AN ABSTRACT OF THE THESIS OF

Brett L. Schaerer for the degree of Master of Science in Entomology presented on March 17, 2000. Title: Arthropod Community Structure in Regenerating Douglas-fir and Red Alder Forests: Influences of Geography, Tree Diversity and Density

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Timothy D. Schowalter

The structuring of canopy arthropod communities was reviewed and investigated in relation to tree species diversity and its component factors, interspersion of different species and density of each tree species. Fifteen treatments of Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*) (various densities and proportions of each) were randomly assigned to 0.073 ha plots, replicated three-fold at each of two locations in Western Oregon: the Cascade Head Experimental Forest and the H. J. Andrews Experimental Forest. The six treatments used in this study were two densities of Douglas-fir and red alder monoculture (1000 trees/ha and 500 trees/ha), and mixtures of Douglas-fir and red alder (500 trees/ha of each) planted simultaneously or red alder planted 6 years after the Douglas-fir. Trees were initially planted in 1985-1986. The arthropod communities were sampled in the summer of 1998 by bagging and pruning branches from the mid-canopy of both tree species.

Multivariate analyses distinguished the arthropod communities found on each tree species and geographical location, but not among the different diversity and density treatments. Many arthropod taxa and functional groups residing on a single tree species had significantly different abundances between locations. The most commonly encountered taxon, *Adelges cooleyi* Gillette (Homoptera: Adelgidae), was most abundant

on Douglas-firs in the 500 trees/ha monoculture and the mixture with younger red alder, and least abundant in the mixture with both species planted simultaneously (the 1000 trees/ha Douglas-fir monoculture was intermediate). Adelgids showed no significant response to location, but did respond to combinations of location×treatment. The functional group of sap-feeders was dominated by adelgids, and showed similar treatment differences on Douglas-fir. Defoliators on red alder responded in abundance to location, treatment (most abundant in the 500 trees/ha monoculture and even-aged mixture, least abundant in the 1000 trees/ha monoculture), and location×treatment.

This study demonstrated that tree species and geographical location are the primary determinants of forest arthropod community composition at this spatial scale. However, tree species diversity and density can affect the abundance of certain arthropod taxa, apparently through some combination of resource quality and plant apparency.

Arthropod Community Structure in Regenerating Douglas-fir and Red Alder Forests: Influences of Geography, Tree Diversity and Density

by

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INTRODUCTION

Insects and other arthropods are ubiquitous in terrestrial ecosystems. Their roles as herbivores, decomposers, predators, and pollinators are important in primary productivity, nutrient cycling, energy flow, and succession. They greatly affect the growth and reproduction of plants (Evans 1984, Urbanek 1989, Doak 1992) as well as regulate ecosystem processes (Mattson and Addy 1975, Romme *et al.* 1986, Schowalter and Sabin 1991, Schowalter *et al.* 1991, Davidson 1993, Haack and Byler 1993). From the human perspective, arthropods can have large beneficial and detrimental impacts on resources of interest. Thus, factors affecting the structure and function of arthropod communities are of immense interest and importance.

The typically coniferous forests of the Pacific Northwest are no exception. Arthropods, though usually not a conspicuous component of the overall community, can have far-reaching effects on the forest. Low to moderate levels of herbivory usually go unnoticed, perhaps even spurring compensatory growth by the consumed plants (Trumble *et al.* 1993). However, during 'pest' outbreaks, the effects of insects on trees become especially apparent: defoliation, reduced growth, damaged wood (collectively, 'growth impact') and mortality can be extensive (Kulman 1971, Speight and Wainhouse 1989, Urbanek 1989, Haack and Byler 1993). Hence, much of the current forest arthropod literature concentrates on the causes, prevention, and treatment of pest outbreaks (e.g. Berryman *et al.* 1987, Speight and Wainhouse 1989, Moore and Francis 1991, Moore *et al.* 1991, Haack and Byler 1993, Schowalter 1996, Mason *et al.* 1992, 1997).

Concentrating on one tree species of major ecological and economic importance in Pacific Northwest forests, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco,

population outbreaks of several species of insect phytophages adversely affect the growth and survival of mature trees. These include: spruce budworm, *Choristoneura occidentalis* Freeman (Mason *et al.* 1992, 1997, Shepherd 1994), Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Berryman 1978, Wright *et al.* 1984, Mason and Wickman 1991, Shepherd 1994), Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Rudinsky 1962, Wright *et al.* 1984), Douglas-fir bud moth, *Zeiraphera hesperiana* Mutuura and Freeman (Furniss and Carolin 1977), and several other minor pests (Furniss and Carolin 1977, Shepherd 1994).

On young Douglas-firs in nurseries or Christmas tree plantations, the Cooley Spruce gall adelgid, *Adelges cooleyi* (Gillette), frequently attains population densities high enough to warrant pest status (Saunders and Barstow 1970, Lasota and Shetlar 1986). *A. cooleyi* is found in greatest abundance in the top two-thirds on 1.5-1.8m Douglas-firs (Lasota and Shetlar 1986), although a mid-canopy sample is representative of the population on the entire tree (Johnson *et al.* 1977).

A. cooleyi is a polymorphic species with a complex life cycle utilizing both spruce and Douglas-fir. On spruce, immatures develop and form galls, emerging as winged parthenogenic, females, which can re-infest spruce or migrate to their alternate host, Douglas-fir. On Douglas-fir, the progeny of the spruce emigrants overwinter as immatures and develop in the spring, sprouting a protective wool-like covering. When they reach adulthood, they can take one of two forms: wingless parthenogenic females and winged parthenogenic females. The wingless morph parthenogenically re-infests Douglas-fir (and can continue this life cycle indefinitely). The winged morph migrates from Douglas-fir back to spruce, producing sexual offspring which mate to produce the galling morph (Lasota and Shetlar 1986).

Red alder, *Alnus rubra* Bong., is another important tree species in Pacific Northwest forests. Insects known to defoliate red alder (often severely) include: the alder flea beetle, *Altica ambiens* LeConte, the alder woolly sawfly, *Eriocampa ovata* (L.),

striped alder sawfly, *Hemichroa crocea* (Fourcroy), the leafroller *Epinotia albangulana* (Walsingham), *Xylomyges simplex* (Walker), which also feeds on Douglas-fir, and the tent caterpillars *Malacosoma californicum* (Packard) and *M. disstria* Hübner (Furniss and Carolin 1977). Of these, the alder flea beetle is well known for its extreme population fluctuations, and at high densities it is capable of completely defoliating alders (T. D. Schowalter and D. E. Hibbs, personal communication).

Research from agricultural systems has demonstrated that incorporating heterogeneity into the plant community (polyculture) tends to lower populations of specialist herbivores, decreasing the possibility of severe insect outbreaks (Pimentel 1961, Tahvanainen and Root 1972, Root 1973, Cromartie 1975, Risch 1981, Brown and Ewel 1987, Stamps and Linit 1998). However, the evidence for this effect is mixed, and many plant diversity-herbivore population studies fail to account for differences in host plant size or quality in the experimental design (Karieva 1983). Two factors might be responsible for minimizing pest outbreaks in more diverse plant communities: plant density and plant diversity (Bach 1980).

Assuming an equal total plant density, the density of any single plant species is necessarily lower in more diverse plant communities. For specialist herbivores, more energy is expended traveling between host plants that are further apart. Also, the carrying capacity for specialist phytophages is lower with lower host plant density because there is less available habitat. Host density within pine monocultures has a demonstrated positive correlation with populations of southern pine beetle, *Dendroctonus frontalis* Zimmerman (Schowalter and Turchin 1993, Schowalter 1996) and mountain pine beetle, *D. ponderosae* Hopkins (Sartwell and Stevens 1975).

The other mechanism that might work to lower populations of specialist herbivores in diverse plant communities is the presence and interspersion of non-host plants. Non-hosts release a variety of chemicals, which can disorient or repel specialist herbivores searching for a host plant, effectively hiding the host plants (Visser 1986, Bell

1990). In addition, interspersed non-hosts provide physical barriers to movements between hosts. Thus, the vegetation surrounding a given plant may provide resistance to certain herbivores by association (Tahvanainen and Root 1972).

No studies have compared the relative importance of these main factors (density alone vs. non-host interspersion) in structuring forest arthropod communities as a whole. Schowalter and Turchin (1993) showed that both of these factors tend to limit the population growth of a single species, southern pine beetle.

The concept of polyculture has received relatively little attention in temperate forests, despite its recommendation as a potential management tool to avoid or mitigate insect outbreaks (Sartwell and Stevens 1975, Franklin *et al.* 1989, Stamps and Linit 1998). This is especially surprising, since forests managed for timber share many important characteristics with agricultural ecosystems: both are dense, even-aged, single-species plantings covering large areas, with harvest cycles shorter than natural plant life cycles, and occasional large-scale disturbances such as pest outbreaks or fires (Franklin *et al.* 1989).

It should be noted that there are also important differences between crop and timber production. Irrigation, fertilization, and pesticide use are common in crop systems but rare in forests. Herbicides are used more extensively to control competing vegetation in timber-managed forests (Rose *et al.* 1999). Also, harvest cycles in timber-managed forests are orders of magnitude greater than in crops, allowing for long-term population growth of herbivores.

Conventional management strategies for regenerating forests are designed to minimize competitive pressures on species of economic interest (Tarrant 1961 and references therein, Franklin *et al.* 1989, Rose *et al.* 1999). Obviously, competition can be a major source of chronic plant stress; reducing or altering growth, causing mortality, and increasing susceptibility to insect attack (Rudinsky 1962, Safranyik 1985, Speight and Wainhouse 1989). However, arthropod damage can also reduce growth (Kulman 1971)

or induce vulnerability to secondary pests (Rudinsky 1962, Wright *et al.* 1984). Insect phytophages often damage young trees and those on plantations more than those in developed forests (Furniss and Carolin 1977, Speight and Wainhouse 1989, Urbanek 1989). This is because defenses in young trees are minimal (growth has priority over defense in energy allocation), and a given amount of consumption causes a relatively greater amount of damage to younger trees. Polyculture in young Douglas-fir plantations may be a viable option to decrease pest damage (Moore *et al.* 1991, Schowalter and Turchin 1993, Schowalter 1996, Stamps and Linit 1998), increase soil fertility and nutrient availability (Tarrant 1961, Binkley 1984, Binkley *et al.* 1984, Moore and Francis 1991, Giardina *et al.* 1995), and better mimic natural forest processes to meet alternative (non-harvest) forest management goals (Swindel and Grosenbaugh 1988, Franklin *et al.* 1989).

The difficulty of manipulating forests on large scales has limited experimental tests of hypotheses concerning plant heterogeneity and arthropod community or population structure. Most of these studies have concentrated on the arthropod communities in forests of different ages or management histories (e.g. old-growth vs. mature or natural succession vs. clear-cut and planted), rather than experimentally manipulated stand diversity (Schowalter 1989, 1995, 1996, Lattin 1993, Greenberg and McGrane 1996, Niemelä 1997). The few experimental studies have shown that some insect species respond in abundance to manipulation of stand diversity (Moore *et al.* 1991, Schowalter and Turchin 1993).

The objective of this study was to compare forest arthropod communities in plots with experimentally manipulated densities and mixtures of Douglas-fir and red alder as part of an established study testing the effects of these treatments on tree performance. Thus, effects of host density and non-host interspersion could be distinguished, allowing each factor's role in structuring arthropod communities to be evaluated separately.

I expected to find differences in arthropod communities residing on each tree species (Murdoch *et al.* 1972, Furniss and Carolin 1977, Southwood *et al.* 1979), and (to a lesser extent) at each location (Progar *et al.* 1999). While I was uncertain whether treatment differences in the entire arthropod community would be apparent, I did expect that some specialist herbivores would respond to the treatments (Moore *et al.* 1991, Schowalter and Turchin 1993).

MATERIALS AND METHODS

STUDY SITES

The sites for this study were the H. J. Andrews Experimental Forest (AF), a Long Term Ecological Research (LTER) site in the western Cascades 100 km east of Eugene, Oregon, and the Cascade Head Experimental Forest (CH) in the Coast Range northwest of Lincoln City, Oregon (Figure 1). As shown in Figure 2, Cascade Head experiences less extreme seasonal fluctuations in temperature than does the Andrews Forest, while receiving slightly more precipitation. Table 1 contrasts other important site characteristics.

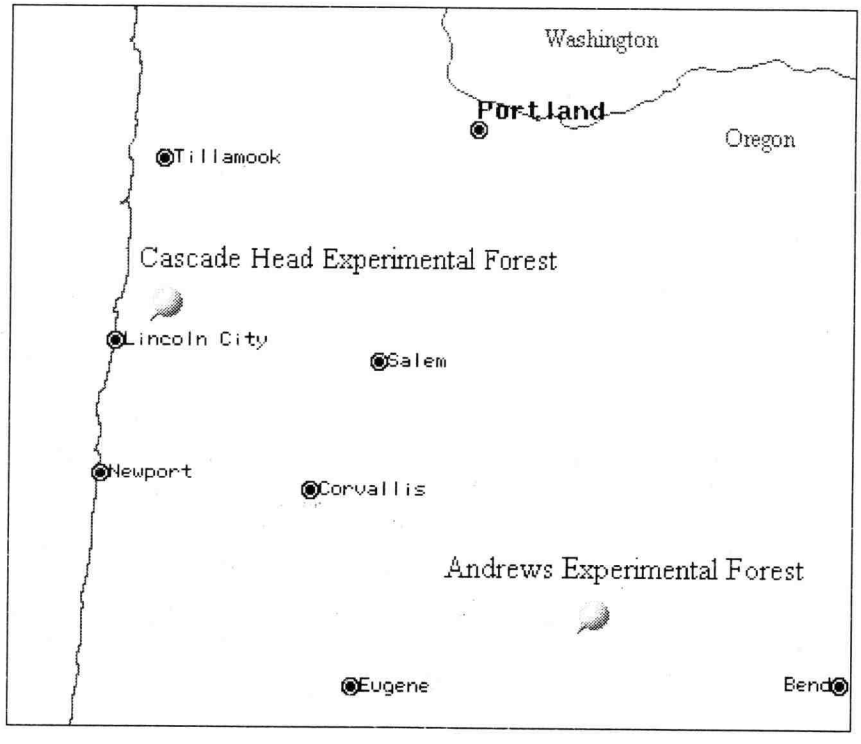

Figure 1. Map showing the relative locations of the Andrews and Cascade Head Experimental Forests in Western Oregon.

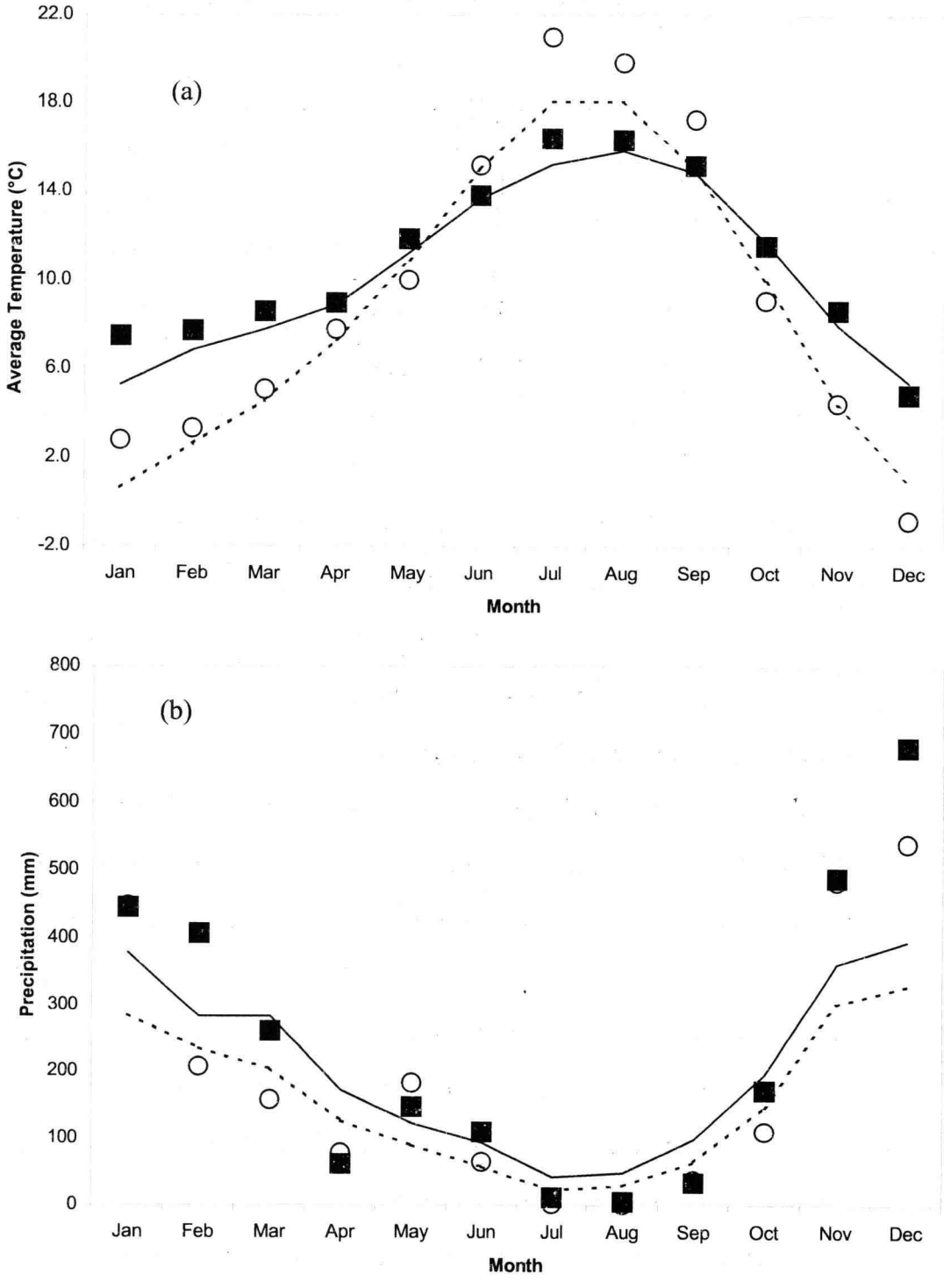

Figure 2. Monthly average (a) temperature and (b) precipitation from 1961-1990 (lines) and 1998 (symbols) at Cascade Head (solid line, filled squares) and Andrews Forest (dashed line, open circles).

Table 1. Site characteristics at the Cascade Head and Andrews Forests.

	Cascade Head	Andrews Forest
Latitude	45° 05' N	44° 15' N
Longitude	125° 58' W	122° 09' W
Elevation (m)	330	660-760
Aspect	E	N, W
Mean Annual Temperature (°C)		
1961-1990	10.3	8.9
1998	10.9	9.6
Mean Annual Precipitation (mm)		
1961-1990	2451	1865
1998	2825	2311

Each site has three replicated blocks containing 15 square 0.073 ha plots randomly assigned to varying mixtures and densities of Douglas-fir and red alder. The six contrasting treatments used in this study are shown in Figure 3. Treatment 1 is full density Douglas-fir (~1000/ha), 2 is half density Douglas-fir (~500/ha), 3 is mixed Douglas-fir and young red alder (alders planted 5 years after Douglas-firs, ~500/ha of each), 4 is mixed (equal-aged Douglas-fir and red alder, ~500/ha of each), 5 is half density red alder (~500/ha), and treatment 6 is full density red alder (~1000/ha). The trees were planted (treatments applied) at Cascade Head in 1985 and at the Andrews Forest in 1986.

This randomized block design permits assessment of separate and interactive influences of diversity or density on arthropod community composition, despite differences among blocks in abiotic factors such as slope, and edaphic composition. The relatively small plot size and lack of buffer strips between plots in this experimental design might mask treatment effects. To minimize edge effects and treatment interference, sampling was concentrated near the center of each plot (see Figure 3).

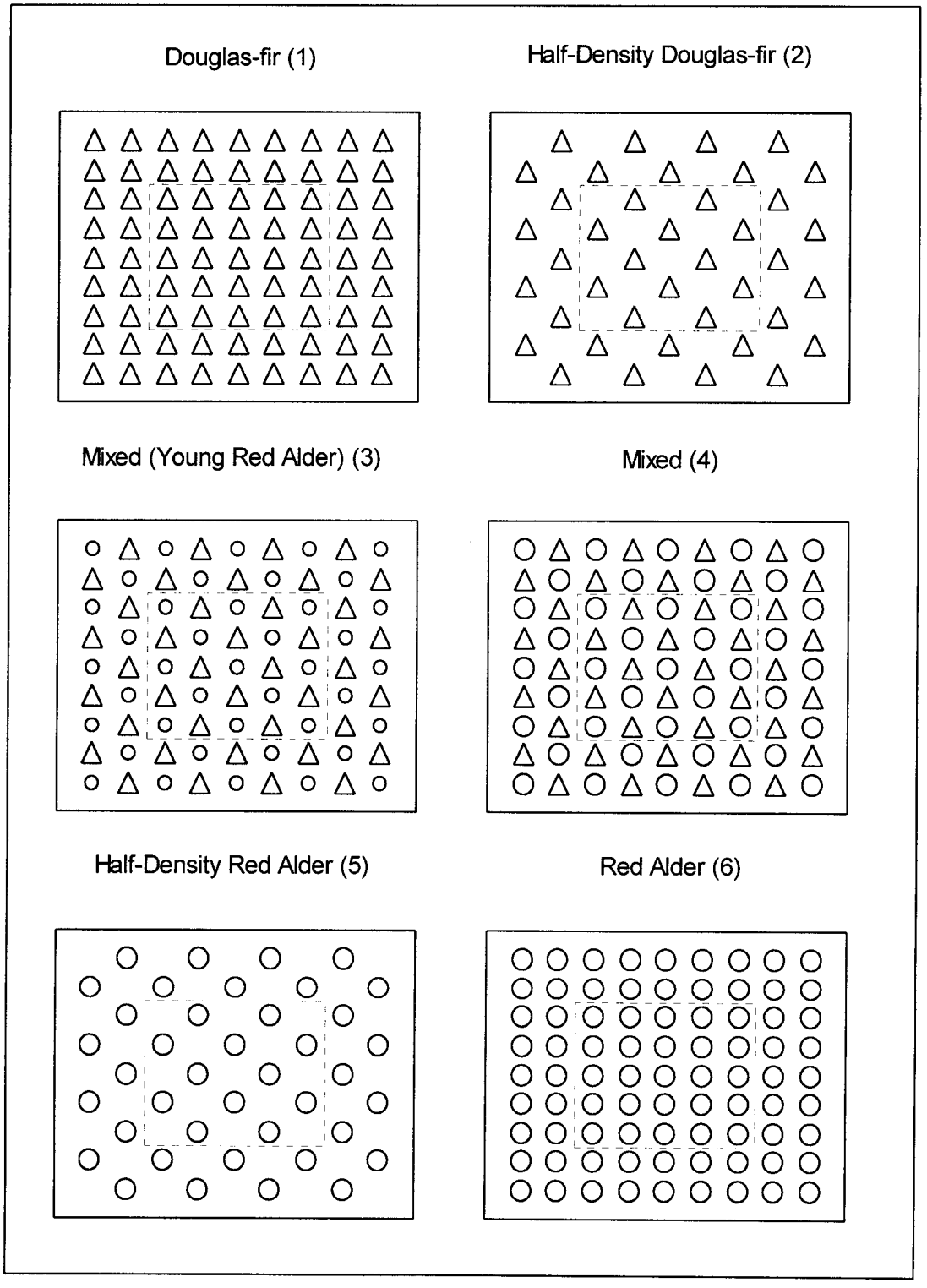

Figure 3. Diagram of the six treatments used in this study. Triangles represent Douglas-fir, circles represent red alder. Samples were taken only from within the area outlined by the dashed line.

The treatments affected the growth and survival of trees subsequent to planting. Table 2 summarizes diameter at 1.4 m, height, and mortality rate of for each tree species in each treatment at Cascade Head prior to sampling. Table 3 summarizes the same information for the Andrews Forest. At Cascade Head, alders in treatment 4 (mixed) outcompeted the Douglas-firs, resulting in short, small-diameter Douglas-firs with high mortality rates (compared to the other Douglas-firs, which were similar in size and mortality). Alders in treatment 3 (planted 5 years later) at both locations were smaller in height and diameter than alders in the other treatments. Douglas-firs at the Andrews Forest were similar in height, diameter and mortality. Andrews Forest alders in treatments 4, 5, and 6 were also similar in height, diameter, and mortality. These data suggest that interspecific competition is intense at Cascade Head, but absent or weak at the Andrews Forest. Red alder growth is slower and mortality rates higher at the Andrews Forest compared to Cascade Head, suggesting a difference in growing conditions.

Table 2. Mean (and standard error of the mean) diameter at 1.4 m high, height, and overall mortality rates for each tree species in each treatment at Cascade Head. Data were collected by D. E. Hibbs (unpublished) in February of 1998. Dead trees were not included in sample size, diameter or height calculations.

	Douglas-fir				Red Alder			
Treatment	1	2	3	4	3	4	5	6
N	71	33	36	23	36	39	35	74
Diameter (mm)	123	125	121	28	87	197	206	164
	(2.4)	(5.2)	(4.8)	(2.6)	(4.0)	(3.7)	(6.3)	(3.2)
Height (m)	8.5	7.8	7.8	3.6	8.5	13.2	13.0	14.2
	(0.2)	(0.2)	(0.3)	(0.2)	(0.3)	(0.1)	(0.3)	(0.1)
Mortality	0.01	0.08	0.03	0.35	0.03	0.00	0.03	0.01

Table 3. Mean (and standard error of the mean) diameter at 1.4 m high, height, and overall mortality rates for each tree species in each treatment at the Andrews Forest. Data were collected by D. E. Hibbs (unpublished) in April of 1998. Dead trees were not included in sample size, diameter or height calculations.

	Douglas-fir				Red Alder			
Treatment	1	2	3	4	3	4	5	6
n	75	34	31	34	23	30	25	54
Diameter (mm)	78	71	72	75	40	133	121	115
	(5.8)	(4.2)	(4.6)	(6.1)	(3.6)	(7.2)	(9.6)	(6.1)
Height (m)	5.4	5.0	5.1	5.8	4.5	9.1	7.8	9.0
	(0.2)	(0.3)	(0.2)	(0.3)	(0.3)	(0.3)	(0.4)	(0.4)
Mortality	0.00	0.03	0.11	0.06	0.22	0.19	0.33	0.29

SAMPLING, IDENTIFICATION, AND ENUMERATION

Samples were collected between June 2 and August 19, 1998. In each plot, three trees (of each species present) were selected according to proximity to the plot center and accessibility of branches. From each of these trees, one ~0.5 m mid-crown branch was selected, quickly enclosed in a plastic bag, and clipped. To minimize disturbance to other experiments at these sites, young alders in treatment 3 were not sampled, and the total amount of foliage removed was less than 5% per tree. Each block was sampled this way in June and August to account for seasonal changes known to occur in forest arthropod communities (Schowalter and Ganio 1998). Thus, each tree species in each plot was represented by a total of 6 branches from 6 individual trees.

The location of branches sampled varied above and below mid-crown, but due to tree structure the upper third of the crown was typically inaccessible. Though this biases the representation of arthropod taxa having varied vertical distributions throughout the canopy, the bias should be relatively constant for all of the samples in this study. Also, the vertical gradients in light, humidity, and temperature in these stands should be less

extreme than those in mature Douglas-fir stands where the arthropod distributions are known to vary vertically (Schowalter and Ganio 1998).

Bagged branches were stored at 4°C for no more than 3 weeks. Arthropods were separated from the foliage and bag, killed and stored in 70% ethanol. The percentage of foliage lost to herbivores was visually estimated for each branch. My estimates were calibrated against measurements made on 130 alder leaf scans (Figure 4). Differences between estimated and measured defoliation were relatively small. Douglas-fir defoliation was underestimated to an unknown extent because missing needles (not necessarily consumed by herbivores) were not counted.

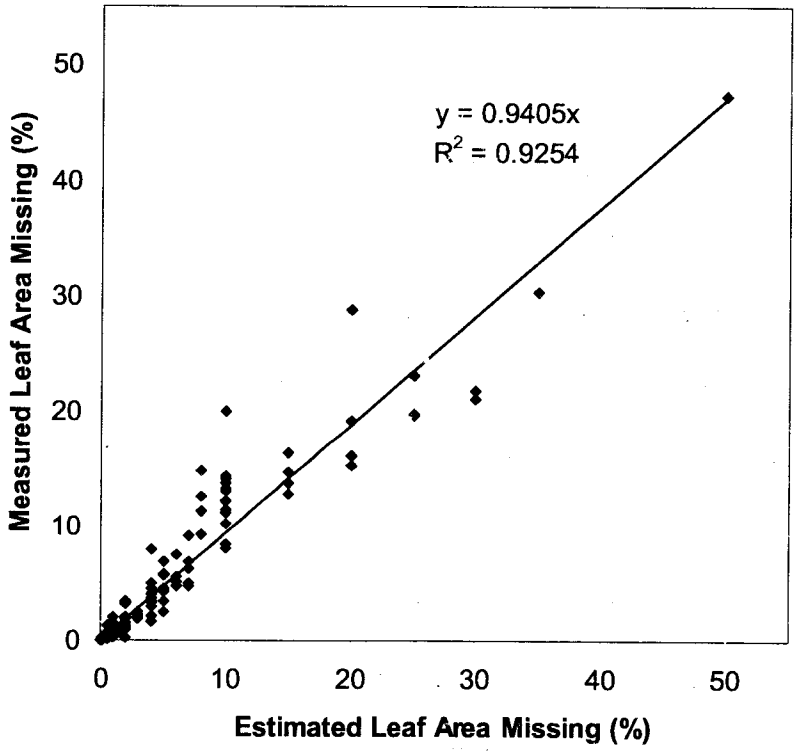

Figure 4. Calibration of my herbivore defoliation estimates against 130 digitally scanned and measured alder leaves. (The correlation was forced through the origin, as estimates of no defoliation were always correct.)

I identified and tabulated arthropods to the lowest possible taxonomic rank (typically family, genus and species whenever possible—see the Appendix for detail on the operational taxonomic units distinguished in this study). Determinations and functional group assignments were made using the keys and descriptions in: Furniss and Carolin (1977), Krantz (1978), Moldenke *et al.* (1987), Moldenke and Fitcher (1988), Chu and Cutkomp (1992), and Daly *et al.* (1998). A voucher collection (in storage at the Oregon State University Forest Insect Laboratory) was created and utilized to ensure consistency of the identifications. The foliage from each sample was dried at 50°C to constant weight.

DATA ANALYSIS

Abundance of each arthropod taxon was defined and calculated as the number per kilogram of dry foliage. Arthropods identified to genus and species in three groups (Diaspididae, Linyphiidae, and Oribatida) were combined into their respective taxa to provide sufficient abundance for analysis. Abundance of each taxon was pooled for each plot by tree species sampled. Percent defoliation for each tree species in each plot was calculated as the weighted mean of percent defoliation of each branch (using the dry mass of each branch as the weighting factor).

The Sørensen similarity measure (a derivative of the "city-block" or "Manhattan" distance) was used throughout the analysis to calculate multivariate distances between plots in terms of arthropod taxa abundance and percent defoliation (Bray and Curtis 1957). The Sørensen distance (D) between two sets of abundances (i and h) comprised of p taxa is calculated as follows:

$$D_{i,h} = \frac{\sum_{j=1}^{p} |a_{i,j} - a_{h,j}|}{\sum_{j=1}^{p} a_{i,j} + \sum_{j=1}^{p} a_{h,j}}$$

Bray-Curtis ordination (Bray and Curtis 1957, Beals 1984) in 3-dimensions served to generate the starting configuration for non-metric multidimensional scaling (NMS). NMS is an ordination technique that iteratively adjusts the locations of data points (plots) to minimize stress (Kruskal 1964, Mather 1976). Stress is defined as the difference between distances between points in the ordination space and the multivariate (Sørensen) distances between points in the data matrix. Thus, NMS is a model-free ordination method: the location of points in taxa space does not depend on a pre-specified correlation structure in the data matrix.

The final stability of each NMS ordination was evaluated using the residual stress after each NMS iteration. In all ordinations, stress remained low and essentially constant over the last several NMS iterations, indicating a stable final configuration. For each NMS run, the number of dimensions was stepped down from three to one. Dimensionality was determined by examining the stress associated with each dimensionality (stress increases as dimensions are decreased). In all NMS runs, a two-dimensional ordination was appropriate (stress increased little from two to three dimensions). Ordinations were performed with PC-ORD software (McCune and Mefford 1999) on untransformed data (#/kg) and ln (#/kg+1) transformed data. To assess the sensitivity to taxanomic resolution, an ordination was performed with species and genera in the Diaspididae, Linyphiidae and Oribatida separated (using ln (#/kg +1) transformed data). Similarly, to assess sensitivity to one extremely abundant arthropod taxon, *Adelges*

cooleyi (Homoptera: Adelgidae), ordinations were performed without this taxon (using transformed data).

Observed grouping patterns recovered by ordination were tested for significance using the Multiple Response Permutation Procedure (MRPP). MRPP is a randomization procedure that determines the likelihood of observed within-group (Sørensen) distances by randomly re-assigning groupings to the real data (Mielke 1984). When significant groupings were found, indicator taxa analysis was used to identify the arthropod taxa that distinguish the groupings, using a multiplicative combination of occurrence frequency and abundance in each group (Dufrene and Legendre 1997). Indicator taxa analysis is an *a posteri* approach, so repeatability is uncertain, as are biologically meaningful associations between significant indicator taxa and the groups that they characterize. MRPP and indicator taxa analysis were performed on ln (#/kg + 1) transformed data using PC-ORD software.

More specific elucidation of location and treatment differences was accomplished by two-way ANOVA (with three replicates, using location and treatment as classifying variables) on percent defoliation, commonly encountered taxa, and functional groups. Three-fold replication permitted testing of the location×treatment interaction by ANOVA. However, ANOVA is extremely vulnerable to violation of the assumption of equal variance (Ramsey and Schafer 1997). The estimate of variance produced with a sample size of three makes this assumption difficult to verify, so significant interaction terms should be viewed skeptically. The sample size for evaluating treatment differences was six, so the assumptions of normality could be better evaluated, but significant treatment differences also deserve some skepticism.

Significant differences between treatment means at each location were elucidated using the student's t test, and are F-protected against spurious treatment effects (Ramsey and Schafer 1997). (When the F-test reported no significant interaction effect, the pairs of means were not t-tested, reducing the probability of encountering spurious differences between means). ANOVAs and t-tests were performed using JMP software (SAS Institute 1998) on transformed data (ln (#/kg + 1), except percentage defoliation, which was not transformed) to normalize distributions. In all cases, transformations improved the normality of the distributions.

RESULTS

In all, 6981 arthropods representing 42 families were sampled. Table 4 summarizes the abundance (raw counts, not standardized by foliage weight) of each taxon sampled in all plots (subdivided by tree species, location, and combinations of tree species×location). To evaluate sufficiency of sampling, taxa-area curves were constructed for each treatment at each (Figure 5). Cascade Head red alders had lower taxa richness than the other samples, and showed a well-defined asymptote (unlike the other tree species×location combinations). The rank abundance diagrams in Figure 6 illustrate how the abundance arthropods are distributed among taxa (from most abundant to least abundant). On Douglas-fir at both locations (Figures 6(c) and 6(d)), the distributions are extremely unequitable due to extremely high abundances of *Adelges cooleyi*.

The NMS ordination in Figure 7 illustrates the overall pattern of arthropod community composition on each tree species at each location (with abundances for each family combined and transformed by ln(#/kg + 1). The final ordination was the result of 42 iterations, and the probability of obtaining the same final stress from randomized data was 0.02. The first and second axes of this ordination captured (respectively) 22% and 64% of the variation in the data set (86% total). Figure 7 distinguishes arthropod assemblages by tree species and location. MRPP found significant groupings of arthropod communities by species sampled (Douglas-fir vs. red alder, $n = 24$ and 18 plots, respectively, $T = -23.2$, $p << 0.0001$) and location (Cascade Head vs. Andrews Forest, $n = 21$ plots for each location, $T = -7.23$, $p = 0.0002$).

Table 4. Summary of family abundances (raw counts) for all plots and each tree species, location, and tree species×location. (CH = Cascade Head, AF = Andrews Forest.)

						Red Alder		Douglas-fir	
	Total	Red Alder	Douglas-fir	CH	AF	CH	AF	CH	AF
Foliage Weight (kg)	6.16	1.29	4.87	1.84	4.40	0.37	0.92	1.47	3.40
Defoliators	**102**	**85**	**17**	**20**	**82**	**10**	**75**	**10**	**7**
Agromyzidae	1	1	0	1	0	1	0	0	0
Cimbicidae	3	3	0	0	3	0	3	0	0
Curculionidae	4	0	4	2	2	0	0	2	2
Geometridae	25	22	3	8	17	6	16	2	1
Gracillariidae	3	3	0	1	2	1	2	0	0
Pyralidae	8	7	1	1	7	0	7	1	0
Thripidae	52	47	5	6	46	2	45	4	1
Tortricidae	6	2	4	1	5	0	2	1	3
Sap-feeders	**6055**	**140**	**5915**	**4631**	**1424**	**60**	**80**	**4571**	**1344**
Adelgidae	5771	0	5771	4504	1267	0	0	4504	1267
Aphididae	55	7	48	26	29	0	7	26	22
Cercopidae	5	2	3	2	3	0	2	2	1
Cicadellidae	78	69	9	45	33	39	30	6	3
Diaspididae	26	0	26	3	23	0	0	3	23
Membracidae	1	1	0	1	0	1	0	0	0
Miridae	6	3	3	3	3	1	2	2	1
Pentatomidae	1	1	0	0	1	0	1	0	0
Psyllidae	46	44	2	10	36	9	35	1	1
Tetranychidae	65	12	53	37	28	10	2	27	26
Tingidae	1	1	0	0	1	0	1	0	0
Predators	**309**	**71**	**238**	**169**	**140**	**49**	**22**	**120**	**118**
Anaphaenidae	14	4	10	12	2	4	0	8	2
Araneidae	76	2	74	3	73	0	2	3	71
Cantharidae	1	0	1	0	1	0	0	0	1
Erythraeidae	69	43	26	63	6	40	3	23	3
Hemerobiidae	5	1	4	2	3	0	1	2	2
Linyphiidae	67	7	60	51	16	4	3	47	13
Nabidae	2	2	0	0	2	0	2	0	0
Philodromidae	21	5	16	12	9	0	5	12	4
Salticidae	19	4	15	0	19	0	4	0	15
Theridiidae	35	3	32	26	9	1	2	25	7
Detritivores	**250**	**44**	**206**	**156**	**94**	**20**	**24**	**136**	**70**
Entomobryidae	50	1	49	29	21	1	0	28	21
Forficulidae	1	0	1	1	0	0	0	1	0
Lepismatidae	2	0	2	1	1	0	0	1	1
Oribatida	59	22	37	38	21	5	17	33	4
Psocidae	106	18	88	59	47	12	6	47	41
Sminthuridae	32	3	29	28	4	2	1	26	3
Other	**77**	**16**	**61**	**46**	**31**	**6**	**10**	**40**	**21**
Chironomidae	30	11	19	19	11	5	6	14	5
Culicidae	18	0	18	18	0	0	0	18	0
Elateridae	3	1	2	1	2	1	0	0	2
Eulophidae	7	2	5	3	4	0	2	3	2
Formicidae	13	0	13	2	11	0	0	2	11
Staphylinidae	2	1	1	0	2	0	1	0	1
Tachinidae	4	1	3	3	1	0	1	3	0
Not Identifiable	**188**	**104**	**84**	**113**	**75**	**68**	**36**	**45**	**39**
Total	**6981**	**460**	**6521**	**5135**	**1846**	**213**	**247**	**4922**	**1599**

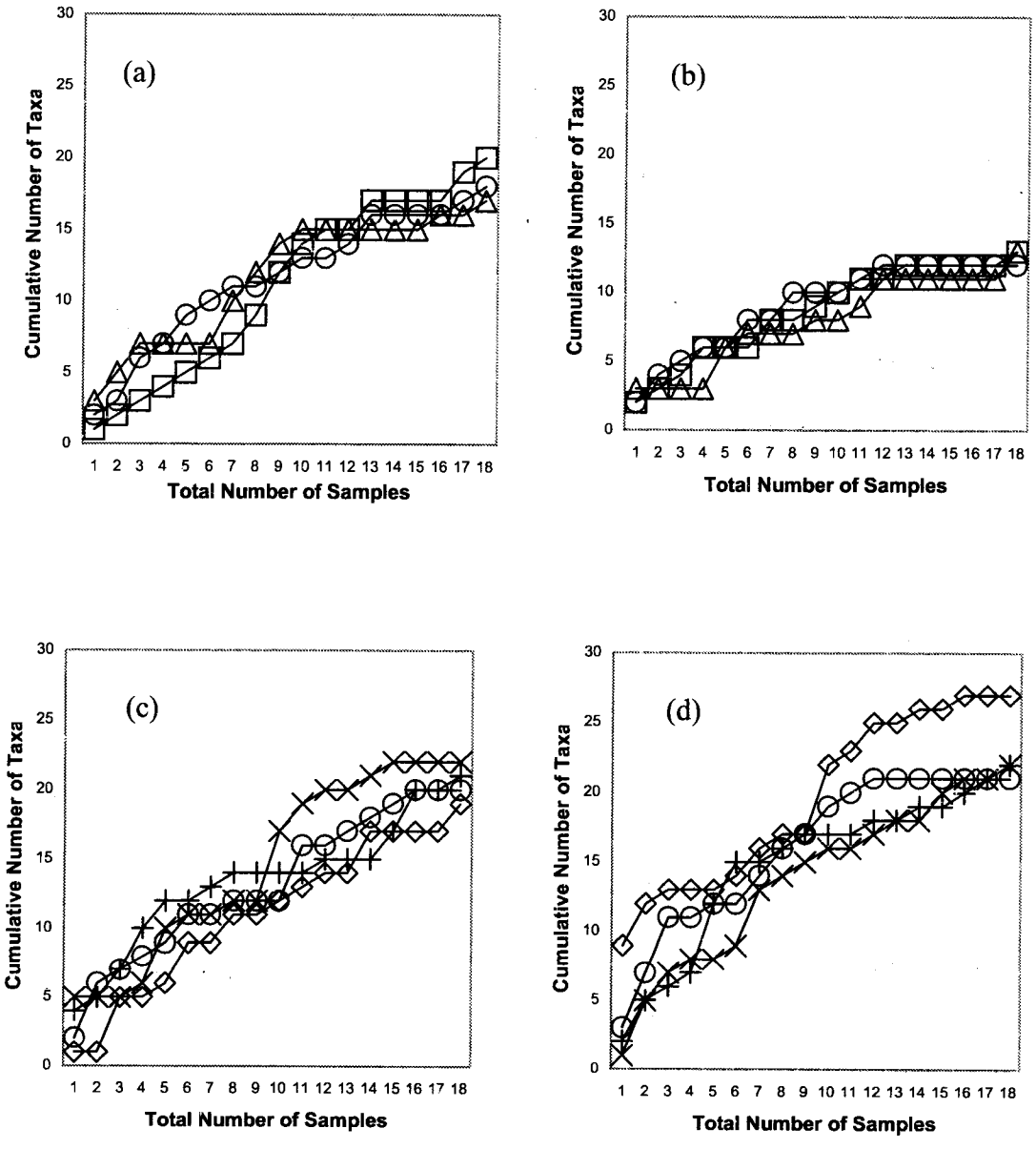

Figure 5. Taxa-sampling effort curves for (a) Andrews Forest red alder, (b) Cascade Head red alder, (c) Andrews Forest Douglas-fir, and (d) Andrews Forest Douglas-fir. Treatments 1-6 are represented by: crosses, x's, diamonds, circles, triangles, and squares, respectively.

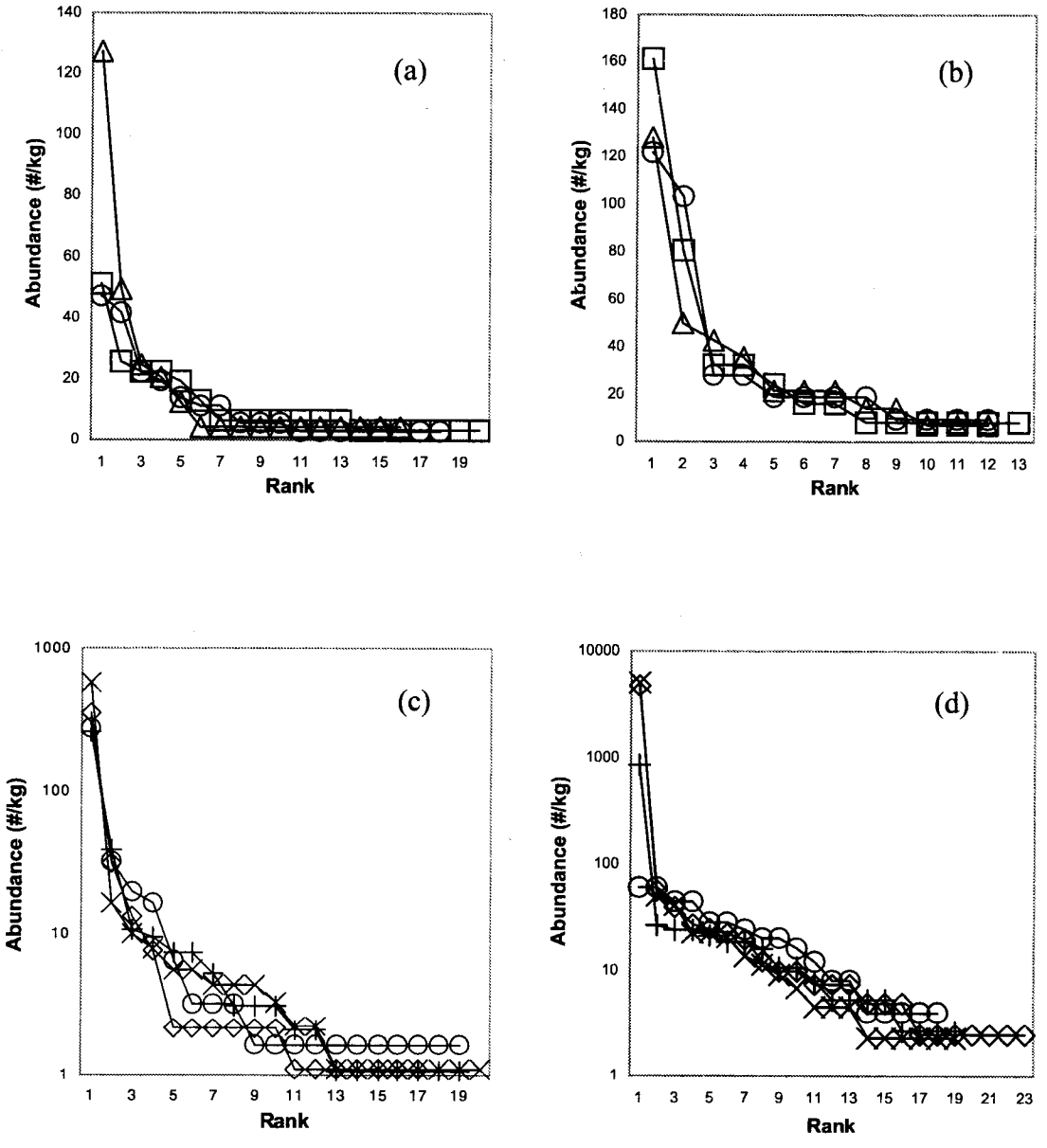

Figure 6. Rank-abundance diagrams for (a) Andrews Forest red alder, (b) Cascade Head red alder, (c) Andrews Forest Douglas-fir, and (d) Andrews Forest Douglas-fir. Treatments 1-6 are represented by: crosses, x's, diamonds, circles, triangles, and squares, respectively. Note the logarithmic abundance scale for Douglas-fir plots (indicating extremely high dominance and low equitability of the taxa-abundance distribution).

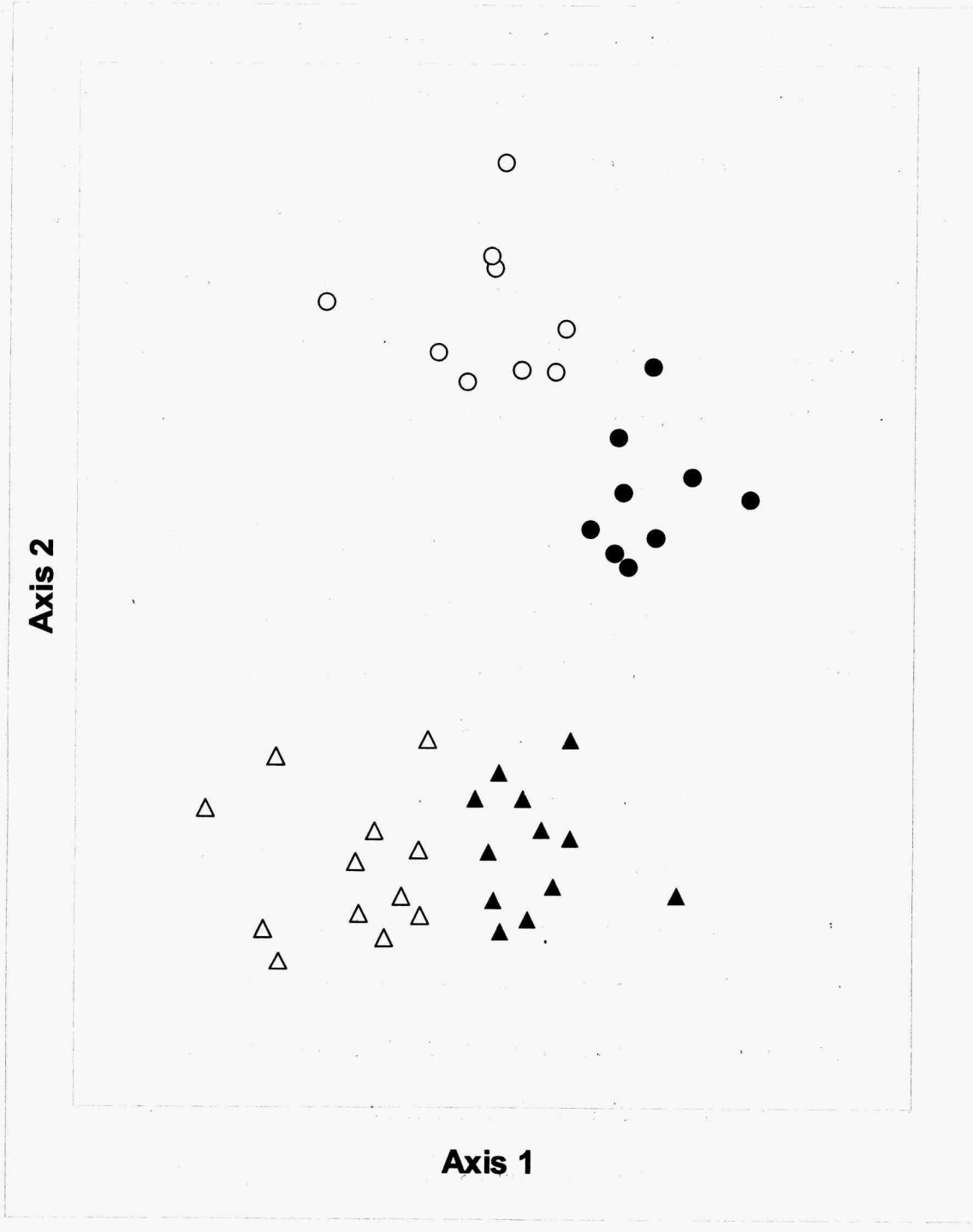

Figure 7. Non-Metric Scaling ordination of all plots showing tree species sampled and location (taxa grouped by family, transformed abundance). Circles represent red alder, triangles represent Douglas-fir, open symbols represent Andrews Forest plots, and filled symbols represent Cascade Head plots.

The NMS ordination in figure 8 is similar to figure 7, except that taxa identified to genus and species were not combined into their respective families. This ordination captured 47% and 32 % of the variation in the data set on axis one and two, respectively (79%) total. Figure 8 also distinguishes the arthropod assemblages by tree species and location, indicating that the ordination is insensitive to taxonomic resolution.

Figure 9 is an NMS ordination performed using untransformed (#/kg) data. Axis one and two account for, respectively, 37% and 36% of the variation in the original data (73% total). Here, the separation of arthropod communities by tree species and location shows that the ordination is not dependent on the natural logarithm transformation.

The NMS ordination in Figure10 excluded *Adelges cooleyi* from the analysis, and captured 49% and 28% of the variation in the data on axis one and two, respectively (77% total). This demonstrates that the distinction of arthropod communities by tree species and location is not driven by the single most abundant arthropod taxon.

Indicator species analyses for all data by tree species sampled and location are presented in Table 5. Red alders are characterized by percentage defoliation, the Cicadellidae and Psyllidae (Homoptera), Geometridae and Pyralidae (Lepidoptera), and Thripidae (Thysanoptera). In contrast, the Adelgidae and Diaspididae (Homoptera), Culicidae (Diptera), Entomobryidae (Collembola), Formicidae (Hymenoptera), Psocidae (Psocoptera), Linyphiidae and Theridiidae (Aranae) characterized Douglas-firs. Cascade Head was typified by the Erythraeidae, Oribatidae and Tetranychidae (Acari), Anaphaenidae and Linyphiidae (Aranae), Sminthuridae (Collembola), Culicidae, and Psocidae, while the Andrews Forest was characterized by the Araneidae and Salticidae (Aranae), and Pyralidae.

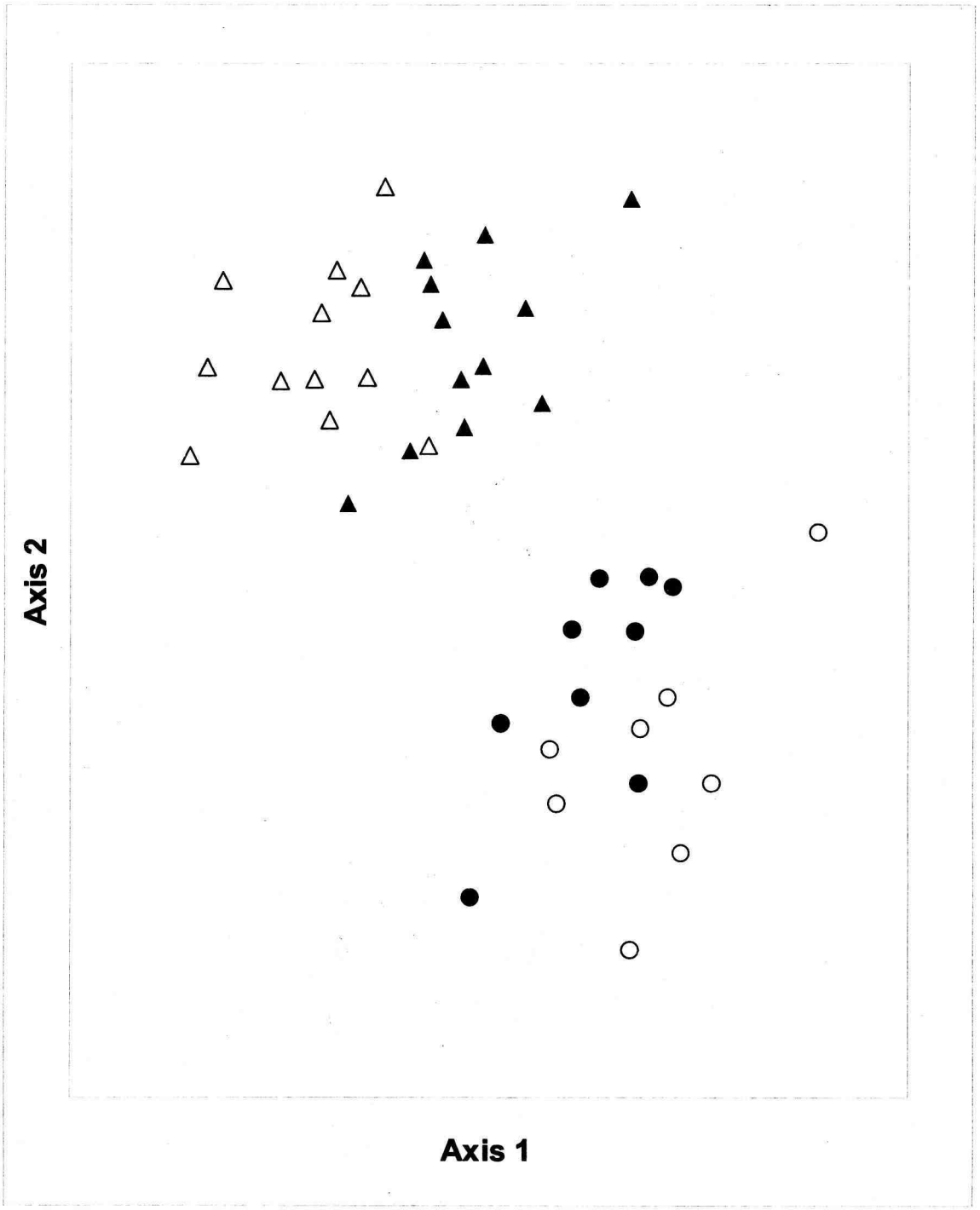

Figure 8. Non-Metric Scaling ordination of all plots, showing tree species sampled and location (taxa separated, transformed abundance). Circles represent red alder, triangles represent Douglas-fir, open symbols represent Andrews Forest plots, and filled symbols represent Cascade Head plots.

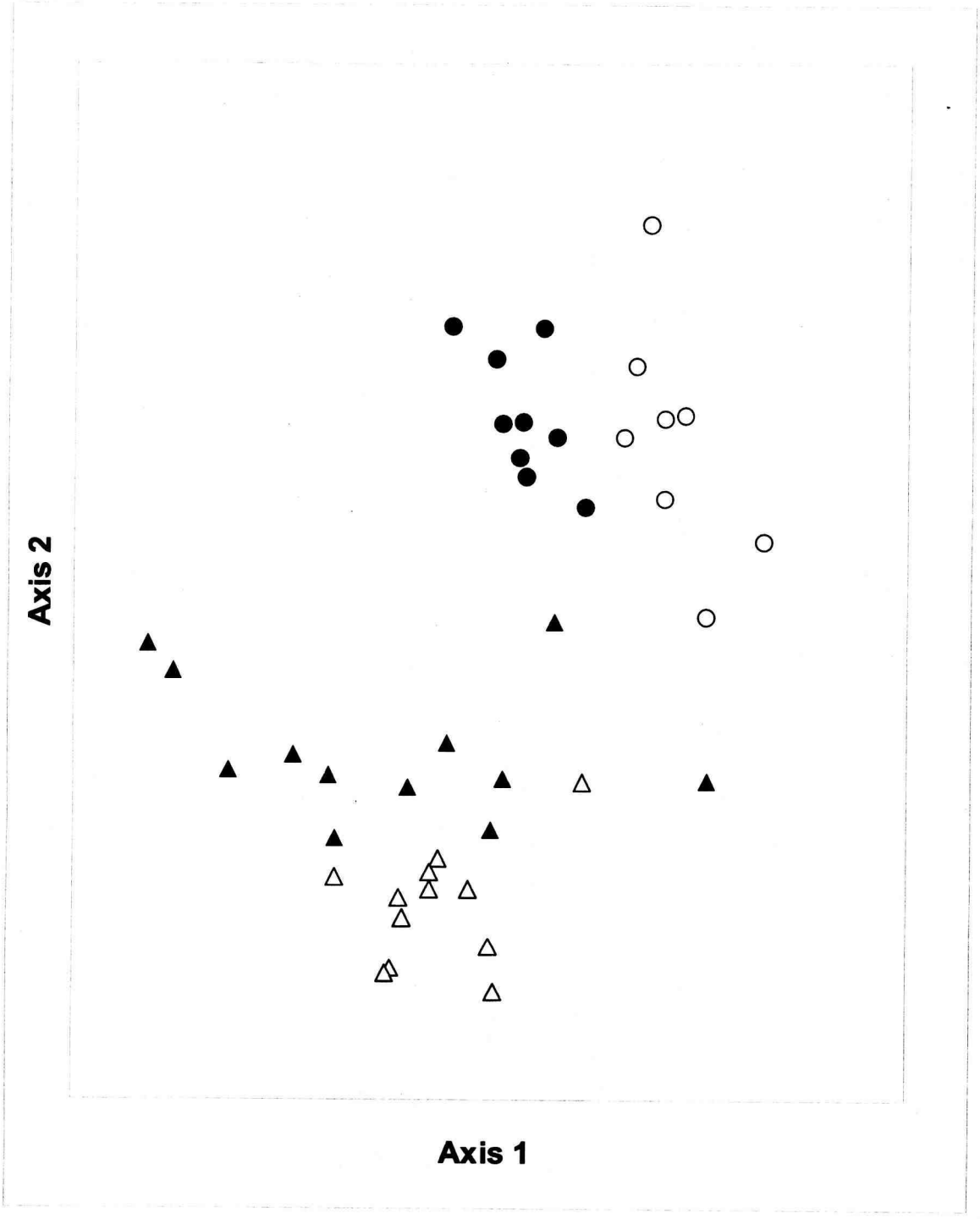

Figure 9. Non-Metric Scaling ordination of all plots, showing tree species sampled and location (taxa grouped by family, untransformed abundance). Circles represent red alder, triangles represent Douglas-fir, open symbols represent Andrews Forest plots, and filled symbols represent Cascade Head plots.

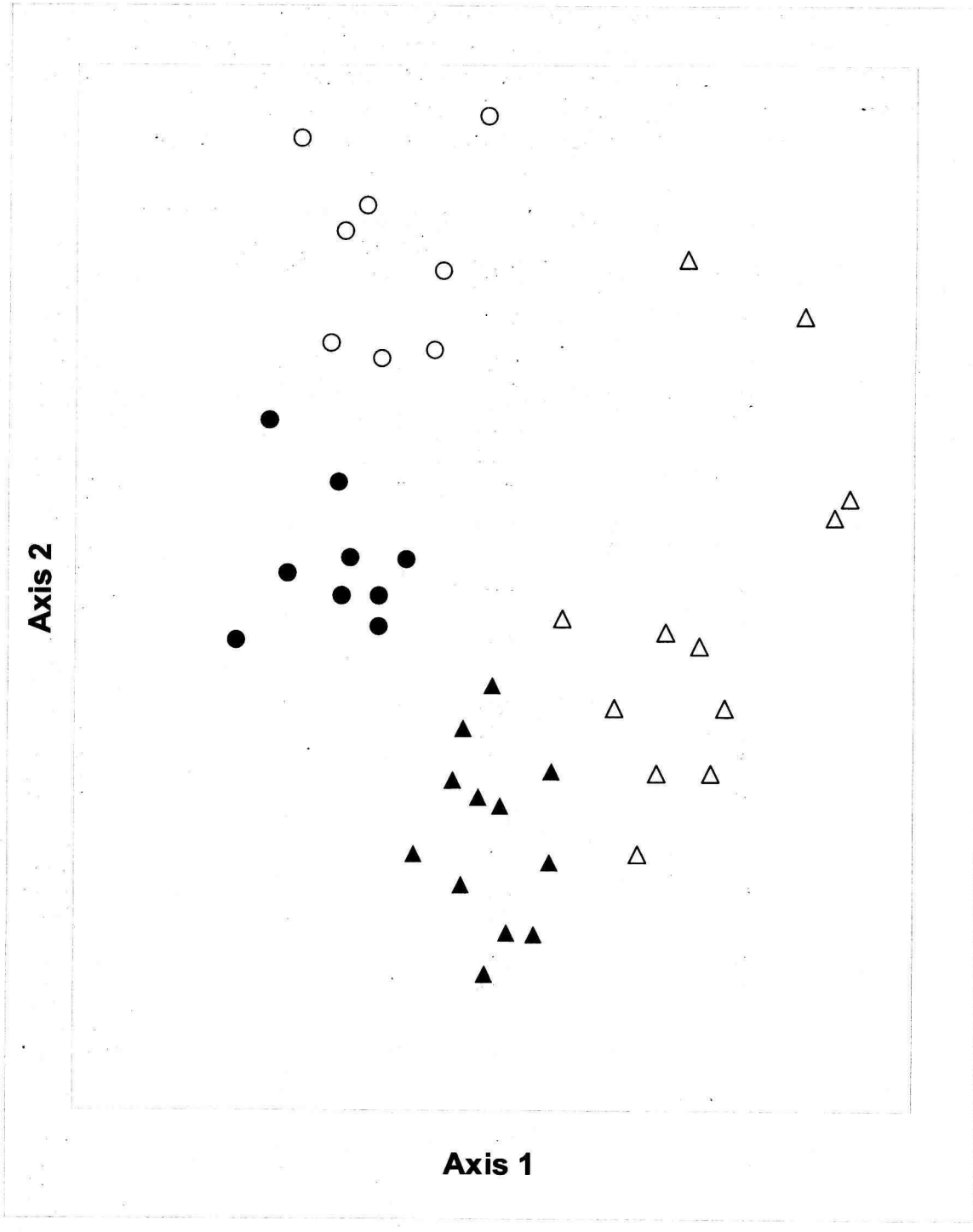

Figure 10. Non-Metric Scaling ordination of all plots, showing tree species sampled and location (taxa grouped by family, excluding *Adelges cooleyi*, transformed abundance). Circles represent red alder, triangles represent Douglas-fir, open symbols represent Andrews Forest plots, and filled symbols represent Cascade Head plots.

Table 5. Indicator taxa analysis for groupings of all plots by tree species sampled and location. The indicator value given for each location or tree species is the percentage of perfect indication, combining occurrence frequency and abundance of each taxa in that group. The p-value is the proportion of 1000 randomized regrouping trials with indicator values equal to or greater than those observed (asterisks mark p-values <0.05).

	Tree Species			Location		
taxon	Red Alder	Douglas-fir	p	CH	AF	p
Defoliation (%)	87	13	0.000*	60	40	0.161
Defoliators						
Agromyzidae	6	0	0.428	5	0	0.999
Cimbicidae	11	0	0.178	0	10	0.446
Curculionidae	0	8	0.520	3	2	0.999
Geometridae	55	1	0.000*	13	21	0.618
Gracillariidae	17	0	0.067	2	5	0.999
Pyralidae	25	0	0.010*	1	21	0.038*
Thripidae	40	4	0.011*	7	30	0.111
Tortricidae	5	6	0.959	1	15	0.172
Sap-feeders						
Adelgidae	0	96	0.000*	27	27	0.999
Aphididae	9	15	0.679	9	16	0.694
Cercopidae	7	3	0.746	1	10	0.495
Cicadellidae	80	5	0.000*	41	20	0.210
Diaspididae	0	42	0.001*	2	29	0.061
Membracidae	6	0	0.432	5	0	0.999
Miridae	7	5	0.885	9	3	0.589
Pentatomidae	6	0	0.417	0	5	0.999
Psyllidae	68	1	0.000*	20	16	0.871
Tetranychidae	25	43	0.243	59	16	0.001*
Tingidae	6	0	0.441	0	5	0.999
Predators						
Anaphaenidae	7	19	0.442	39	1	0.003*
Araneidae	2	29	0.080	1	41	0.001*
Cantharidae	0	4	0.999	0	5	0.999
Erythraeidae	38	13	0.124	61	3	0.000*
Hemerobiidae	2	11	0.502	5	7	0.866
Linyphiidae	8	56	0.003*	51	12	0.015*
Nabidae	11	0	0.177	0	10	0.453
Philodromidae	14	12	0.828	5	24	0.159
Salticidae	7	17	0.519	0	48	0.001*
Theridiidae	3	53	0.003*	41	10	0.061
Detritivores						
Entomobryidae	1	49	0.002*	16	17	0.931
Forficulidae	0	4	0.999	5	0	0.999
Lepismatidae	0	8	0.508	3	2	0.999
Oribatida	14	37	0.194	56	6	0.002*
Psocidae	18	50	0.030*	49	20	0.050*
Sminthuridae	5	33	0.089	39	4	0.019*
Other						
Chironomidae	25	18	0.634	35	11	0.125
Culicidae	0	29	0.024*	33	0	0.008*
Elateridae	3	3	0.999	2	5	0.999
Eulophidae	2	11	0.388	4	8	0.950
Formicidae	0	25	0.033*	1	18	0.181
Staphylinidae	4	1	0.753	0	10	0.493
Tachinidae	2	8	0.640	10	1	0.598

To evaluate the significance of treatment effects, plots were first separated by tree species sampled. Figure 11 is an NMS ordination of red alder plots. This ordination was the result of 32 NMS iterations. The probability of obtaining the same stress by randomization was 0.02. The first and second dimensions explained 42% and 37%, respectively, of the variation in the data (79% total). While the arthropod communities separated by plot location, there is no discernible grouping by treatment. MRPP of red alder plots showed no significant grouping by treatment ($T = 1.08$, $p = 0.88$). In essence, the treatments have no effect on the arthropod communities of red alder as a whole.

NMS ordination of Douglas-fir plots is displayed in Figure 12. Iterations numbered 70 for this ordination. The probability of achieving lower stress with randomized data is 0.02. Axis 1 and 2 accounted for 36% and 47%, respectively, of the variation in the data (83% total). As with the red alder plots, NMS ordination displayed grouping of plots by location, but failed to show any grouping of arthropod assemblages by treatment on Douglas-fir. MRPP showed no significant groupings of Douglas-fir plots by treatment ($T = 0.59$, $p = 0.70$). Thus, after accounting for differences in tree species sampled, there appeared to be no difference in the overall arthropod communities for different treatments.

The results of two-way ANOVA for defoliation, abundant families, and functional groups in red alder plots are presented in Table 6. Alders at Cascade Head sustained greater defoliation, and had a greater abundance of Cicadellidae, predators, and Erythraeidae than did alders at the Andrews Forest, which in turn had more Thripidae and defoliators. Defoliators also showed a treatment effect and location×treatment interaction.

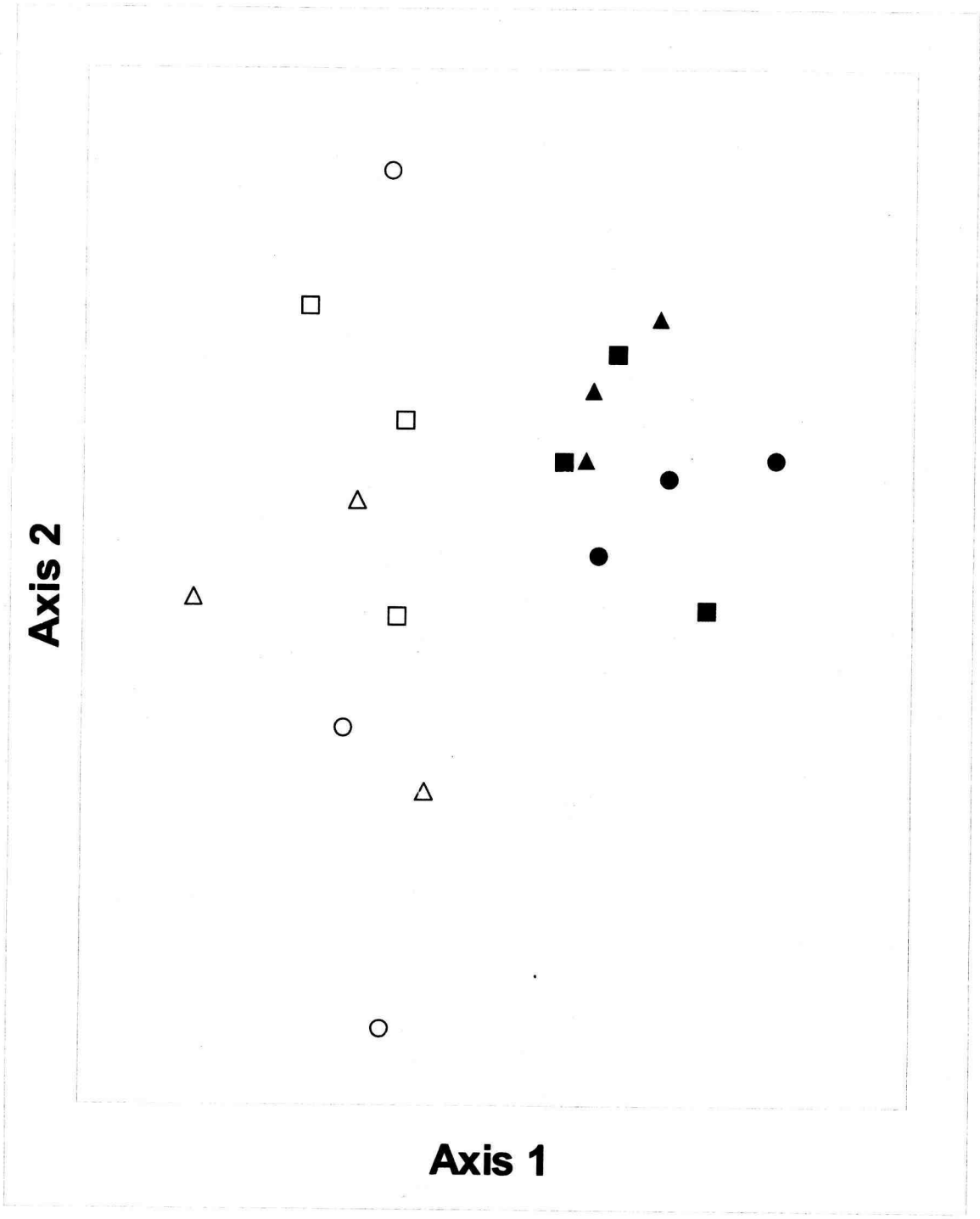

Figure 11. Non-Metric Scaling ordination of red alder plots, showing location and treatments (taxa grouped by family, transformed abundance). Circles represent treatment 4 (mixed), triangles represent treatment 5 (half density), and squares represent treatment 6 (full density). Open symbols represent Andrews Forest plots, while closed symbols represent Cascade Head plots.

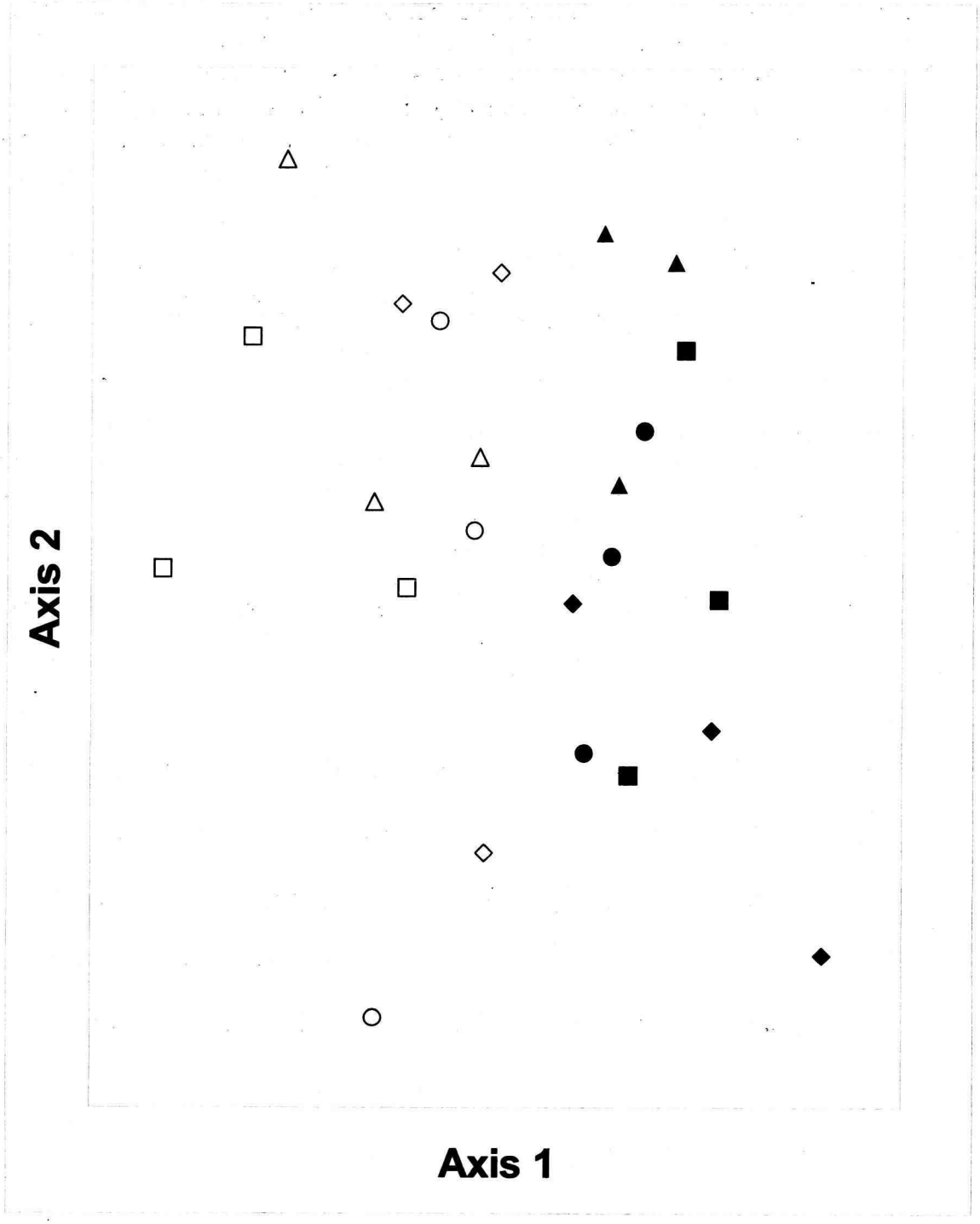

Figure 12. Non-Metric Scaling ordination of Douglas-fir plots, showing location and treatments (taxa grouped by family, transformed abundance). Circles represent treatment 1 (full density), triangles represent treatment 2 (half density), squares represent treatment 3 (mixed with young alder), and diamonds represent treatment 4 (mixed). Open symbols represent Andrews Forest plots, while closed symbols represent Cascade Head plots.

Table 6. Results of two-way ANOVA for common response variables in red alders. Median abundance (#/kg of dry foliage) and average defoliation (%) (and standard error) are listed for each location (CH = Cascade Head, AF = Andrews Forest) and treatments 4, 5, and 6. ANOVAs were performed on data expressed as ln (#/kg +1) (except defoliation). Degrees of freedom for location, treatment, location×treatment interaction, and error were 1, 2, 2, and 12, respectively. Significant ($p < 0.05$) effects found by ANOVA are marked with an asterisk.

	Location		Treatment				Location		Treatment		Loc×Trt	
Taxon	CH	AF	4	5	6	MSE	F	p	F	p	F	p
Defoliation (%)	5.6 (0.38)	3.6 (0.24)	4.6 (0.71)	4.5 (0.46)	4.7 (0.57)	1.10	15.93	0.002*	0.12	0.89	0.28	0.76
Defoliators	25	55	38	41	30	0.86	10.97	0.006*	4.4	0.04*	4.5	0.03*
Geometridae	0	21	4	19	11	3.46	0.85	0.38	0.40	0.68	0.11	0.89
Thripidae	0	23	5	7	11	1.70	19.92	0.001*	0.32	0.73	2.64	0.11
Sap-feeders	173	82	94	159	118	0.58	3.598	0.082	0.3	0.71	0.5	0.60
Cicadellidae	87	30	59	63	66	1.00	9.11	0.011*	0.67	0.53	1.82	0.20
Psyllidae	25	34	27	24	27	3.81	0.00	0.95	0.35	0.71	0.62	0.56
Predators	143	18	53	48	102	1.17	13.22	0.003*	0.6	0.55	0.4	0.65
Erythraeidae	90	0	38	6	66	1.79	31.66	0.0001*	1.21	0.33	1.75	0.22
Detritivores	58	9	37	18	16	2.72	3.384	0.09	0.6	0.55	3.6	0.06

The results of two-way ANOVA for defoliation, abundant families, and functional groups on Douglas-firs are presented in Table 7. Cascade Head Douglas-firs showed greater defoliation, and had a greater abundance of Linyphiidae, Theridiidae, Eyrthraeidae, Oribatida, predators, and detritivores than did Andrews Forest Douglas-firs, which in turn had a greater abundance of Diaspididae. The abundance of Adelgidae was significantly affected by treatment, as were sap-feeders (a functional group dominated by adelgids). Significant location×treatment interactions were found for Adelgidae and Diaspididae on Douglas-fir.

Significant location×treatment interactions are analyzed in Table 8. At Andrews Forest, defoliators on red alder were similar in abundance in each treatment, while at Cascade Head, they were most abundant in treatment 4 (mixed). Adelgidae on Douglas-

fir at Cascade Head were less abundant in treatment 4 (mixed), than in the other treatments (which were all similar in abundance). Adelgidae were similarly abundant in all treatments at the Andrews Forest. The location×treatment interaction of Diaspididae is characterized by total absence from treatments 2 and 3 at Cascade Head and treatment 1 at the Andrews Forest.

Table 7. Results of two-way ANOVA for common response variables in Douglas-firs. Median abundance (#/kg of dry foliage) and average percent defoliation (and standard error) are listed for each location (CH = Cascade Head, AF = Andrews Forest) and treatments 1, 2, 3, and 4. ANOVAs were performed on data expressed as ln (#/kg +1) (except defoliation). Degrees of freedom for location, treatment, location×treatment interaction, and error were 1, 3, 3, and 16, respectively. Signifcant ($p < 0.05$) effects found by ANOVA are marked with an asterisk.

	Location		Treatment					Location		Treatment		Loc×Trt	
	CH	AF	1	2	3	4	MSE	F	p	F	p	F	p
Defoliation (%)	0.76 (0.05)	0.57 (0.06)	0.77 (0.06)	0.59 (0.08)	0.68 (0.07)	0.63 (0.11)	0.03	6.00	0.03*	0.95	0.44	0.91	0.46
Defoliators	4	0	6	0	5	0	1.24	1.89	0.19	1.39	0.28	1.36	0.29
Sap-feeders	904	390	369	1111	461	131	1.96	1.21	0.29	5.08	0.01*	2.84	0.07
Adelgidae	883	365	325	1091	444	103	1.87	0.87	0.36	6.92	0.003*	3.80	0.03*
Diaspididae	0	4	0	1	3	2	0.96	5.82	0.03*	0.89	0.47	3.71	0.03*
Tetranychidae	21	7	12	13	3	17	1.33	2.21	0.16	1.90	0.17	0.97	0.43
Predators	91	20	54	41	46	67	0.53	17.93	0.0006*	0.35	0.79	1.44	0.27
Araneidae	0	3	0	2	0	0	2.03	4.67	0.05*	0.02	0.99	1.15	0.36
Erythraeidae	8	0	1	2	0	0	1.96	5.56	0.03*	0.31	0.82	0.43	0.73
Linyphiidae	27	4	8	21	7	12	0.91	29.00	0.00001*	0.77	0.53	0.29	0.83
Theridiidae	14	0	6	3	7	9	0.98	20.33	0.0004*	0.69	0.57	1.02	0.41
Detritivores	87	13	30	24	29	78	0.51	28.82	0.00006*	2.65	0.08	0.85	0.48
Entomobryidae	0	5	1	6	0	7	2.76	0.01	0.93	0.78	0.52	0.68	0.58
Oribatida	21	0	6	2	5	8	1.00	32.17	0.00003*	0.38	0.77	0.40	0.75
Psocidae	27	8	10	5	18	48	1.83	2.58	0.13	1.81	0.19	0.96	0.44

Table 8. Median abundance of arthropods showing significant location×treatment interactions on red alder and Douglas-fir. Pairs of medians sharing the same letter (at the same location) are not significantly different at $\alpha = 0.05$, using the student's t-test on ln (y+1) transformed data (n=3, degrees of freedom = 4 for each comparison).

	Cascade Head				Andrews Forest			
Red Alder Treatment	4	5	6		4	5	6	
Defoliators	40a	20b	0b		36a	109a	53a	
Douglas-fir Treatment	1	2	3	4	1	2	3	4
Adelgidae	623a	4098a	2468a	11b	254a	416a	424a	292a
Diaspididae	0a	0b	0b	0a	0b	4.2a	7.9a	4.6a

DISCUSSION

The distinction of arthropod communities on Douglas-fir and red alder was as expected. Different tree species are known to harbor unique and characteristic arthropod faunas (Moran and Southwood 1982, Costa and Crossley 1991, Schowalter and Ganio 1998). This phenomenon results in large part from the presence of specialist herbivores, whose phylogeny frequently mirrors that of their host plants on an evolutionary scale (Farrell *et al.* 1992, Beccera 1997). Similarly, microhabitat differences between different tree species might influence their associated arthropod communities. For example, differences in foliage structure and branching patterns can affect the microclimate and set limits to arthropod size or range of within-plant travel (see Lawton 1986). Even within a single tree species, morphology plays an important role in structuring arthropod communities (Waltz and Whitham 1997). All of these factors help to explain the observed correlation between plant and insect species richness (Murdoch *et. al* 1972, Southwood *et. al* 1979).

The observed geographical separation of arthropod communities was also as expected (Progar *et al.* 1999). Climate is a primary explanation for unique arthropod faunas at different locations. Stiling and Rossi (1995) have shown that local climatic variation can overwhelm other factors in structuring insect communities. Precipitation and temperature patterns are different between the Cascade Head and Andrews Forests, with Cascade Head being warmer in the winter, cooler in the summer, and slightly wetter throughout the year (Figure 2). This could affect how certain arthropod populations develop at each location.

Alternatively, regional variation in populations of certain arthropod taxa might result in unique arthropod faunas at any two distant locations. Also, if tree structure is affected by location (due to differences in genotype or growing conditions), then this could create distinct arthropod communities (on a single tree species) at different locations (see above).

With the exceptions of defoliators and Thripidae on red alder and Diaspididae and Araneidae on Douglas-fir, defoliation and abundance of specific arthropod taxa or functional groups were generally greater at Cascade Head. This may be a direct result of climate (the ocean-moderated climate allows greater survival through the winter and higher rates of population growth) or perhaps reflects a host-mediated climate effect (tree productivity was higher at Cascade Head).

The greater percentage defoliation but lower defoliator abundance on Cascade Head alders compared to Andrews Forest alders seems paradoxical. Because of climate differences, we would expect Cascade Head alders to break bud and leaf out earlier than Andrews Forest alders. Defoliators (typically Lepidoptera and Hymenoptera) also might develop and pupate earlier at Cascade Head because foliage is available earlier. At the time of initial sampling in June, perhaps the majority of defoliators at Cascade Head had already pupated, while those at the Andrews Forest were feeding larvae (not yet attaining maximum leaf damage). Leaf phenology has been shown to play an important role in the life cycles of associated herbivores (Hunter 1992, Mopper and Simberloff 1995).

Defoliator abundance on red alder was also affected by treatment (depending on the location). At Cascade Head, defoliators were most abundant in treatment 4 (mixed), with other treatments being similar. At the Andrews Forest, all treatments were similar in

defoliator abundance. Given the small sample size (n = 3) and generally low defoliator abundance at Cascade Head, the biological meaning of this interaction is uncertain.

The treatment differences in *A. cooleyi* abundance on Douglas-firs are best explained by host productivity. At Cascade Head, treatment 4 had low *A. cooleyi* abundance in comparison to other treatments. At the Andrews Forest, all treatments were similar. From Table 2, we see that there was strong interference competition between red alders and Douglas-firs in treatment 4 at Cascade Head, but not at the Andrews Forest. In treatments where Douglas-firs had more energy available for tree growth (1, 2, and 3 at Cascade Head) we would expect more energy to be available for *A. cooleyi* to utilize (resulting in higher abundance). Also, greater Douglas-fir size and diameter would make trees in these treatments more likely to intercept *A. cooleyi* dispersing from spruce. While trees with greater resource availability might be better defended, sap-suckers utilize a poorly defended resource compared to leaves or bark. At the Andrews Forest, Douglas-firs were similar in size and mortality, and no treatment differences were seen in *A. cooleyi* abundance. The high abundance of *A. cooleyi* at Cascade Head relative to the Andrews Forest dominated the analysis and contributed to an overall significant treatment effect (regardless of location).

An alternative explanation is non-host interference. Douglas-firs in treatments 2, 3, and 4 were equally dense (~500/ha), but there were differences among the interspersed trees: no alder, young alder, or alders planted simultaneously, respectively. At Cascade Head, alders in treatment 4 outgrew the Douglas–firs, and might reduce the vagility of dispersing *A. cooleyi*. Young alders in treatment 3 at Cascade Head were similar in size to the Douglas-fir, and would be less of barrier to *A. cooleyi* movement. Distinguishing

between host-quality (productivity) and host-apparency is not possible in this experiment, as the two factors are inter-dependent. Note that when Douglas-fir are at high density in treatment 1 (and presumably most apparent), *A. cooleyi* abundance is lower than in treatments 2 and 3 at either location (though not by a significant margin), so host quality is probably at least part of the explanation.

These results are contrary to many other studies, where plant stress from competition, drought, or other factors usually increases plant susceptibility to herbivory (Safranyik 1985, Schowalter *et al.* 1986, Franklin *et al.* 1987, Waring 1987, Müller-Schärer 1991, Bonser and Reader 1995). However, others have shown that some phytophages prefer more productive plants (Lightfoot and Whitford 1987, 1989, Waring and Price 1990, Siemann 1998, Schowalter *et al.* 1999). In light of this controversy, we must consider the resource being used by sap-suckers such as *A. cooleyi*. In stressed plants, resource quality typically declines along with plant defenses (making resources relatively easy to utilize). However, sap is generally low in defensive chemicals (compared to leaves or bark). In response to plant stress, sap quality declines (reduced growth results in a lower rate of resource translocation), but defenses are approximately constant. Thus, sap-feeders might be expected to favor more productive hosts.

The communities as a whole and most common taxa or functional groups, showed no significant responses to the treatments. It is possible that these treatments did not affect these arthropods (Karieva 1983). Another possibility is that these treatments did or could affect other arthropods, but the spatial scale or low replication of this study precluded detection of significant treatment effects. The plots used in this study were small relative to the dispersal capacity of most arthropods. Larger plots would reduce the

influx of arthropods from neighboring plots, perhaps making treatment differences easier to detect. Sensitivity to treatment effects might have also been reduced by the geographical locations of treatments. Plot location significantly affected community composition as a whole as well as many component arthropod taxa. Replicating the treatments six-fold at one location would be more likely to elucidate treatment differences than three-fold replication at two locations.

The amount of replication necessary to detect a treatment effect in a t-test (or ANOVA) is easily calculated from the estimated variation in the population and the biologically meaningful difference in means (see Ramsey and Schafer 1997). Similarly, for diversity studies (especially those concerned with species richness), the relationship between the total number of species encountered and number of samples taken defines the adequacy of sampling effort—when the rate of species accumulation per sample approaches zero, sampling is considered adequate. In this study, red alders at Cascade Head were the only group to meet this condition (due to low taxa richness), making comparisons of taxa richness difficult.

For ordinations or other multivariate analyses, the relationship between replication and statistical sensitivity is not mathematically defined, but the effect is similar. Increased replication facilitates interpretation of ordinations: more data points confer greater confidence (because of probability) that the observed groupings (or lack of groupings) demonstrate a real pattern (or lack thereof). Increasing the amount of replication could only increase the sensitivity of the study, as well as capture a greater proportion of the available taxa (Figure 5).

Another factor that might have influenced the results of this study was the understory vegetation. Both geographical locations had additional unplanted (and unquantified) vegetation. For example, salmonberry, hemlock, blackberry, and spruce were all common at Cascade Head. These species were occasionally codominant with the planted Douglas-firs and red alders. The presence of these and other species likely affected arthropod presence on sampled Douglas-firs and red alders (Altieri and Schmidt 1986, Szentkiralyi and Kozar 1991) and might affect herbivory rates (Brown and Ewel 1987). Without sampling the surrounding vegetation, it is much less obvious exactly how they might affect the communities on Douglas-fir and red alder. However, I would expect this associated vegetation to increase the abundance of transients on Douglas-fir and red alder, thereby increasing variation in my data. Sedentary arthropods such as *A. cooleyi* and Lepidoptera larvae are likely less affected by the surrounding vegetation than more mobile taxa, but population sources from alternate hosts (such as spruce in the case of *A. cooleyi*) is still a possible source of variation.

The family level taxonomic resolution achieved by this study was detailed enough to separate arthropod communities by tree species and geographic location. Increasing the taxonomic resolution in the Diaspidiade, Linyphiidae, and Oribatida resulted in a similar overall pattern of arthropod assemblages (communities distinguished by tree species and geographic location). It cannot be determined whether finer taxonomic resolution in the other families would result in similar patterns or better detection of treatment effects. If we assume that each morphospecies encountered in this study corresponds to a formally identified species (Beattie and Oliver 1994, Oliver and Beattie 1996), then only three families of Coleoptera would have more than one species per

family (Curculionidae, Elateridae, and Staphylinidae, with a total of 9 individuals among them—see Appendix). Thus, I would expect species-level taxonomic resolution to result in a similar pattern of overall arthropod assemblages (distinction of communities by tree species and location).

The functional group of sap-suckers captured the treatment response of *A. cooleyi* alone but not the interaction, so a more inclusive grouping of arthropods is less informative (even though the sap-suckers were heavily dominated by *A. cooleyi*). The only other treatment effect to be detected was in a functional group (defoliators on red alder). Perhaps combining defoliators corrected for geographical differences in taxa (same roles filled by different families), or integrated consistent, but non-significant treatment responses. More likely is that this treatment effect is defined by chance absence of defoliators from certain treatments (see above). Combining taxa increases abundance, making values easier to compare (and helping to satisfy assumptions of normality in statistical analyses). However, there is a risk of missing complementary responses among component taxa. Also, specific knowledge on the biology of component taxa is lost as taxa are combined

The applications of this study depend greatly on the forest management objectives. If the goal of forest regeneration is commercial growth of Douglas-fir, absence of competitors (monoculture) appears to be the best strategy (Rose *et al.* 1999). Even if herbivore loads and defoliation increase somewhat as the result of monoculture (which was not seen here, but might occur in some situations), the growth effects will typically be minor west of the Cascade Mountains (Osman and Sharrow 1993). When soil nitrogen and phosphorous depletion hinders this goal, incorporating alders can enrich

the soil (Binkley 1984, Giardina *et al.* 1995). In the unlikely scenario that adelgid populations increase to pest levels, mixed stands would work to alleviate the problem (essentially growing stressed Douglas-firs incapable of supporting high adelgid abundances).

If the goal of forest management is arthropod biodiversity, mixing several tree species will maximize this aim. Since the communities of each tree species are distinct, adding tree species to the plant community adds entire arthropod communities (and their component taxa). Progar *et al.* (1999) and this study have demonstrated geographical differences in forest arthropod communities, so conserving geographically distinct forests should conserve their unique arthropod faunas.

In conclusion, this study supports two previously identified trends: arthropod communities of different tree species are distinct, as are the communities in different geographical locations. This study did not clearly indicate that density and/or non-host interspersion limit herbivore abundance in diverse plantations, at least at this spatial scale. Instead, resource quality, abundance, and/or apparency may be the key factors in determining abundance of certain arthropod taxa. Improved experimental design might increase the chances of detecting diversity or density effects on community structure.

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APPENDIX

Operational Taxonomic Units Identified:

Functional Group	Family	Genus/Species	Morhpospecies	Individuals
Defoliators	Agromyzidae		1	1
	Cimbicidae		1	3
	Curculionidae		2	4
	Geometridae		1	25
	Gracillariidae		1	3
	Pyralidae		1	8
	Thripidae		1	52
	Tortricidae		1	6
Sap-Feeders	Adelgidae	*Adelges cooleyi*	1	5771
	Aphididae		1	55
	Cercopidae		1	5
	Cicadellidae		1	78
	Diaspididae	*Chionaspis pinifoliae*	1	14
		Stramenaspis kelloggi	1	12
	Membracidae		1	1
	Miridae		1	6
	Pentatomidae		1	1
	Psyllidae		1	46
	Tetranychidae		1	65
	Tingidae		1	1
Predators	Anaphaenidae		1	14
	Araneidae	*Araniella displicata*	1	76
	Cantharidae		1	1
	Erythraeidae		1	69
	Hemerobiidae		1	5
	Linyphiidae	*Gnathantes ferosa*	1	10
		Pityophantes	1	31
		Spirembolus	1	26
	Nabidae		1	2
	Philodromidae		1	21
	Salticidae		1	19
	Theridiidae		1	35
Detritivores	Entomobryidae		1	50
	Forficulidae		1	1
	Lepismatidae		1	2
	Oribatida	*Camisia*	1	26
		Ctenacarus	1	24
		Eupterotegaeus	1	4
		Peloribates	1	5
	Psocidae		1	106
	Sminthuridae		1	32
Other	Chironomidae		1	30
	Culicidae		1	18
	Elateridae		3	3
	Eulophidae		1	7
	Formicidae		1	13
	Staphylinidae		2	2
	Tachinidae		1	4