0.940	1.62	0.209
Treat	3	15.12	<.0001	7.31	0.001
Block*Treat	9	2.68	0.023	1.55	0.183
Season*Treat	3	0.25	0.859	1.11	0.360
Block*Season*Treat	9	0.18	0.994	0.43	0.907

Table 3. Indicator values (IV, %) based on relative abundance from window traps over two seasons (Early, June to August; Late, August to October) and in four thinning treatments (CN, control; LT, light-thin; HT, heavy-thin; L/G, light-thin with gaps) during 2000 and 2001.

Taxa	Season		Treatment			
	Early	Late	CN	LT	HT	L/G
Buprestis	17.7	-	-	-	-	52.4**
Cerambycidae	58.4**	-	-	-	-	18.7
Ampedus	84.7**	-	-	-	-	26.9
Mordella	30.9*	-	-	-	-	25.6
Mycetophagidae	18.7*	-	-	12.3	-	-
Acrocera	32.5*	-	-	-	-	17.8
Asilus	52.1*	-	-	-	-	28.1
Bradysia	15.6*	-	3.0	-	-	-
Tachinidae	4.5	-	21.4*	-	-	-
Aradidae	12.6	-	19.5*	-	-	-
Pentatomidae	23.3*	-	-	-	-	-
Reduviidae	9.6	-	-	-	-	26.6*
Thyreocoridae	12.6	-	-	-	-	25.8*
Cercopidae	18.7*	-	-	-	-	11.3
Vespidae	13.4	-	-	-	-	27.4*
Melanoplus	-	21.3	-	-	-	29.2*

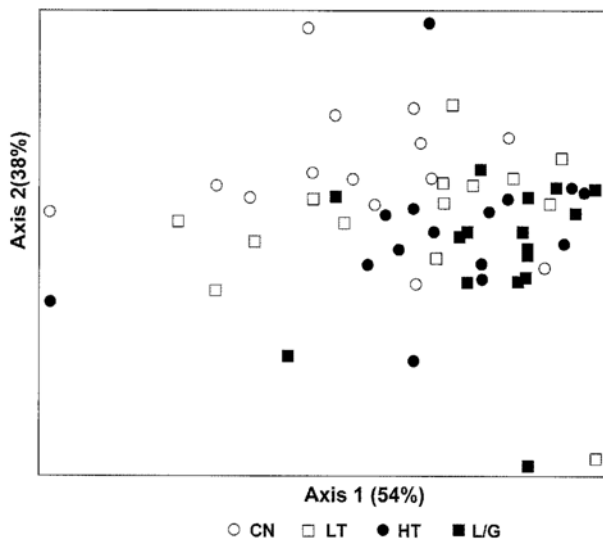


Figure 3. Nonmetric Multidimensional Scaling for evaluation of flying insect responses to four thinning intensities in Willamette National Forest, Blue River District, in Oregon. CN, open circles; LT, open rectangle; HT, solid circles; L/G, solid rectangle.

on both species richness and mean abundance (Fig. 2; Table 2). From the three-way ANOVA tests, the seasonal responses of flying insects revealed a statistically significant difference in species richness ($F=22.21$, $P < 0.001$) and mean abundance ($F=34.87$, $P < 0.001$). The interaction effects were not significant for all the species richness and mean abundance values ($P > 0.05$).

Indicator species analysis (ISA) selected 16 taxa that responded to one thinning treatment or season, with indicator values (IVs) being presented as percentiles with $P \leq 0.05$ (Table 3). Larger IVs meant a greater association between a particular taxon and treatment or season. Most of the taxa generated by ISA indicated early-season and L/G treatment. For example, *Buprestis* wood borers (Buprestidae) were strongly associated with L/G (IV=52.4, $P \leq 0.001$), whereas two taxa, Cermabycidae (IV=58.4, $P \leq 0.001$) and *Ampedus* (IV=84.7, $P \leq 0.001$), were significantly associated with early-season while *Melanoplus* (Acrididae) was associated with both late-season (IV=21.3, $P > 0.05$) and L/G (IV=29.2, $P \leq 0.05$).

In the NMS ordination, Axis 1 (65%) and Axis 2 (27%) explained 92% of the variance between sampling points (Monte Carlo test based on 50 randomizations; Fig. 3). Its final stress was 13.1673% and final instability was 0.00498. Axis 1 was strongly associated with thinning intensity, with higher coefficients of species richness ($r=0.645$) and species diversity ($r=0.583$). Coefficient values of the indicator species selected by ISA were evaluated with NMS results, and demonstrated that *Buprestis* ($r=0.842$), Cermabycidae ($r=0.760$), *Ampedus* ($r=0.451$), *Mordella* ($r=0.867$), Mycetophagidae ($r=0.807$), *Acrodera* ($r=0.700$), and *Asilus* ($r=0.824$) had higher coefficients with Axis 1; while higher coefficients with Axis 2 were found with Tachinidae ($r=-0.552$), Aradidae ($r=0.533$), Pentatomidae ($r=0.656$), Reduviidae ($r=0.481$), Thyreocoridae ($r=0.468$), Vespidae ($r=0.643$), and *Melanoplus* ($r=0.431$).

MRPP tests were applied to find statistically explicit differ-

ences among treatments, using the graphical results shown by the NMS ordination (Fig. 3). These tests revealed statistically significant differences for thinning treatments (T -statistics = -4.6322, A -statistics = 0.0479, $P < 0.0001$).

DISCUSSION

This project was conducted as a part of a multi-disciplinary study, the goal of which is to determine to what extent different thinning strategies accelerate the return of old-growth characteristics and promote more diverse forests. Concerns over the protection of biological diversity and forest health under various management scenarios require that quantitative data from replicated plots be available for assessing insect responses to changing environmental conditions (Showalter, 1995). Although various previous research has demonstrated that litter-dwelling invertebrates are highly responsive to thinning intensity when habitats are altered (Showalter et al., 2003; Yi, 2003; Yi and Moldenke, 2005), it is also valuable for ornithologists, forest managers, other scientists, and the public to monitor the response of mobile invertebrates to such practices. Therefore, this study with window traps was designed to examine the effects of thinning activity on the behavior of flying insects. Here, the greatest response was to heavier thinning (Table 1). Evaluating these trends, as they are associated with forest species and management regimes, may prove important to our understanding of changes in the diversity and dynamics of forest communities (Progar et al., 1999; Hunter, 2002).

All insect taxa representing functional groups have shown significant reactions to thinning treatments (Progar, 1999; Yi and Moldenke, 2005). Because vegetation communities also respond afterwards (Bohac et al., 1997), the hypothesis tested in the current research was that the abundance of herbivorous arthropods, including wood borers (Buprestidae) and bark beetles (Scolytidae), would increase in thinned stands. In fact, numbers of the latter type did grow in LT during the early season (Table 1). Likewise, as hypothesized, the abundance of predators was higher in thinned stands. A reduction in host-tree density should have strong effects on herbivore populations because of changes in microclimate, host-plant conditions, and the proximity of new hosts (Lorio, 1980; Schowalter et al., 1986; Amman et al., 1988; McMillin and Wagner, 1993; Hunter, 2001). Many predators and detritivores, as well as some herbivores, are already known to be less abundant or absent in disturbed stands (Kruess and Tscharrntke, 1994; Schowalter, 1994, 1995), and some defoliators are sensitive to tree spacing, decreasing their populations in thinned stands (Batzer, 1976; Lance, 1983; Schowalter, 1995). Nevertheless, it is useful to obtain data from the use of intercept traps because effects on the composition of functional groups provide further information about potential influences on ecosystem processes (Progar et al., 1999). Some plant-association invertebrates are considered vectors for plant pathogens (Progar et al., 1999), and measurements of such groups are useful when monitoring disease epidemiology, including Pine Wilt Disease in Europe and Asia (Hasegawa et al., 2004). Because many of those plant-associated invertebrates

are prey for some vertebrates, e.g., birds, broader generalizations of vertebrates can be derived from the data used to assess the availability of that prey (Pettersson et al., 1995; Lehmkuhl et al., 1999). By evaluating the results of tests on insect abundance after various thinning operations, mammalogists, ornithologists, herpetologists, and other ecologists can glean useful knowledge about the balance of roles between populations of prey and insectivores, which can then be utilized in efforts to better manage forest ecosystems that will increase the biodiversity of insects as prey for mammals, birds, amphibians, etc. Because so little is known about the distribution of flying insect diversity and biomass across the forested landscape, data collected from unthinned control stands contribute substantially to the beginnings of a baseline. This information is significant not only for the study of insect ecology, but also insofar as it estimates the abundance, temporal presentation, and range of food items available for vertebrate predation. Other investigations of vertebrate groups have provided similar results, with some species decreasing and some increasing in response to thinning (Hooven and Black, 1976; Sullivan, 1979; Gunther et al., 1983; Garman, 2000, 2001; Larson, 2001; Sullivan et al., 2001; Hagar and Starkey, 2002; Hager, 2003; Hayes et al., 2003). Although the study of diversity among insects is less often utilized than that of vertebrates when making forest-management decisions, primarily because of the taxonomic complexity and un-replicated nature of the former type, it is true that insect research should receive more attention so that the resulting data can be incorporated into evaluations of prey availability within the forest ecosystem.

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