

AN ABSTRACT OF THE THESIS OF

Peter T. Oboyski for the degree of Master of Science in Entomology presented on June 28th, 1995. Title: Macroarthropod communities on vine maple, red alder and sitka alder along riparian zones in the cnetral Western Cascade Range, Oregon.

Abstract approved: _____

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This study addresses the structure and distribution of the arthropod communities on vine maple, red alder and sitka alder of riparian zones in the Western Cascade mountain range. Samples were collected from the riparian zones of ten montane streams in and around the H.J. Andrews Experimental Forest, Linn/Lane County, Oregon from May to July of 1992 and May to November of 1993. Arthropod taxa were sorted and tabulated for calculations of intensity (# individuals per biomass of plant sampled) and diversity. The study was designed to test if host tree species and riparian morphology (summarized as stream order) correlate with the organization of arthropod communities.

The arthropod communities were dominated by Homoptera (particularly Aphididae), spiders (Aranea) and a leaf mining weevil (Curculionidae). Less abundant, but consistently present were Lepidoptera, Hymenoptera (Symphyta) and Diptera (Mycetophilidae).

Multivariate (ordination and classification) and two-sample statistical analyses revealed that arthropod species inhabiting these riparian areas were segregated by host tree and stream order. Of the 24 dominant taxa, 12 taxa (10 herbivores and 1 fungivore) showed significant affinities to particular host tree species while 7 taxa (3 predators, 2 fungivores, 1 scavenger and 1 herbivore) significantly differed in intensity with stream order.

Macroarthropod communities collected from red alder represented the greatest diversity, a result of both high species richness and evenness. Vine maple showed the least diversity, but highest intensity as a result of high aphid abundance. Guild structure

revealed that the proportions of sap-sucking to chewing herbivores differed among the host tree species. The high abundance of aphid species resulted in a ratio of nearly 80:1 of sap-suckers to chewing herbivores on vine maple. High abundance of the weevil *Isochnus goniophallus* resulted in a ratio of nearly 3:5 of sap-suckers to chewing herbivores on sitka alder. The same ratio on red alder was nearly 4:1.

Spiders were the most abundant of the predator trophic level. Webspinning spiders were significantly more abundant at the more shaded and humid low order sites, while hunting spiders were more abundant at the more open and sunny mid order sites. This segregation of taxa implies that diversity within the compound community of the riparian zone is a function of the different component communities existing therein.

Macroarthropod communities on vine maple, red alder and sitka alder along riparian
zones in the central Western Cascade Range, Oregon

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed June 28, 1995
Commencement June 1996

Master of Science thesis of Peter T. Oboyski presented on June 28, 1995

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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1. INTRODUCTION

Lotic waters have been recognized as ecosystems since the early part of this century (Hynes 1970, Leopold *et al.* 1964, Thienemann 1925). More recently, however, the role of stream ecosystems has been placed within the context (and as a subset) of a larger perspective - the watershed ecosystem (Gregory *et al.* 1991, Fontaine & Bartell 1983, Edmonds 1982, Naimann & Sedell 1981, Hynes 1975). The riparian zone is a multi-dimensional zone of interaction (an ecotone) between a stream and a terrestrial ecosystem (Gregory *et al.* 1991, Swanson *et al.* 1982b, Meehan *et al.* 1977). Precise definitions and delineation of riparian zones are difficult because they are "comprised of mosaics of landforms, communities and environments within the larger landscapes" (Gregory *et al.* 1991). Most definitions include the presence of hydric soils, wet adapted vegetation and a near surface water table during at least part of the growing season (Frenkel, personal communication).

Although it occupies relatively little land area, the riparian zone may be considered a "hot spot" of activity due to the overlap of communities and functions (Gregory *et al.* 1991, Oakley *et al.* 1985, Thomas *et al.* 1979). These small areas of high resource availability are therefore disproportionately important to wildlife, agricultural and recreational uses (Thomas *et al.* 1979). As an ecotone, the riparian zone supports arthropods of both the stream community and upland community as well as those adapted to the unique conditions established in the riparian zone *per se* (Andersen 1985, Merritt & Lawson 1981).

The extent of the riparian zone is largely dependent on local geomorphology (Gregory *et al.* 1991, Thomas *et al.* 1979). Mid and higher order, lower elevation, stream channels (third order and greater) are subject to lateral migrations due to a lack of barriers

that would otherwise contain the channel (Thomas *et al.* 1979). The local terrain may rise less than a meter above the stream bed for tens of meters away from the stream channel. As a result water tables are relatively high while direction of water movement is dependent upon water levels in the channel relative to the surrounding areas, particularly during high water events (Junk *et al.* 1989). Lower order montane streams (zero to second) often have steep rocky banks with bedrock outcrops that inhibit lateral channel migration and maintain lower water tables in surrounding areas (Triska *et al.* 1982).

Canopy cover of small, montane streams is often 100% (Triska *et al.* 1982). The high amount of shading greatly reduces primary production by aquatic plants (autochthonous inputs) within the stream channel. Therefore, the resource base is dependent upon processing of organic input from riparian vegetation (allochthonous inputs) and sediment erosion into the channel (Vannote *et al.* 1980, Cummins 1974). The type and extent of the vegetation is largely dependent on erosional history and local geomorphology and may show high heterogeneity along a stream reach (Gregory *et al.* 1991, Swanson *et al.* 1982b).

Nutrient flow in the form of particulate matter (litter, sediments) and dissolved nutrients (surface and groundwater flow) all must pass through the riparian zone before entering the stream channel for downstream movement (Swanson *et al.* 1982a,b). Therefore, water quality (Taylor & Adams 1986) and downstream nutrient availability (Elwood *et al.* 1983) may be greatly affected by riparian community composition. Though most allochthonous inputs are associated with flood pulses (Junk *et al.* 1989) and leaf senescence (Taylor & Adams 1986, Swanson *et al.* 1982a) lower levels of continuous organic input may occur through arthropod herbivory (and subsequent defecation) of riparian vegetation and as dead arthropods fall into the stream.

The importance of understanding riparian zone form and function has implications for ecosystem management of wildlife habitat, water flow dynamics, material transfer and nutrient flow. The current ecological and political emphasis on biodiversity (Wilson 1988) stresses the importance of maintaining habitat heterogeneity. Since riparian zones are relatively small in area and high in heterogeneity (Gregory *et al.* 1991, Swanson *et al.* 1982b, Thomas *et al.* 1979) they are particularly attractive for conservation efforts.

Removal of riparian vegetation by clear-cutting of timber (Triska *et al.* 1982, Swanson *et al.* 1982a,b) or for recreational or agricultural use (Oakley *et al.* 1985, Thomas *et al.* 1979) results in reduced retention of organic material due to greater wind erosion and less primary production in the riparian zone. The removal of stream shading vegetation can also cause a shift in the resource base for the aquatic community from allochthonous to autochthonous sources.

The riparian zones of Pacific Northwest montane forests are dominated by broadleaf trees (willow, alder, cottonwood and maple) that are adapted to regularly disturbed environments, such as riparian zones (Oakley *et al.* 1985, Campbell & Franklin 1979). Several of these species are also adapted to the hydric conditions of riparian soils and stream beds. All are common components of lower elevation flood plains, but only alder and maple are found at upper elevation, low order stream sites in the western Cascades. As a result, the arthropods associated with these plants, and the habitats in which they are found, are also limited in their distribution.

The organization of arthropod communities is affected, in part, by host specificity and climatic requirements. In this respect, communities can be subdivided into compound and component communities depending on the habitat being considered. According to Root (1973), component communities are assemblages of species associated with a particular microenvironment or resource (*e. g.* a particular plant taxon, rotting logs, tree holes), that when taken together represent a compound community (*e. g.* communities on all the plant species in a meadow or riparian area).

Host nutrition, in the form of unbound nitrogen and carbohydrates, as well as secondary plant compounds, dictate the complement of herbivores that can potentially feed on a plant. Host preference by herbivores is well documented, and reaches its greatest specificity where herbivores have evolved to exploit the secondary defense compounds of their hosts (Berenbaum 1981). The abundance of herbivores in a particular environment, in turn, dictates the complement of predators that may specialize on them. Karr (1975) suggests that the diversity within a community is closely linked with the resource packages that the habitat has to offer. Price (1983) outlines several factors that

influence the composition of insect communities, including resource availability and enemy impact.

The riparian zone is dominated by a small number of hardwood tree species, thus providing an opportunity to investigate host relationships of herbivores in a limited environment. The distribution of host plants is patchy as a result of scouring and deposition during periods of flood, providing conditions for metapopulation exchange and predator refugia. Periodic disturbance of the riparian habitat, in the form of seasonal flooding, results in the continued establishment of immature vegetation while haphazard deposition may result in complex architectural features.

The three host plants under investigation are red alder (*Alnus rubra* Bong.), sitka alder (*Alnus sinuata* [Reg.] Rydb.) and vine maple (*Acer circinatum* Pursh). Red alder is a common, early colonizing, hardwood of near coastal landscapes in the Pacific Northwest. Nitrogen fixation by symbiotic bacteria takes place in nodules of alder roots, thus allowing the plants to persist in nitrogen poor soils. Red alder's ability to exploit poor growing conditions may result in a nutrient rich food source to herbivores where other plants are less successful. The availability of sequestered nutrients to wildlife, however, has not been well documented. McComb (1994) suggests that the astringent nature of alder leaves may render much of their nitrogen unavailable to herbivores. Insect associations with red alder have been documented by Furniss and Carolin (1977) and include significant feeding by tent caterpillars (*Malacosoma* spp.), fall webworm (*Hyphantria cunea* Drury), sawflies (*Eriocampa ovata* Ross, *Hemichroa crocea* (Geoffroy)) and leaf beetles (*Altica ambiens* LeConte, *Pyrrhalta* spp.). Also noted are colonization by the alder aphid (*Pterocaulis alni* (DeGeer)), the alder leaf miner (*Lithocolletis alnicolella* Wlsm.), flatheaded borers (*Agilus* spp.) and bark beetles (*Alniphagus aspericollis* LeConte).

Sitka alder has not been investigated to the same extent as red alder. The distribution of sitka alder is generally limited in the Pacific Northwest to sites above 1200 meters (4000 ft), where it often forms thickets around stream channels (Ross 1978). Furniss and Carolin (1977) report only one insect species from sitka alder, (*Alniphagus hirsutus*

Schedl: Scolytidae), while no other wildlife interactions are documented for the Pacific Northwest.

Vine maple, like sitka alder, lacks the economic significance necessary to warrant extensive biological and ecological research. Vine maple is distributed throughout the northwestern states along talus slopes, riparian zones and as a shade-tolerant understory component of coniferous forests (Franklin & Dyrness 1973). Russel (1974) observed that vine maple comprises a vast amount of the biomass that recolonizes sites after disturbance (*e. g.* fire, clearcutting) on the H. J. Andrews Forest. The percent nitrogen content of vine maple foliage is more than twice that of the shrubs and herbs with which it is associated (Russel 1974). Del Moral and Cates (1971) demonstrated, however, that vine maple leaf extracts showed inhibitory effects to decomposition and establishment of conifer seedlings. Furniss and Carolin (1977) do not list vine maple in their host index for common insects of western forests, although it probably harbors aphids and caterpillars common to other species of maple.

The goal of this study was to characterize the arthropod communities along the riparian zones of several streams in and around the H.J. Andrews Experimental Forest, Oregon. In particular, I wished: (1) to test if arthropod intensity and diversity were correlated with host tree species and riparian morphology, (2) to determine if the arthropods on vine maple, red alder or sitka alder contributed the greatest diversity and intensity to riparian communities, and (3) to identify those arthropod species that dominated these communities. By studying an entire community I hoped to uncover community patterns and associations not revealed by species specific sampling efforts. This study is intended to provide baseline data for further analysis of riparian communities with possible implications for the management of riparian habitat in the central western Cascades of Oregon.

2. MATERIALS & METHODS

2.1 H.J. Andrews Experimental Forest

Sample sites for this study were located in and around the H.J. Andrews Experimental Forest (HJA) in the Blue River Ranger District of the Willamette National Forest (lat. 44°13' x long. 122°08'). The HJA is part of a nationwide network of Long-Term Ecological Research (LTER) sites that promote and facilitate long term studies of ecosystem properties and processes. Interdisciplinary research projects have resulted in a vast accumulation of silvicultural, hydrogeological and ecological data that are drawn upon to improve the interpretation and inference of individual projects.

The past emphasis of the HJA has been on applied forestry, though basic research on forest and stream ecosystem properties has become the focus of most contemporary studies (Swanson *et al.* 1979). The forest lies along the central eastern margin of the western Cascade Range and ranges in elevation from 600 to 1300 m (2000 to 4400 ft). Precipitation averages 230 cm (90 in) annually, mostly in the form of winter rains. As a result of highly permeable soils with high water retention potential, free water enters the soil and travels by subsurface flow to stream channels (Swanson *et al.* 1979).

The HJA is located within the *Tsuga heterophylla* Zone (Franklin & Dyrness 1973) and is dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn), some stands of which are 400-500 years in age. The major hardwood species are red alder in disturbed and riparian sites, bigleaf maple (*Acer macrophyllum* Pursh) along breaks in the overstory, sitka alder generally above 1200 meters, willow (*Salix* spp.) in riparian areas, and vine maple in riparian zones and the conifer understory. The specific distribution of tree species is a result of burns from the last century, experimental harvest plots (with their subsequent regeneration) and the natural landscape features of the drainage basin.

2.2 Sites

Sample sites were selected by identifying two riparian habitat types (low and mid order stream reaches) that supported three hardwood species (vine maple, red alder and sitka alder). Though several hardwood species may be found in montane riparian zones in the Pacific Northwest, only maple and alder were encountered at an abundance necessary for sampling at higher elevation sites. Low order sites, (upper Lookout Creek, Cold Creek, Earth-flow Creek, Shorter Creek, upper MacRae Creek, upper Tidbits Creek, upper Mona Creek), range 700-1340 meters in elevation and are characterized by closed canopy, well shaded stream reaches with channels well defined by bedrock formation. Mid order sites, (middle Lookout Creek, lower Mack Creek, lower MacRae Creek, lower Tidbits Creek, North Quartz Creek and Blue River), range 450-750 meters in elevation and are characterized by open canopy and sunny stream reaches with marginal flood plains that show signs of lateral stream movement. The sites represent many different slopes and aspects and encompass a range of 13 km (8 mi.) within the Lookout Creek drainage basin and adjacent Buck Mountain. See Table 1 for a summary of sample sites.

Table 1: Summary of Sample Sites

List of sites with corresponding host plants, habitat types and elevations found at each. ACCI = *Acer circinatum*, ALRU = *Alnus rubra*, ALSI = *Alnus sinuata*, Low = low order stream sites, Mid = Mid order stream sites, Elevation (meters).

Stream name	ACCI	ALRU	ALSI	Low	Mid	Elevation
upper Tidbits Creek	x		x	x		1340
upper Lookout Creek	x		x	x		1200
Cold Creek	x		x	x		1000
upper MacRae Creek		x		x		900
Earth-flow Creek	x		x	x		850
Shorter Creek	x		x	x		800
upper Mona Creek	x	x		x		700
middle Lookout Creek	x	x			x	730
lower Mack Creek	x		x		x	680
lower MacRae Creek	x	x			x	560
North Quartz Creek	x	x			x	470
lower Tidbits Creek	x	x			x	460
Blue River	x	x			x	450

2.3 Samples

Samples of vine maple, red alder and sitka alder were collected from within 2 to 3 meters of the stream channel. These three tree species were chosen because they showed the greatest consistency of occurrence at the different sites. While willow and bigleaf maple are common riparian inhabitants, they were not found consistently at low order sites. Collecting took place from May to July in 1992 and from May to November in 1993 at 3-4 week intervals. All samples were collected during daylight hours (10 a.m. to 6 p.m.) from a random order of sites for each date.

Samples of arthropods from riparian vegetation were collected using a bagging technique similar to that of Schowalter (1989). Selection of branches for the three host plants was arbitrary but without preconceived bias due to a lack of conformity of plants to potential transects. Single branches (approximately 0.5 m in length) were quickly enclosed in 60 liter plastic bags, clipped from the plant and sealed for return to the lab. Although this sampling protocol is biased against nocturnally active and highly mobile species, it does adequately represent sedentary species that comprise the vast majority of the community (personal observation) and leaf-mining species that go undetected by other sampling methods, such as beating the foliage or using sticky traps. Furthermore, great care was taken not to disturb foliage prior to enclosure. The list of collected species reveals a number of highly mobile taxa.

Since vine maple sites outnumber each of the alder sites (nearly two to one), five branches of alder and three branches of vine maple were collected for each site, resulting in nearly equal biomass of foliage for each plant when samples were pooled. Samples were stored at $\sim 5^{\circ}\text{C}$ until they could be processed. Storage at this temperature allowed the survival of most taxa, which greatly facilitated detection during sorting. Immature holometabolous insects were placed in 4 oz. plastic containers along with host plant material in order to rear individuals to adulthood for identification.

The processing of samples began with the partitioning of leaves, stems and arthropods. Foliage was dried to constant weight and biomass of leaves and stems was

recorded. Arthropods were separated by sight into morphospecies and tabulated. Each morphospecies was then identified to its greatest resolution using keys from Peterson (1948), McAlpine *et al.* (1987), Grissel (unpublished), Borror *et al.* (1989), Merritt and Cummins (1984) and the H.J. Andrews voucher collection (Parsons *et al.* 1991) housed at the Systematic Entomology Laboratory at Oregon State University. Dominant taxa were identified to species where authorities were available. Arthropods from each tree species at each site were pooled and considered one sample for each sample date.

2.4 Data

Intensity for each taxon was calculated by dividing the number of individuals by the biomass (in kg) of the dried foliage. The natural log transformation was applied to intensity measures to normalize variance. Taxa showing relatively low intensities were lumped according to taxonomic, trophic and ecological similarities. For example, spiders were grouped first by family, then by similarities in prey capture strategies. Taxa were also segregated by guilds (chewing herbivores, sucking herbivores, fungivores, predators, scavengers and tourists) to examine trends in community organization. Analyses are based on the 24 dominant taxa which were delineated by a 5% presence in samples (at least 15 out of 296 samples).

Samples were then pooled across all sample dates for each of the 25 site types, resulting in 12 replicates from vine maple, 7 replicates from red alder and 6 replicates from sitka alder. Alternatively, pooling resulted in 13 low order sites and 12 mid order sites. The sample dates from 1992 and 1993 did not form complete replicates to test seasonal components of the communities, though data were examined for apparent seasonal trends.

2.5 Statistics

To test hypotheses on community organization both multivariate and two-sample test statistics were used. The pooled samples matrix includes only the 24 dominant taxa and excludes the rare taxa, for the 25 different host x habitat sites. The full samples matrix includes all taxa (126) for the 25 sites. Student's T-test and one way analysis of variance (ANOVA) were used (Systat software package) to detect significant differences in diversity and taxon intensities among the three host tree species and the two habitat types, based on the mean and variance of the replicate sites. All p-values reported are two-tailed values unless otherwise stated.

Diversity measures were used to calculate the number of species and their relative abundances for each pooled site. The Shannon-Wiener index was used on the pooled samples matrix. The Simpson index (which places greater weight on more dominant taxa) was used on the full samples matrix to determine total diversity for the sample season. Total number of species and total species intensity were also tabulated and compared for the pooled and full samples matrices. When applied to the transposed matrix, the Shannon-Wiener index was used as a measure of niche breadth for each taxon.

Multivariate techniques used were cluster analysis and ordination (PCORD statistical software package). Cluster analysis was performed, using *Ward's method* to calculate sample distances, to reveal which samples showed the greatest similarities in terms of species abundance. Ordination using Non-metric Multidimensional Scaling (NMS) was performed to determine the strongest axes of separation between sample sites based on species abundance. NMS was preferred to other ordination techniques because of the nature of the data set. High beta diversity among samples (high species turnover) resulted in many zero entries in the data matrix. Metric scaling, in this situation, tends to place disparate communities in proximity based on the absence of species. NMS uses ranked scaling, thereby avoiding this problem. NMS also employs flexible dimensional axes that allow axes to be drawn through prominent gradients without the restriction of orthogonality used by PCA procedures. In this way, axes may more accurately represent environmental gradients, but may not be completely independent.

Multi-Response Permutation Procedure (MRPP) was also used to evaluate the designation of samples based on tree species and habitat type (see Appendix of Biodini *et al.* 1985). MRPP calculates and ranks the distances (in species space) between all combinations of samples. It then averages the rank scores from an imposed grouping scheme (*e. g.* samples from three host plants). By comparing imposed group averages with all other combinations of samples MRPP is able to return a probability term that relates how natural a grouping scheme is (*e. g.* Is the grouping of samples by stream order and host plant more enlightening than by other variables?).

Chi-square (X^2) procedures were used to test for significant seasonal trends in diversity and taxon intensities. The observed intensities for the 1993 season were tested against equal intensities throughout the season (null hypothesis) to determine significant peak abundances. The critical chi-square value is 3.84 for one degree of freedom (observed vs. expected for one season) at the $\alpha = 0.05$ level. X^2 values greater than this indicate a significant difference. The chi-square test was used to test seasonal trends because only one complete season of pooled data was available, allowing no estimate of variance for parametric procedures.

Comparisons of guild structure were also made between the different host plants and habitat types. The percent of each guild (chewing herbivores, sucking herbivores, fungivores, predators, scavengers and tourists) was compared. The predator trophic level was furthered divided into insect predators, parasitoids, hunting spiders, webspinning spiders and ambush spiders.

3. RESULTS

3.1 Dominant Taxa

Arthropod specimens (5417 individuals) were extracted from 296 samples. These specimens were sorted into 336 morphospecies by sight then lumped back into 126 taxa after identifications were made to the greatest possible resolution. Further lumping was performed for analytical purposes based on trophic and ecological similarities. The total intensity for the sampling period was 5955 (Indiv / kg dry foliage) for the 3733 grams of foliage collected.

Homopteran insects, primarily aphids (Aphididae), scales (Coccidae), and leafhoppers (Cicadellidae), were most abundant and together represented 38% of the arthropod intensity collected. Five species of aphids (*Euceraphis gillettei* [Davidson], *Periphyllus californiensis* [Shinji], *P. testudinacea* [Ferne], *Boernerina variabilis* Richards and *Pterocallis alni* [DeGeer]) represented 26% of the intensity collected, with *B. variabilis*, *P. californiensis* and *E. gillettei* being three of the seven most dominant taxa. Leafhoppers (3-4 species, 7.6% of intensity) and scales (2 species, 4.3% of intensity) were of various nymphal stages that were difficult to separate taxonomically and so were left at the family level. Aphid mummies (4.9% of intensity) were included as a taxonomic category because of their high abundance and unique trophic significance (hosts of parasitoids).

Spiders (Aranea) were the next most abundant taxon (16% of intensity). Spiders were identified to genus (12 families, 15 genera) then lumped by feeding strategies (*i.e.* webspinning, mobile hunters, ambush predators). The leaf-mining weevil *Isochnus goniophallus* (Curculionidae) dominated collections from sitka alder for much of the sampling season (5.3% of total intensity, 21% of intensity on sitka alder). Insects of the orders Lepidoptera, Hymenoptera, Diptera and Coleoptera were grouped at the family level due to their lower abundance and the taxonomic difficulties of immature stages.

Species of Ephemeroptera, Plecoptera, Trichoptera, Thysanoptera and Psocoptera were grouped at the level of order for reasons of low abundance and taxonomic difficulty.

Individuals of 24 taxa were present in at least 15 of the 296 samples (5% of samples). The mean and standard error for each taxon intensity is illustrated in Figure 1. These 24 dominant taxa each had at least 19 specimens represented over the course of the study and are listed in Table 2 along with their total abundance, intensity, number of times present in a collection and niche breadth. The following taxon references will be of these 24 dominant groups unless otherwise stated.

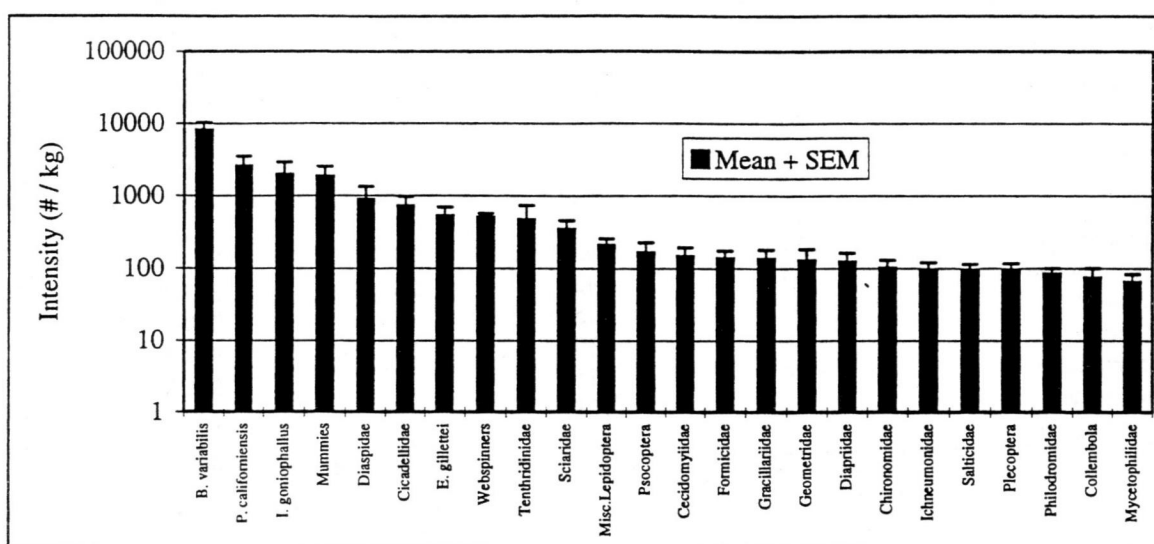


Figure 1: Mean Intensity of 24 Dominant Taxa

Mean intensity (ln [# Indiv / kg dry foliage]) + SEM for each of the 24 dominant taxa collected over the course of the study, ranked by intensity.

Table 2: Summary of 24 Dominant Taxa

List of 24 dominant taxa ranked by intensity. # Individuals = total absolute abundance, Intensity = # Indiv / kg dry foliage, Present = # of samples collected in (out of 296), Niche breadth = Shannon information index.

Taxon	# Individuals	Intensity	Present	Niche Breadth
<i>Boerneria variabilis</i>	1608	203947	66	4.156
<i>Periphyllus californiensis</i>	431	64396	39	3.641
<i>Isochnus goniophallus</i>	659	49253	52	3.925
Aphid mummies	303	45917	35	3.518
Diaspidae	375	22390	34	3.487
Cicadellidae	230	18085	59	3.633
<i>Euceraphis gillettei</i>	232	13280	37	3.576
Web-spinning spiders	130	12713	71	4.064
Tenthredinidae	123	11811	33	3.114
Sciaridae	88	8741	34	3.487
Lepidoptera (Misc.)	66	5285	34	3.505
Psocoptera	46	4170	24	3.162
Cecidomyiidae	43	3671	19	2.913
Formicidae	42	3457	25	3.201
Gracillariidae	44	3376	28	3.311
Geometridae	32	3239	16	2.757
Diapriidae	38	3095	16	2.757
Chironomidae	31	2550	22	3.078
Ichneumonidae	31	2420	23	3.125
Salticidae	32	2358	30	3.387
Plecoptera	26	2301	24	3.165
Philodromidae	24	2112	21	3.038
Collembola	19	1857	18	2.873
Mycetophilidae	21	1617	17	2.824

3.2 Diversity Indices

Diversity indices (# individuals, intensity, # species, Shannon [H_e]) were calculated for the pooled and full matrix for samples grouped by vine maple (12 sites for the pooled matrix, 142 samples for the full matrix), red alder (7 sites, 89 samples) and sitka alder (6 sites, 60 samples) and with samples grouped by low order (13 sites for the pooled matrix, 152 samples for the full matrix) and mid order (12 sites, 144 samples).

The pooled samples matrix contains only the 24 most dominant taxa used in the analyses of the 25 sites. The full samples matrix contains all the taxa identified for the 296 samples collected. The totals, means and ranges for each index are listed in Table 3.

Table 3: Diversity Measures

Totals, means (+ SEM) and ranges of diversity measures. # Individuals = absolute abundance, Intensity = # Individ / kg dry foliage, # Spp = species richness, H' = Shannon Diversity Index. Pooled Samples = 25 sites pooled across all dates for 24 dominant taxa, All Samples = 296 samples pooled across all dates for all 127 taxa identified. Measures reported for: a. All sites pooled, b. Sites pooled by vine maple, c. Sites pooled by red alder, d. Sites pooled by sitka alder, e. Sites pooled by low order habitat and f. Sites pooled by mid order habitat.

	Pooled Samples					All Samples				
	Total	Mean	SEM	Min	Max	Total	Mean	SEM	Min	Max
a. All Samples	(n = 25 sites)					(n = 296 samples)				
# Individuals	4,674	187.0	25.0	40	424	5,417	18.3	1.7	0	271
Intensity	492,042	19,682	2,898	2,423	59,702	566,364	1,913	219	0	38,277
# Spp	24	14.0	0.7	7	20	127	4.0	0.2	0	14
H'	3.01	2.38	0.05	1.71	2.76	2.71	0.90	0.04	0.00	2.50
b. Vine Maple	(n = 12 sites)					(n = 144 samples)				
# Individuals	2,335	194.6	32.7	40	424	2,673	18.6	2.87	0	271
Intensity	321,099	26,758	4,681	9,642	59,702	367,173	2,550	418	0	38,277
# Spp	24	11.8	0.78	7	16	81	3.0	0.0	0	12
H'	2.68	2.23	0.07	1.71	2.52	1.96	0.70	0.05	0.00	2.31
c. Red Alder	(n = 7 sites)					(n = 80 samples)				
# Individuals	1,016	145.1	38.8	62	362	1,227	15.3	2.4	0	157
Intensity	59,006	8,429	2,004	2,423	17,910	72,208	903	129	0	7,085
# Spp	24	16.9	1.0	13	20	91	5	0.4	0	13
H'	2.88	2.63	0.05	2.44	2.76	3.15	1.20	0.07	0.00	2.40
d. Sitka Alder	(n = 6 sites)					(n = 72 samples)				
# Individuals	1,323	220.5	53.1	71	343	1,517	21.1	3.1	0	125
Intensity	111,937	18,656	4,018	4,253	34,248	126,983	1,764	257	0	11,231
# Spp	24	15.3	1.4	9	19	81	5	0.5	0	14
H'	2.70	2.37	0.08	2.01	2.58	2.42	0.95	0.09	0.00	2.50
e. Low Order	(n = 13 sites)					(n = 152 samples)				
# Individuals	2,798	215.2	35.8	40	424	3227	21.2	2.8	0	271
Intensity	283,445	21,803	3,834	4,270	59,702	327,456	2,154	335	0	38,277
# Spp	24	13.5	1.1	7	19	105	4	0.3	0	14
H'	2.92	2.29	0.08	1.71	2.72	2.75	0.89	0.06	0.00	2.50
f. Mid Order	(n = 12 sites)					(n = 144 samples)				
# Individuals	1,876	156.3	25.8	62	331	2190	15.2	1.9	0	137
Intensity	208,597	17,383	4,459	2,423	54,198	238,908	1,659	278	0	18,150
# Spp	24	14.7	0.9	10	20	97	4	0.2	0	12
H'	2.96	2.47	0.06	0.21	2.76	2.35	0.92	0.06	0.00	2.40

3.3 Host and Habitat Affinities of Arthropods

Diversity indices and taxon intensities were calculated to determine if the arthropods collected showed significant affinities for either of the three tree species or for the two habitat types being investigated. Student's t-test for each pair of comparisons between site types revealed significant differences between sap-sucking and chewing herbivore intensities on the different host tree species. Comparisons also revealed significant differences in some predator and fungivore intensities for the different habitat types. Of the dominant taxa only Formicidae, Plecoptera, Ichneumonidae, Chironomidae, Collembola, Philodromidae, and Sciaridae showed no significant differences in mean intensity with respect to host tree species or habitat type.

Red alder consistently supported the greatest diversity of arthropods, followed by sitka alder, with vine maple supporting the least of the three (Figure 2). Samples were pooled across the sampling period for each tree species to compare H_e (minimum = 0 for 1 taxon, maximum = 3.18 for 24 equally abundant taxa) and species intensities for each host. Red alder supported a significantly greater diversity of arthropods ($H_e = 2.10$) than did sitka alder ($H_e = 1.65$) ($T = 2.6$, $df = 11$, $p = 0.024$). Vine maple supported significantly less diversity ($H_e = 1.22$) than either alder ($T = 2.4$, $df = 16$, $p = 0.024$, compared to sitka alder). Average species richness was greatest on red alder (17 species) and sitka alder (15 species) ($T = 0.9$, $df = 11$, $p = 0.384$) compared to vine maple (12 species) ($T = 2.4$, $df = 16$, $p = 0.026$). Average arthropod intensity, however, was significantly greater on vine maple (26,758 individuals / kg foliage) than on red alder (8,429 individuals / kg foliage) due to high aphid intensities. Average intensity on vine maple was also greater than on sitka alder (18,656 individuals / kg foliage), though not significantly so ($T = 1.2$, $df = 16$, $p = 0.260$).

Boernerina variabilis and *Periphyllus californiensis* showed significant host relationships with vine maple (Figure 3) compared to red alder ($T = 5.9$, $df = 17$, $p < 0.001$ and $T = 8.5$, $df = 17$, $p < 0.001$, respectively), while *Euceraphis gillettei* displayed an affinity for red alder, relative to sitka alder and vine maple ($T = 2.4$, $df = 16$, $p = 0.032$).

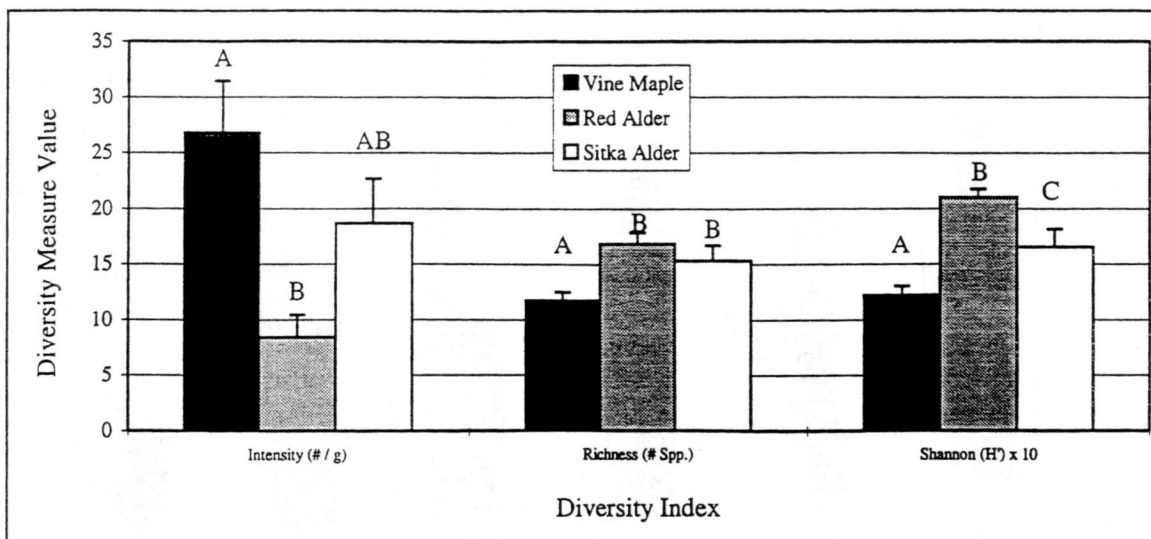


Figure 2: Diversity Measures of Arthropods for Host Plants

Intensity (# Indiv / g dry foliage), Richness (# species) and Shannon Diversity Index ($\times 10$) for Vine Maple, Red Alder and Sitka Alder. Note Intensity measured per gram (not kilogram). Data labels represent statistical significance within each diversity measure only.

Aphid mummy intensities were significantly greater on maple than the two alders ($T = 9.2$, $df = 17$, $p < 0.001$) and probably represent parasitized individuals of *B. variabilis* and *P. californiensis*. Cicadellid intensities were significantly greater on alder foliage than on vine maple ($T = 3.0$, $df = 17$, $p = 0.008$). Scale intensities were also greater on alder foliage than on vine maple ($T = 2.9$, $df = 17$, $p = 0.009$). Although the above Homoptera intensities on vine maple are in many cases greater than those on red alder, the number of taxa found on red alder results in greater taxonomic diversity.

Alder also played host to a greater intensity of lepidopteran, hymenopteran and coleopteran chewing herbivores (including Gracillariidae, Geometridae and Tenthredinidae, Curculionidae) than did maple (Figure 4). *Isochnus goniophallus* (Curculionidae) showed a strong affinity to sitka alder, reaching intensities of 110 individuals per one-half meter of branch (9167 individuals / kg), though some adults were collected from vine maple. Oviposition and larval survival were also noted on red alder foliage along with adult feeding.

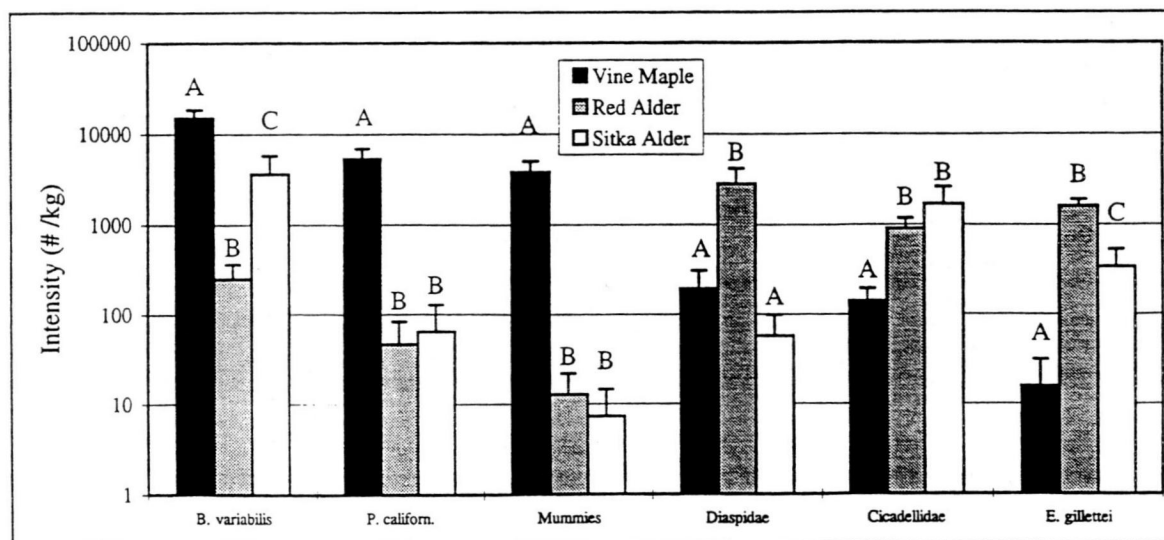


Figure 3: Sap-sucking Herbivore Intensity for Three Host Plants

Intensities for sap-sucking herbivore taxa pooled by host plant. Data labels represent statistical significance for within taxon comparisons only.

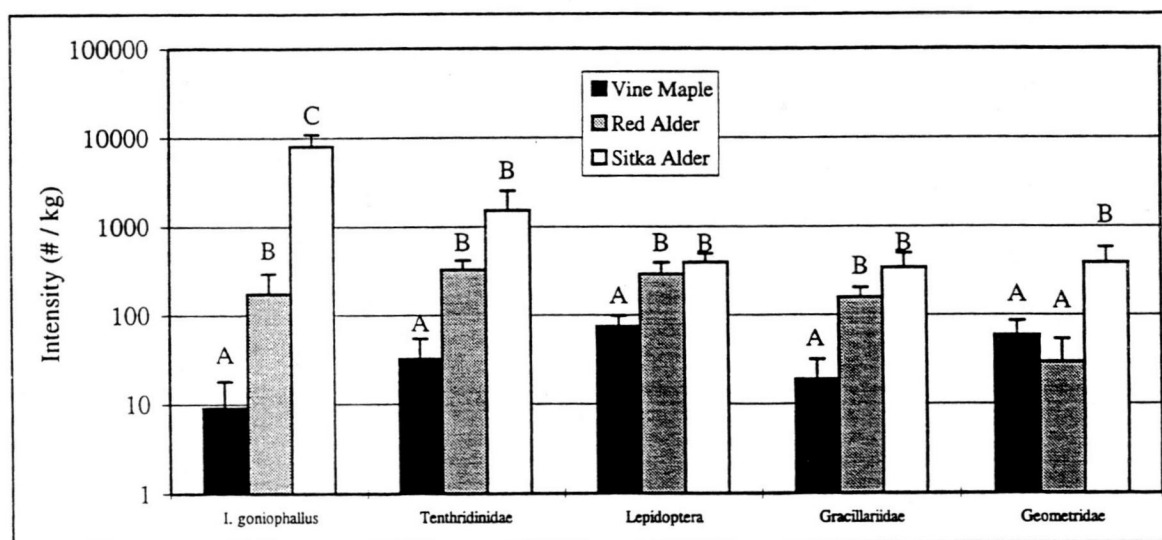


Figure 4: Chewing Herbivore Intensity for Three Host Plants

Intensities for chewing herbivore taxa pooled by host plant. Data labels represent statistical significance for within taxon comparisons only.

None of the predator guilds showed significant affinity to any of the three host tree species (Figure 5). All the hymenopterans collected (except Tenthredinidae: Symphyta and Formicidae) are parasitoids of homopterans, lepidopterans and dipterans. Although their hosts (homopterans and lepidopterans) showed greater abundance on alder the

ichneumonid parasitoids showed no significant differences in intensity between alder and maple. Ants (Formicidae) also foraged without preference for substrate or association with honeydew producing aphids. Of the remaining taxa, only the Cecidomyiidae showed a significant difference between host trees (Figure 6).

Segregation of taxa by habitat type (stream order) was less common, although several taxa showed a significant difference in intensity. None of the diversity measures analyzed (intensity, richness, Shannon diversity) showed significant differences between the two habitat types. (Figure 7). None of the herbivores showed a significant difference in intensity between low and mid order sites (Figures 8, 9), except for the weevil, *I. goniophallus* ($F = 5.9$, $df = 1,23$, $p = 0.023$; after accounting for host tree species).

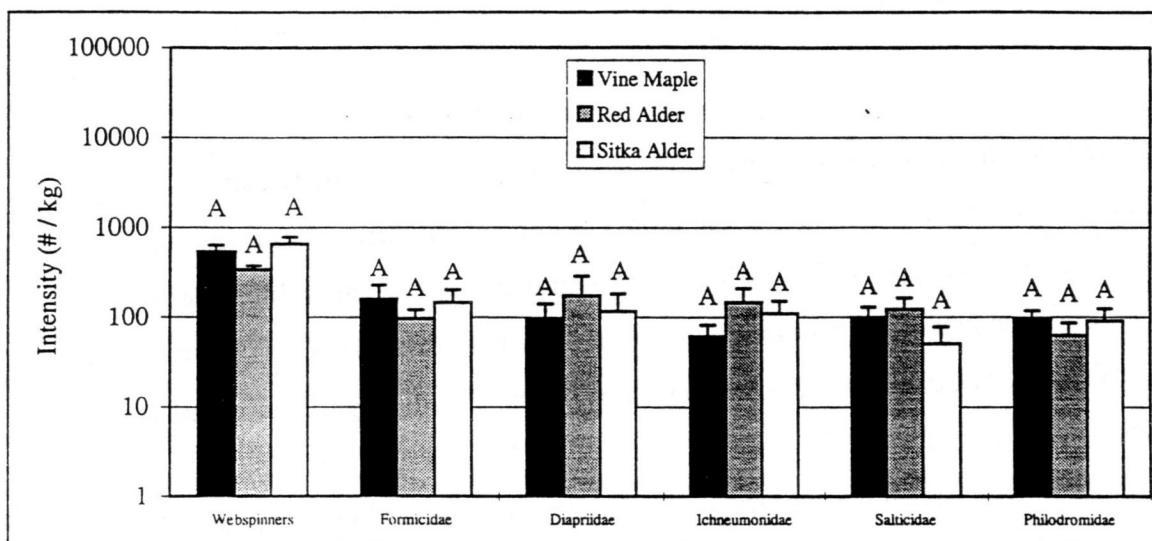


Figure 5: Predator Intensity for Three Host Plants

Intensities for predator taxa pooled by host plant. Data labels represent statistical significance for within taxon comparisons only.

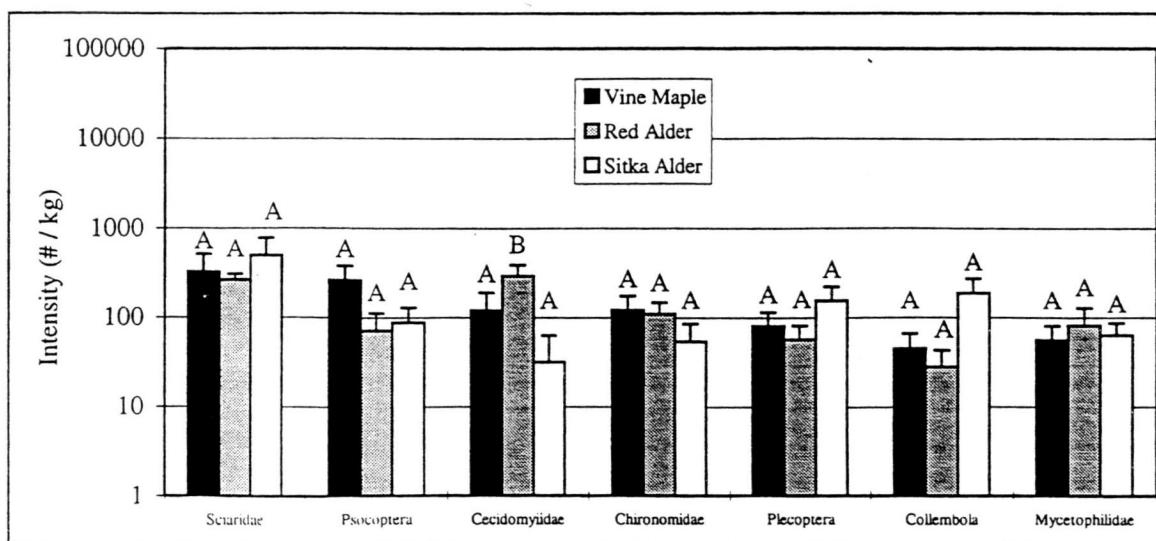


Figure 6: Intensity of Miscellaneous Taxa for Three Host Plants

Intensities for fungivore, scavenger and tourist taxa pooled by host plant. Data labels represent statistical significance for within taxon comparisons only.

There was a significant segregation of the dominant predators by stream order (Figure 10). Webspinning spiders were more common at low order sites than mid order sites ($T = 2.9$, $df = 23$, $p = 0.009$), while jumping spiders of the family Salticidae were much more abundant at the sunnier mid order sites than at low order sites ($T = 4.1$, $df = 23$, $p < 0.001$). The diapiiid parasitoids (Hymenoptera) showed significantly greater intensities at low order sites than mid ($T = 2.2$, $df = 23$, $p = 0.033$), reflecting a significantly greater abundance of their host (Mycetophilidae) at low order sites ($T = 3.1$, $df = 23$, $p = 0.004$).

Barklice (Psocoptera) and cecidomyiid fly larvae and adults, scavengers of a variety of food items, were more abundant at mid order sites than low order ($T = 2.4$, $df = 23$, $p = 0.027$ and $T = 2.2$, $df = 23$, $p = 0.035$, respectively) (Figure 11). No other taxa showed significant difference with respect to habitat type.

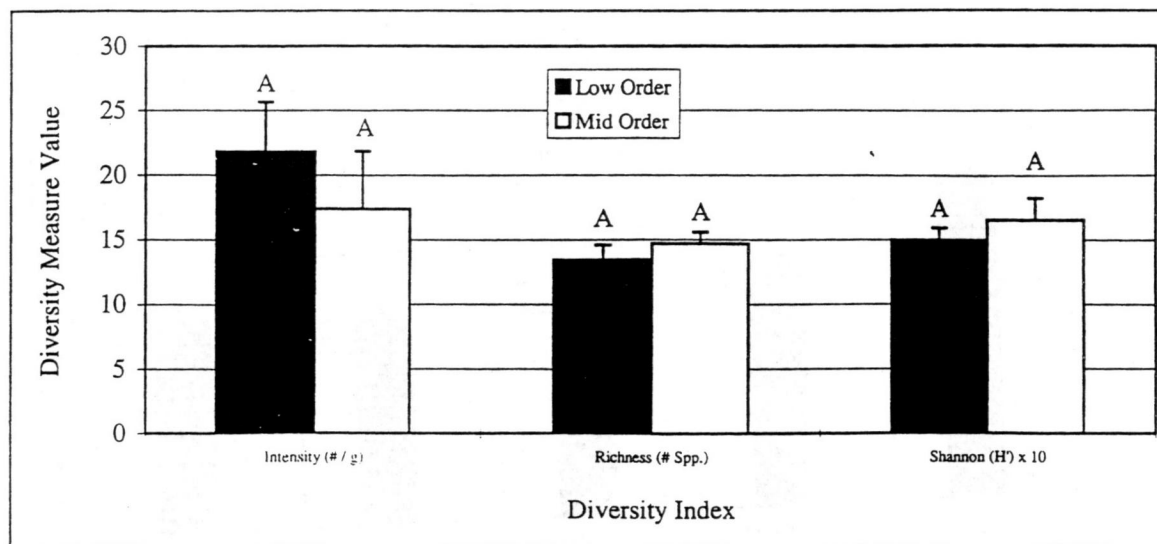


Figure 7: Diversity Measures of Arthropods for Habitat Types
Intensity (# Indiv / g dry foliage), Richness (# species) and Shannon Diversity Index (x10) for Low Order and Mid Order stream habitat types. Note intensity measured per gram (not kilogram). Data labels represent statistical significance within each diversity measure only.

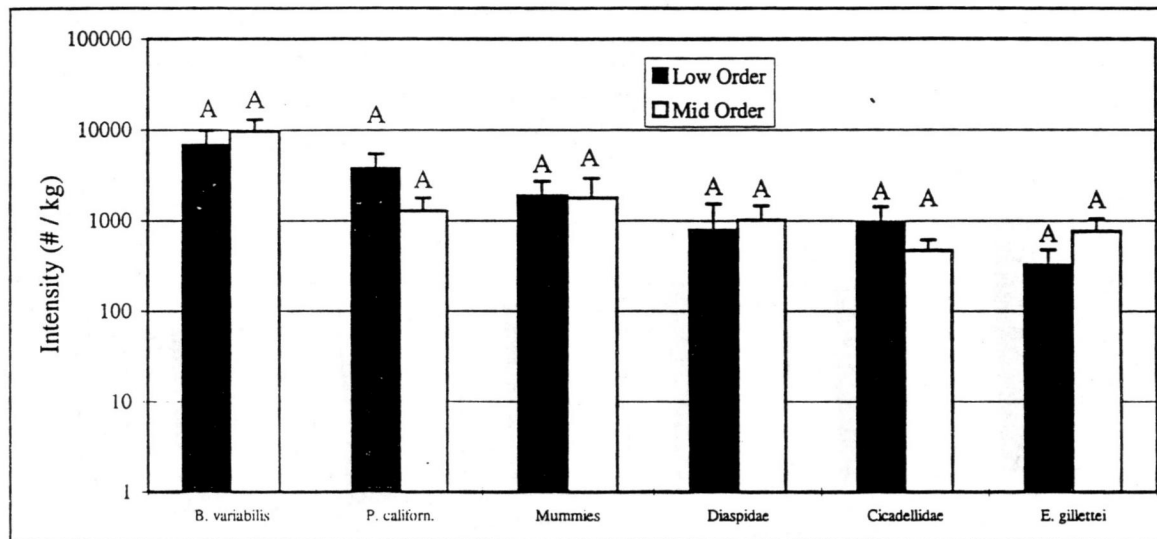


Figure 8: Sap-sucking Herbivore Intensity for Two Habitat Types
Intensities for sap-sucking herbivore taxa pooled by habitat type. Data labels represent statistical significance for within taxon comparisons only.

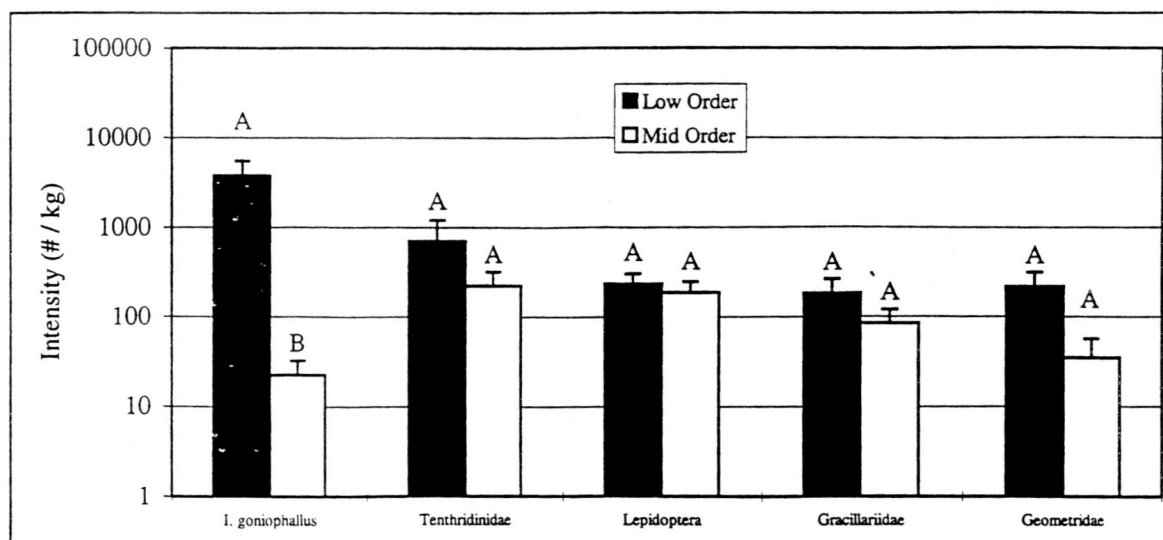


Figure 9: Chewing Herbivore Intensity for Two Habitat Types

Intensities for Chewing herbivore taxa pooled by habitat type. Data labels represent statistical significance for within taxon comparisons only.

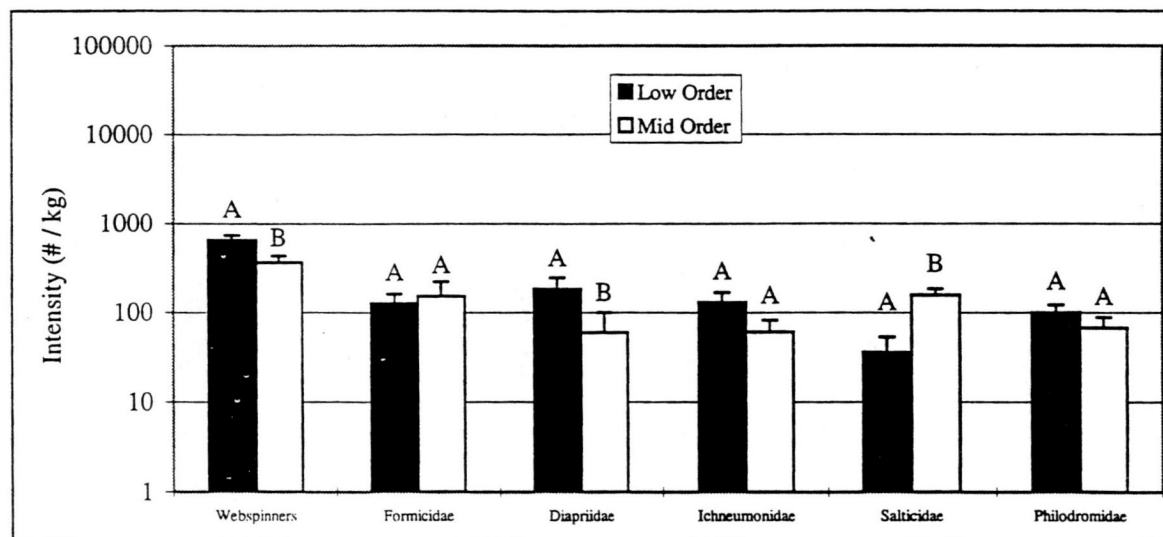


Figure 10: Predator Intensity for Two Habitat Types

Intensities for predator taxa pooled by habitat type. Data labels represent statistical significance for within taxon comparisons only.

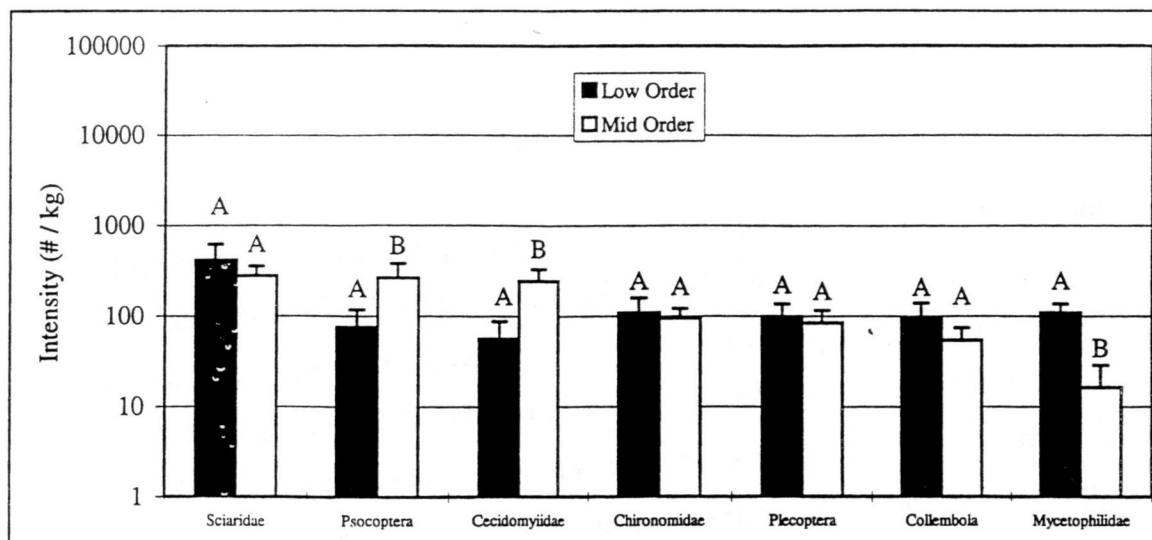


Figure 11: Intensity of Miscellaneous Taxa for Two Habitat Types

Intensities for fungivore, scavenger and tourist taxa pooled by habitat type. Data labels represent statistical significance for within taxon comparisons only.

3.4 MRPP

Multiple-response permutation procedure (MRPP) is a statistical test used to determine the significance of grouping samples by categories. The procedure returns a test statistic and probability value indicating if grouping samples by a given parameter (in this case host tree species or habitat type) is more significant than by a chance grouping. A low test statistic (T-statistic < 2.4) indicates that the categories by which the samples are being grouped are not statistically significant.

The MRPP result for the group variable **tree** (vine maple, red alder, sitka alder) indicates that the within group statistical distance between samples is significantly less than between group distances (T-statistic = 11.8, $p < 0.001$). Likewise, MRPP analysis of the group variable **order** (low and mid order) indicates that the within group statistical distance between samples is less than the between group distance (T-statistic = 2.6, $p < 0.025$). This test signifies that of all the possible ways that the sites could have been grouped, grouping by **tree** and **order** placed samples closer together than would have been expected by chance.

3.5 Cluster Analysis

Cluster analysis was used to determine which samples were most similar in terms of the taxon richness and abundance. Sites most similar are linked together at distances proportional to how similar the sites are. Analysis revealed clear patterns based on tree species. Cluster distances, using Ward's Method, ranged from 250 units to 45,000 units with three primary groups (vine maple, red alder and sitka alder) forming below 20,000 units (Figure 12). The primarily red alder cluster contained two sitka alder sites, one of which is the only mid order sitka site (Mack Creek). The other rogue sitka alder site (Earth-flow Creek) is geographically and topographically situated between the remaining sitka alder sites, leaving interpretation of this alignment unclear. The two closest subgroups within the red alder cluster are both of mid order sites (Blue River and lower LookOut) while the remaining subgroups do not reveal any clear patterns with respect to the variables being tested.

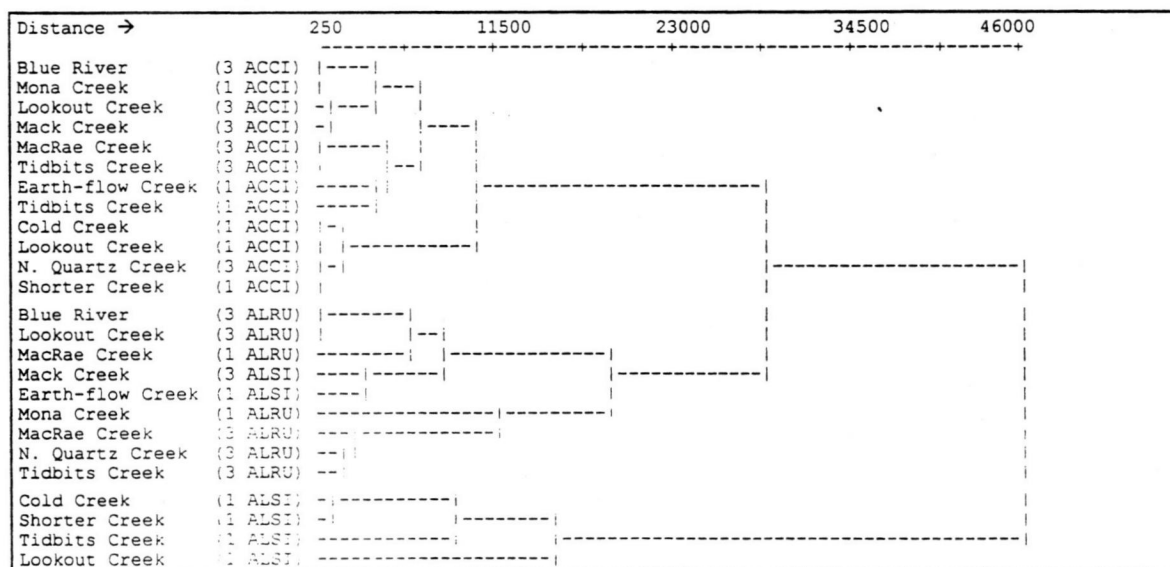


Figure 12: Cluster Analysis (Ward's Method) of 25 Sites

Cluster analysis of 25 sites using Ward's Method for sample distance (Euclidean). 1 = Low Order habitat types, 3 = Mid Order habitat types, ACCI = *Acer circinatum*, ALRU = *Alnus rubra*, ALSI = *Alnus sinuata*.

The four sites in the sitka alder cluster consist of three that are geographically close (within 5 km, along upper Lookout Creek) and one that is over 13 km from the rest (Tidbits Creek), all low order sites. The maple cluster contains three subgroups that do not reveal any obvious pattern relative to the variables being tested. Of the three major clusters, the red alder and vine maple groups cluster together first (at 28500 units), with the sitka alder group joining last at 45500 units. This analysis reveals that habitat type and local topography are less influential to the organization of macroarthropod communities than are the host tree species sampled. Other factors may correlate with the clustering of these sites but were not part of the design of this study.

3.6 Ordination

Nonmetric multi-dimensional scaling (NMS) ordination was used to determine if the factors being tested (host tree species and habitat type) correlate with the composition of the macroarthropod communities sampled. The abundance of each taxon represents one axis (or dimension) in species space. Since each site reported a different complement of the 24 dominant taxa, each site occupies a different point in species space. NMS attempts to regress the most significant line (new axis) through these points, which may then be correlated to other parameters (*i. e.* host tree species and habitat type).

NMS ordination showed strong correlation between the first three axes and **alder**, **sitka** and **order**, respectively. Axis **NMS 1** strongly correlated with **alder** ($r = 0.942$, $p < 0.001$), which separates sites with vine maple from those with either alder, while **NMS 2** separated sites with the two different alder species using the variable **sitka** ($r = 0.607$, $p = 0.001$) (Figure 13a). Axis **NMS 3** (Figure 13b) correlated most strongly with **order** ($r = 0.688$, $p < 0.001$), but did not significantly correlate with **NMS 2** even though most low order sites contained sitka alder and most mid order sites contained red alder.

A plot of species abundance vectors (direction of abundance increase) overlaid on ordinated samples reveals which species have the greatest influence on the ordination process. Figure 14a of **NMS 1** and **NMS 2** confirms that *Periphyllus californiensis*,

Boernerina variabilis and aphid mummies were the major taxa inhabiting samples from vine maple, while *I. goniophallus* and sawflies dominated samples from sitka alder. *Eucерaphis gillettei*, ichneumonids, and cecidomyiids dominated samples from red alder. Webspinning spiders, gracillariids, cicadellids and miscellaneous lepidopterans have abundance vectors that bisect the two alders in the ordination space. It is tempting to suggest that these combinations of taxa represent typical communities on the three tree species, but correlation analysis between each taxon on a site by site basis revealed that these taxa did not typically cooccur (nor indicate exclusion of one another by a negative correlation) (Pearson correlation, $p > 0.2$). However, interaction on a spatial or temporal scale not explored by this design may occur.

A similar overlay for NMS 1 and NMS 3 (Figure 14b) confirms that salticid abundance ordinated with mid order sites while webspinning spider abundance ordinated towards low order sites. *I. goniophallus* abundance also ordinated with low order sites, but may be confounded with its preference for sitka alder which is typically found at low order sites. Analysis of variance, however, revealed a significant interaction effect between **sitka** and **order** for intensities of *I. goniophallus* ($F = 5.6$, $p = 0.027$) indicating that both factors play a role in the weevil's distribution. The remaining taxa did not have vectors that extended significantly along any of the three axes.

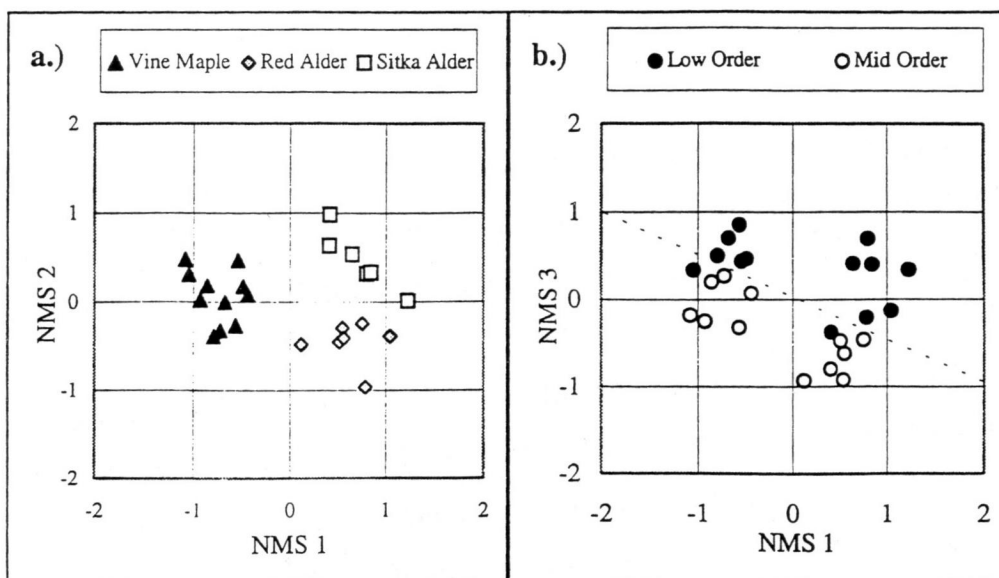


Figure 13: Sites Plotted in Ordination Space

Sample communities from: a.) three host plants and b.) two habitat types, plotted in ordination space. First three ordination axes used from Non-metric Multidimensional Scaling ordination method.

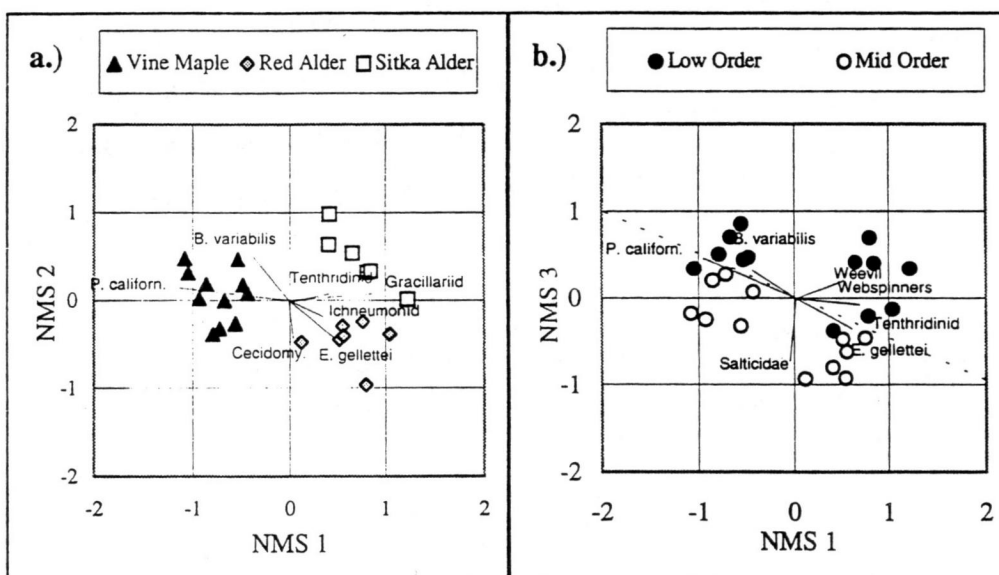


Figure 14: Species Abundance Vectors Overlaid on Ordination

Vectors represent the direction of increase in taxon intensity from the center of the ordination space. Only taxa showing the strongest gradient along the ordination axes are figured and labeled. Taxon vectors are overlaid for: a.) three host plants and b.) two habitat types, for the first three ordination axes NMS 1, 2 and 3.

3.7 Seasonal Trends

Diversity and average taxon intensities were calculated for each sample date to determine if particular taxa showed significant differences in intensity throughout the season. While most taxa fluctuated in intensity throughout the season, only a few showed significant changes for the different sample dates.

Red alder sites generally showed higher diversity (Simpson Index) than both sitka alder and vine maple sites throughout the season (Figure 15). Vine maple generally had the lowest mean values for intensity, number of species and diversity throughout the sample period, though statistical significance was not detected. None of the three hosts showed a significant change in arthropod diversity throughout the sampling period ($X^2 < 1$, $df = 1$, $\alpha = 0.05$).

Lower than average diversity values for each tree species occurred during mid summer (August 18, 1993 and September 13, 1993 collections). Weather conditions at the time of sampling during the mid summer sample dates included warm, dry air and 5% - 10% cloud cover. Both alder and maple leaves during this period were showing signs of senescence (browning, stiff surfaces), followed by dropping of many leaves at later sample dates.

Diversity for low and mid order sites fluctuated throughout the season. No statistical difference was detected for the different sample dates using chi-square analysis, though the two site types differed from each other for most of the season.

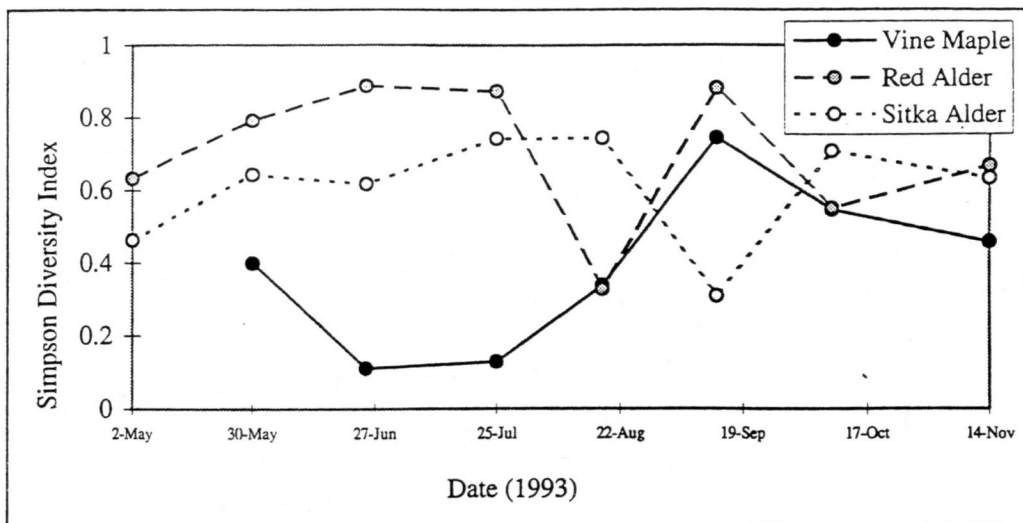


Figure 15: Seasonal Diversity Trends for Host Plants

The Simpson Index for arthropod diversity shows no significant differences throughout the 1993 sampling season for each host plant.

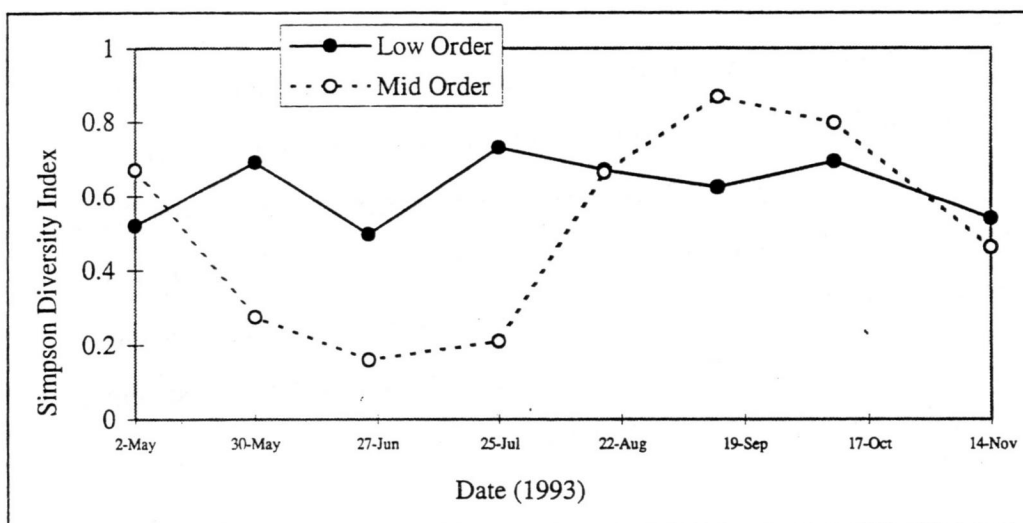


Figure 16: Seasonal Diversity Trends for Habitat Types

The Simpson Index for arthropod diversity shows no significant differences throughout the 1993 sampling season for each habitat type.

Aphid species showed two peaks during the sample period, one in early summer and one in late summer. *Euceraphis gillettei* (Figure 17) showed significantly greater abundance in late summer (October) than the rest of the season ($X^2 > 3.8$, $df = 1$, $\alpha = 0.05$) on red alder. *Periphyllus californiensis* (Figure 18) showed two periods of high abundance on vine maple in early and late summer ($X^2 > 4.2$, $df = 1$, $\alpha = 0.05$). *Boernerina variabilis* (Figure 19) had its greatest abundance on both vine maple ($X^2 > 4.5$, $df = 1$, $\alpha = 0.05$) and sitka alder in the early summer period (May, June, July), indicating that a seasonal host shift did not occur between the two tree species on which it was collected. Aphid mummies were significantly more abundant in October and November ($X^2 > 4.5$, $df = 1$, $\alpha = 0.05$) mostly on vine maple (Figure 18). Most of the mummies collected were already vacated by their parasitoids, which may have occurred between sample dates, leaving the parasitoids under-represented. At the family level aphids had their lowest abundance during the late summer (September) sample date.

Leafhoppers (Cicadellidae) had their greatest abundance on red and sitka alder during May ($X^2 > 3.3$, $df = 1$, $\alpha = 0.05$) and steadily declined the rest of the season (Figure 17) with no shift in host during the season. The parasitoid family, Diapriidae, was more abundant in September, October and November ($X^2 > 2.8$, $df = 1$, $\alpha = 0.05$), particularly on red alder (Figure 20). This coincides with fungivore populations in September and October ($X^2 > 2.7$, $df = 1$, $\alpha = 0.05$), particularly for the sciarid (Figure 20) and mycetophilid fungus flies on which diapriid parasitoids are known to prey.

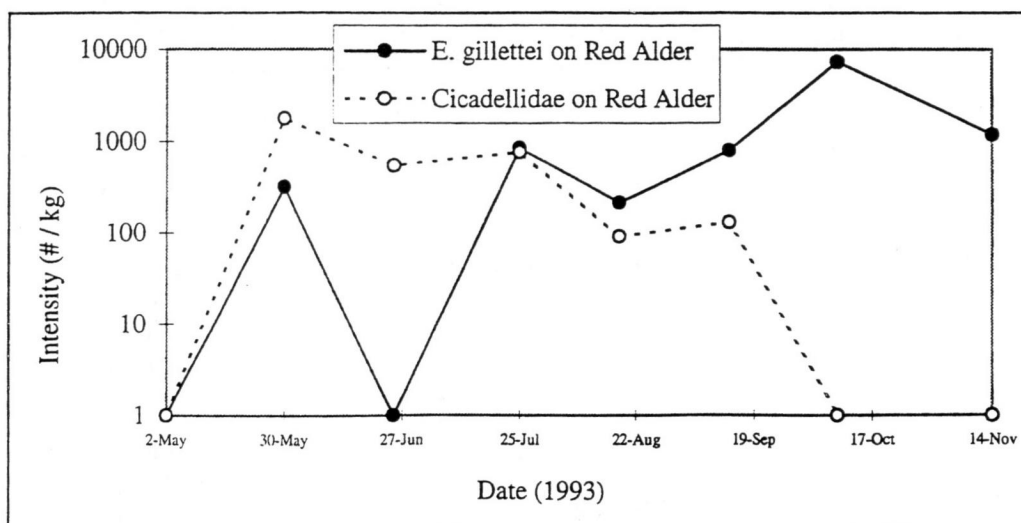


Figure 17: Seasonal Trends for *Eucерaphis gillettei* and Cicadellidae
 Intensities for the aphid, *Eucерaphis gillettei*, and leafhoppers (Cicadellidae) pooled from red alder for each sample date in 1993. Data labels represent statistic significance (X^2) for within taxon comparisons only.

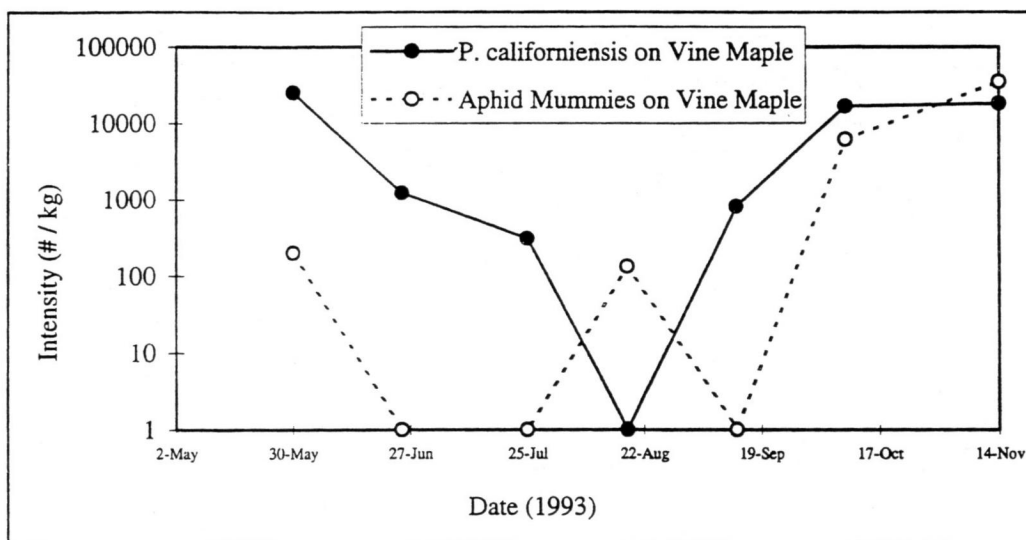


Figure 18: Seasonal Trends for *Periphyllus californiensis* and Aphid Mummies
 Intensities for the aphid, *Periphyllus californiensis*, and aphid mummies pooled from vine maple for each sample date in 1993. Data labels represent statistic significance (X^2) for within taxon comparisons only.

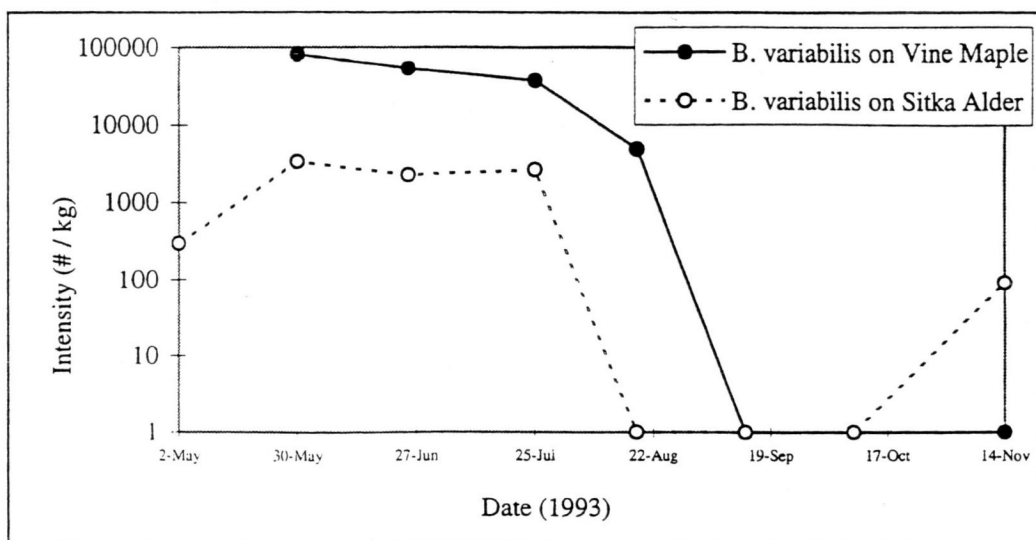


Figure 19: Seasonal Trends for *Boernerina variabilis*

Intensities for the aphid, *Boernerina variabilis*, pooled from vine maple and from sitka alder for each sample date in 1993. Data labels represent statistic significance (X^2) for within host plant comparisons only.

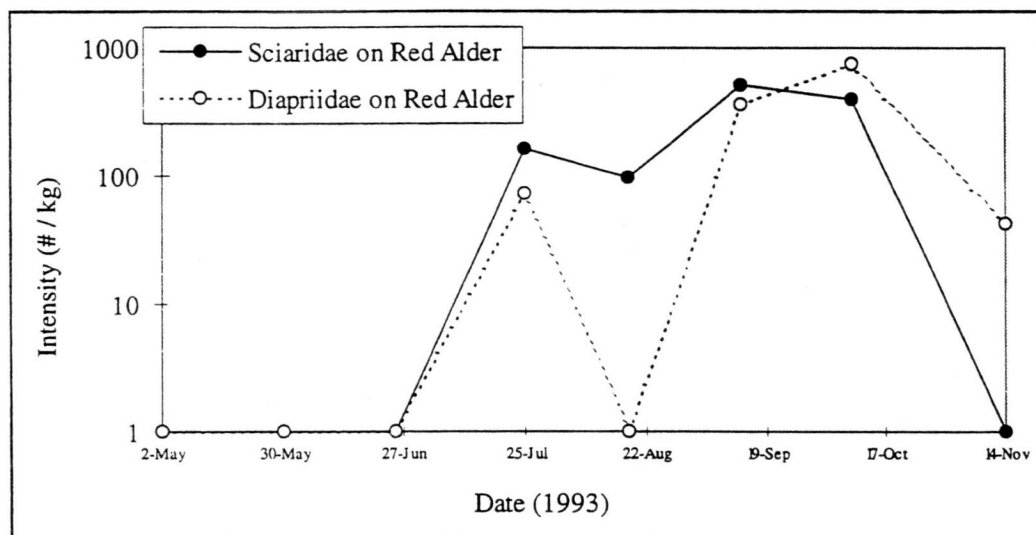


Figure 20: Seasonal Trends for Sciaridae and Diapriidae

Intensities for darkwing fungus flies (Sciaridae) and their parasitoids (Diapriidae) pooled from red alder for each sample date in 1993. Data labels represent statistic significance (X^2) for within taxon comparisons only.

3.8 Niche Breadth

Niche breadth measures were calculated to determine which species were the most ubiquitous and the most restricted in their distributions. The range of niche breadth values (nb) for each site, using the Shannon-Weiner Diversity Index, is 0 to 3.22 units. The actual range for the 24 dominant taxa was 1.92 to 3.11 units with a mean of 2.50 units (Table 2). The most ubiquitous taxon was the webspinning spiders (nb = 3.10), which were collected at all 25 sites. This group includes the families Araneidae, Linyphiidae and Tetragnathidae, each of which showed a similar breadth of sites collected from and evenness among those sites when the full (252 x 127) matrix was analyzed. *Boernerina variabilis* was the next most ubiquitous taxon (nb = 2.95), being collected at 23 of the 25 sites. All the rest of the taxa collected were at 20 or fewer sites ($\leq 80\%$ of the sites).

The taxon most restricted in its distribution was the weevil *Isochnus goniophallus* (nb = 1.92) which was found at only 11 of the 25 sites, all but one of which were alder sites and all of which were low order sites. The coccid family of scale insects was restricted to 11 sites (nb = 2.05), 8 of which were pairs of tree species found at a site (*i. e.* both maple and alder at four sites). Diapriid parasitoids were found at the least number of sites (10) of the 24 dominant taxa, but were more evenly distributed among those sites than the previous two taxa and so had a slightly higher niche breadth measure (nb = 2.17). Diapriids prey on mycetophilid fungus flies and were found to have a similar niche distribution as the genus *Mycetophila* (same 10 sites).

3.9 Guild Structure

Guild structure was determined to illustrate the relative abundances of functional groups for the different site types. Different proportions of feeding groups may suggest different selective pressures acting in the environments sampled.

Guild structure was calculated as the percent intensity that a functional feeding group represented in a given community throughout the sampling period. The six major groups considered were sap-sucking herbivores, chewing herbivores, fungivores, predators, scavengers and tourists, with predators being further subdivided into insect predators (flies and beetles), parasitoids, webspinning spiders, hunting spiders and ambush (crab) spiders. The scavenger group is a non-homogeneous group (Collembola, Psocoptera, Formicidae, *et al.*) representing a number of different feeding strategies and food sizes consumed. The tourist group consists of non-feeding adult insects that use the foliage as a resting site (Chironomidae, Plecoptera, Trichoptera, Ephemeroptera). See Appendix A for a summary of the taxa collected.

Differences in guild structure among the three host tree species were most obvious for the sap-sucking and chewing herbivores (Figure 21). Sucking herbivores represented 84% of the community on vine maple, 58% of that on red alder and 30% of that on sitka alder ($T > 3.0$, $df = 454$, $p < 0.005$ for each comparison). Conversely, chewing herbivores represented a significantly lower percentage of the the community on vine maple (0.8%) than on red alder (16%, $T=10.2$, $df=670$, $p=0.000$) and sitka alder (52%, $T=22.2$, $df = 646$, $p = 0.000$). Together sap-sucking and chewing herbivores represented $80\% \pm 7\%$ of the community on each of the three tree species.

The percentage of the community represented by fungivores and scavengers also differed for the three tree species. The percentage of the community represented by fungivores was significantly greater on red alder (6.9%) than on either vine maple (1.9%, $T=3.2$, $df = 670$, $p = 0.001$) or sitka alder (3.1%, $T = 3.1$, $df = 454$, $p = 0.002$), while no significant difference was detected between the vine maple and sitka alder ($T = 0.62$, $df = 646$, $p = 0.539$). Arthropod communities on vine maple had a significantly greater percentage of scavengers (1.9%) than did red alder (0.8%) and sitka alder (1.1%) ($T = 3.3$, $df = 670$, $p = 0.001$ and $T = 2.6$, $df = 646$, $p = 0.008$, respectively), while there was no significant difference between the two alders ($T = 0.5$, $df = 454$, $p = 0.635$).

The percentage of the community represented by predators also showed significant differences between host trees, especially for webspinning and hunting spiders. Vine maple supported a significantly lower percent of webspinning spiders (28% of predators)

than did red alder (38% of predators) and sitka alder (43% of predators) ($T = 2.0$, $df = 670$, $p = 0.049$ and $T = 2.6$, $df = 646$, $p = 0.008$, respectively). Hunting spiders showed a greater percentage on red alder (11% of predators) than on vine maple (4.3% of predators) and sitka alder (5.5%) ($T = 2.0$, $df = 670$, $p = 0.043$ and $T = 3.5$, $df = 454$, $p = 0.001$, respectively). The predator trophic level, however, was dominated by parasitoids (57%, 39% and 38%) and webspinning spiders (28%, 38% and 43%) (for vine maple, red alder and sitka alder, respectively) (Figure 22).

Guild structure relative to habitat type showed similar differences in percent composition (Figure 21). Sap-sucking herbivores represented 59% of the community at low order sites and 81% at mid order sites ($T = 4.5$, $df = 886$, $p = 0.000$), while chewing herbivores represented 22% of the community at low order sites and 3.8% of mid order sites ($T = 7.4$, $df = 886$, $p = 0.000$). Parasitoids made-up a greater percentage of the predator trophic level at low order sites (61%) than at mid order sites (25%) ($T = 5.2$, $df = 886$, $p = 0.000$), while hunting spiders were a greater percentage of the predator trophic level at mid order sites (13%) than at low order sites (2.4%) ($T = 7.3$, $df = 886$, $p = 0.000$) (Figure 22). And although webspinning spiders showed significantly greater intensity at low order sites than mid order sites (above), they represented 3% of the community at both low order sites (27% of predators) and mid order sites (48% of predators) when measured in terms of percent contribution to the community.

The average guild structure for all sites is given in figures 22 and 23 for comparison with the individual component communities (on vine maple, red alder, sitka alder and at low and mid order sites). The remaining taxa showed no significant differences in the percent of the community they represented for each site type.

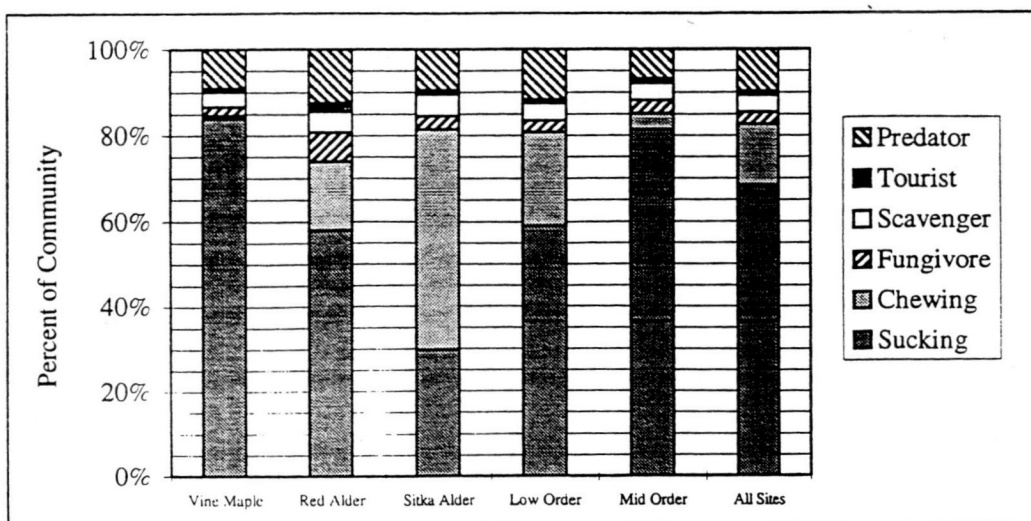


Figure 21: Arthropod Guild Structure

Percent of the total macroarthropod community found on vine maple, red alder and sitka alder and at low and mid order site types. Significant differences are explained in the text. Members of each guild may be found in Appendix A.

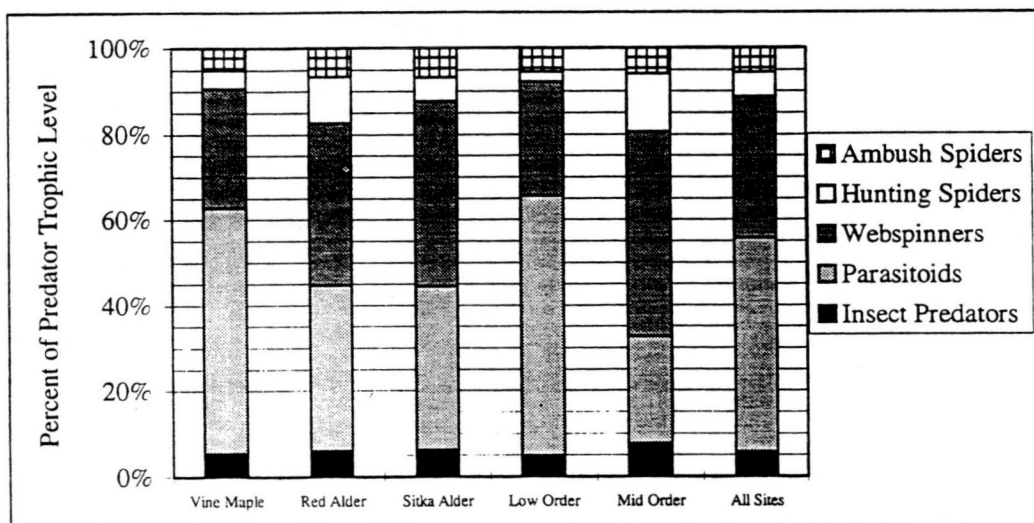


Figure 22: Predator Guild Structure

Percent of the predator trophic level for predator guilds on vine maple, red alder and sitka alder and at low and mid order site types.. Significant differences are explained in the text. Members of each guild may be found in Appendix A.

4. DISCUSSION

This study indicated that riparian arthropod communities segregate significantly by both host tree species and riparian habitat type. Communities collected from red alder represented the greatest diversity, a result of both high species richness and evenness. The greatest intensities of arthropods were collected from vine maple due to high herbivore loads. Low and mid order habitat communities showed no significant differences with respect to intensity, richness or Shannon diversity, but were composed of different assemblages of arthropods.

A clear delineation was observed between communities collected from the three different hosts. Host association of the dominant herbivores appears to have the strongest influence on the composition of the community. Homopteran species, particularly the aphids *Boernerina variabilis*, *Periphyllus californiensis* and mummies of parasitized aphids, dominated samples from vine maple. As a result, the guild structure of communities on vine maple were highly skewed towards sap-sucking (Homoptera) herbivores with relatively few chewing herbivores represented. The sap-sucking and chewing herbivores together represented 80% of the community.

Red alder arthropod communities were dominated by the aphid *Euceraphis gillettei*, several species of leafhoppers (Cicadellidae) and a soft scale (probably *Lecanium* sp.: Coccidae). Sap-sucking herbivores represented a greater proportion of the community than chewing herbivores, which together represented approximately 80% of the community. Predator populations were composed primarily of parasitoids and webspinning spider guilds. Though the intensities of fungivores were not significantly different among the tree species the percentage of the community composed of fungivores was greatest on red alder.

Sitka alder samples were dominated by a small leaf mining weevil, *Isochnus goniophallus* (Curculionidae), and to a lesser extent the aphid, *Boernerina variabilis*, and leafhoppers (Cicadellidae). The weevils were consistently present in high abundance throughout the sampling season. Both adults and leaf mining larvae were found actively

feeding on (in) sitka alder leaves throughout the season, resulting in decimated foliage. As a result, sitka alder communities were skewed towards chewing herbivores. Webspinning spiders represented nearly half of the predator populations on sitka alder, although total predators were comparable to red alder. Larvae of Tenthredinidae and Lepidoptera were found in greater abundance on the two alder species than on vine maple, but at lower intensities than the homopteran insects.

Segregation by riparian habitat (low order *versus* mid order streams) was observed in several predator and fungivore-scavenger taxa. Spiders (Aranea) were the most abundant predators for all sites, but showed segregation of functional feeding groups by riparian habitat type. Jumping spiders (Salticidae) are visual hunters and were significantly more abundant at the more open and sunny mid order sites. Webspinning spiders (mostly Linyphiidae and Araneidae) were the most abundant predators at all sites, but showed a significantly greater abundance in the closed canopy low order sites.

Parasitoids in the family Diapriidae (Hymenoptera) showed greater intensities at low order sites. Sites with high abundances of parasitoids coincided with high abundances of fungus gnats (Mycetophilidae), on which diapriids are known to prey. The seasonal distribution of both the parasitoids and the gnats also follow similar dynamics of abundance. Though correlation analysis revealed that these taxa did not typically co-occur in the same samples at the same time, it is likely that the parasitoid populations are tightly coupled with the fungus gnat populations on a broader temporal-spatial scale.

Other taxa also showed segregation by habitat type. The weevil, *I. goniophallus*, showed greater abundance at low order sites (after accounting for host tree species). Psocoptera and cecidomyiid flies (both larvae and adults) were found in greater abundance at mid order sites. Although both groups at the family level feed on a variety of food items, each was found free living and probably scavenging for fungi, detritus, and small prey items that use the sunny, mid order riparian vegetation as a resting site.

The factors by which populations and communities are organized have been suggested by models of competition (Wiens 1977), predation (Bodini 1991, Hairston et al. 1960), keystone species (Paine 1969) and trophic cascades (Polis 1994). Strong *et al.* (1984) proposed that the majority of insect populations are regulated by density-

dependent processes while being perturbed by density-independent factors. Price (1983) recognized that the evolution of adaptations by both herbivores and their host plants, including secondary plant compounds (Berenbaum 1981), results in increased specialization and a finer separation of niches. Plants that provide diverse microenvironments (Strong *et al.* 1984, Williams 1964) and resource packages (Karr 1975) also may support a greater diversity of inhabitants.

This study suggests that host plant association plays a primary role in the organization of the riparian arthropod communities collected in the central western Cascades. The low arthropod diversity collected from vine maple may reflect the astringent nature of maple leaves (Del Moral & Cates 1971), while the higher diversity collected from red alder may be a result of its capacity to provide nitrogen, through fixation, in resource-poor habitats (Hibbs *et al.* 1994). Red alder foliage is also known to support many species of endophytic fungi (Sieber *et al.* 1991), which may account for the higher proportion of fungivores found in red alder communities.

The change in riparian character as one progresses from headwaters to mouth of montane streams, particularly in the Pacific Northwest, has been well documented (Vannote *et al.* 1980, Campbell & Franklin 1979). Most studies, however, have focused on stream habitat and nutrient and material flow between the stream channel and the terrestrial environment (Edmonds 1982, Cummins 1980). Though the riparian zone has been suggested as a corridor of movement for several classes of animals (Thomas *et al.* 1979), little work has been done to assess how the resident fauna utilize these regions (except see Doyle 1990, Rice *et al.* 1983). The present study reveals that changes in arthropod communities can occur as one progresses from low order to mid order stream riparian habitats.

The different habitat types along a riparian zone and the different host tree species available for colonization represent different component communities in the compound community of a riparian zone. Each component community presents different biotic and abiotic hurdles for the occupying fauna to overcome and resources to exploit. As a result, the distribution of macroarthropods within the riparian zone is dependent on the distribution of the resources to which they are tied. This study indicates that a diversity

of component communities is an important feature of the maintenance of arthropod diversity within the riparian zone.

Further investigation is required to determine to what extent the riparian zone supports a unique complement of species relative to the adjacent upslope environment and the level of biotic exchange between riparian zones and their neighboring communities.

5. CONCLUSIONS

Arthropod communities collected from three tree species in riparian areas of the Blue River District of the central Western Cascade Range of Oregon showed significant segregation by host plant and habitat type. Communities on vine maple and red alder were dominated by aphids, while sitka alder communities were dominated by a leaf mining weevil. Spiders represented the greatest predator abundances, while spider guilds showed habitat preferences by functional feeding groups. Several herbivore taxa showed significant host affinities, while several fungivore-scavengers showed significant habitat affinities. Although arthropod species did not typically cooccur at the collection sites, many taxa were typical to particular hosts and habitats forming loose, resource-based communities.

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APPENDIX A - Annotated List of Taxa

Aphid mummies (Aphididae: Homoptera): Sap-sucker (parasitized). Collected primarily off of vine maple leaves and twigs in early autumn (October and November). Probably parasitized individuals of *Boernerina variabilis* and *Periphyllus californiensis*. Maximum abundance was 68 individuals per one-half meter branch of vine maple in November 1993.

Boernerina variabilis (Aphididae: Homoptera): Sap-sucker. Collected from leaves and twigs of sitka alder and vine maple. Present in greatest abundance from May to August. Maximum abundance was 157 individuals per one-half meter branch of vine maple in May 1993.

Cecidomyiidae (Diptera): Fungivore and other trophic levels. Individuals collected were primarily adults of fungivorous species resting on vegetation. Collected at moderate abundance throughout the sample season with a maximum of 5 individuals per one-half meter branch of vine maple in May 1993.

Chironomidae (Diptera): Tourist. All appeared to be of the subfamily Orthocladiinae. Collected as adults resting on vegetation. Collected from May to July and October through November with a maximum of 3 individuals per one-half meter branch of vine maple in May 1992.

Cicadellidae (Homoptera): Sap-sucker. Most individuals were immature and appeared to represent 2 or 3 species. Primarily collected from twigs of alder. Abundance was greatest in May and declined slowly throughout the sample season. Maximum abundance was 32 individuals per one-half meter branch of sitka alder in May 1993.

Collembola: Scavenger. Several species, mostly of the family Entomobryidae. Present mostly from May to July and October through November, with a maximum abundance of 2 individuals per one-half meter branch of sitka alder in July 1992.

Diapriidae (Hymenoptera): Parasitoid. Known as parasitoids of Diptera (primarily Mycetophilidae, Sciaridae and Syrphidae). No species documented for the Pacific Northwest. All collected as adults resting on vegetation. Greatest abundance achieved

in October and November with a maximum of 10 individuals per one-half meter branch of red alder in October 1993.

Diaspididae (Homoptera): Sap-sucker. Probably species of *Lecanium*. Collected mostly as first and second instars on leaves and few as adults on twigs. Present throughout the sample season with a maximum abundance of 146 individuals per one-half meter of red alder branch in August 1993.

Eucерaphis gелlettei (Aphididae: Homoptera): Sap-sucker. Collected on leaves and stems, mostly of alder. Populations increased later in the season (October - November) with a maximum abundance of 37 individuals per one-half meter branch of red alder in October 1993.

Formicidae (Hymenoptera): Omnivore (Scavenger). Mostly of the genus *Formica*, but a few of the genus *Camponotus*. Collected from stems, but not in association with aphids or other Homoptera. Highest populations were from May through July with a maximum of 7 individuals per one-half meter branch of vine maple in July 1992.

Geometridae (Lepidoptera): Chewing herbivore. *Rheumaptera subhastata* was the most prevalent species on alder, but several other species were collected (unsuccessfully reared). Abundance was greatest in May and June with a maximum of 8 individuals per one-half meter branch of sitka alder in June 1992.

Gracillariidae (Lepidoptera): Chewing herbivore. Predominantly *Caloptilia* species on alder. All specimens collected were larvae mining leaves and were present from after leaf flush until leaf senescence. Maximum abundance was 5 individuals per one-half meter branch of sitka alder in June 1992.

Ichneumonidae (Hymenoptera): Parasitoid. Several species were collected throughout the sample season, with a maximum abundance of 5 individuals per one-half meter branch of red alder in September 1993.

Isochnus goniophallus (Curculionidae: Coleoptera): Chewing herbivore. Holotype described from the H.J. Andrews Experimental Forest. Larvae mine the leaves of alder and pupate within the mines. Adults feed on alder leaves by chewing pin-holes through the leaf resulting in leaves nearly covered with holes and mines. Mating occurs on the leaf surface. Overwintering sites have not been discovered, but are probably in soil or

crevices of tree bark. Abundance was high throughout the sampling season, with larvae primarily present from early June through August. Maximum abundance was 110 individuals per one-half meter branch of sitka alder in September 1993.

Miscellaneous Lepidoptera: Chewing herbivore. Includes the family Noctuidae and microlepidoptera that were not identified and not successful reared, and excludes Geometridae and Gracillariidae (which were found in far greater abundance). Because this group represents many different species there was no strong seasonal or host trend. Maximum abundance was 7 individuals per one-half meter branch of sitka alder in June 1992.

Mycetophilidae (Diptera): Fungivore. Several genera collected as adults. Present throughout the sampling season with a maximum of 3 individuals per one-half meter branch of red alder in September 1993.

Periphyllus californiensis (Aphididae: Homoptera): Sap-sucker. Virtually all specimens collected from leaves and twigs of vine maple. Abundance was greatest in spring and late fall with a maximum of 108 individuals per one-half meter branch of vine maple in May 1993.

Philodromidae (Aranea): Ambush predator. Principally *Philodromus* along with *Misumena* (Thomisidae), representing crab spiders which prey on insects by ambushing from twigs and undersides of leaves. Most abundant in early to mid summer with a maximum of 2 per one-half meter branch of red alder in July 1992.

Plecoptera: Tourists. Several families represented, but primarily Chloropidae. Adults which emerged from the neighboring stream channel were apparently using vegetation as a resting site and not for feeding purposes. Abundance was low, but consistent, throughout the sample season with a maximum of 3 individuals per one-half meter branch of sitka alder in July 1993.

Psocoptera: Scavenger. Several families represented which consume a wide variety of food items. Most were immature forms. Presence was patchy throughout the sample season with a maximum of 12 individuals per one-half meter branch of vine maple in June 1992.

Salticidae (Aranea): Hunting predator. The genera *Eris* and *Metaphidippus* of the jumping spider family. Visually oriented predators that stalk and pounce on prey on foliage surfaces. Present throughout the sampling season, but tended more towards the open sunnier sites of mid order streams, with a maximum of 2 individuals per one-half meter branch of red alder in July 1992.

Sciaridae (Diptera): Fungivore. Virtually all specimens were of the genus *Bradysia*. Mostly collected as adults resting on the leaf surface, though two larvae were reared from senescing vine maple leaves that had been picked from a live tree. Greatest abundance was in September and October with a maximum of 14 individuals per one-half meter branch of vine maple in September 1993.

Tenthridinidae (Hymenoptera): Chewing herbivore. Primarily *Nematus oligospilus* collected from alder. Apparently with several generations per year and present throughout the sampling season. Maximum abundance was 25 individuals per one-half meter branch of sitka alder in July 1993.

Webspinning Spiders (Aranea): Webspinning predators. Primarily the spider families Araneidae, Tetragnathidae and Linyphiidae. Present at high abundance throughout the sampling season with abundance slightly greater at low order sites. Webs were extended between branches, which may have led to under-representation, since the sample unit was one branch. Maximum abundance was 3 individuals per one-half meter branch of vine maple in October 1993.