AN ABSTRACT OF THE THESIS OF

Juraj Halaj for the degree of Doctor of Philosophy in Entomology presented on May 6, 1996. Title: Abundance and Community Composition of Arboreal Spiders: The Relative Importance of Habitat Structure, Prey Availability and Competition.

This work examined the importance of structural complexity of habitat, availability of prey, and competition with ants as factors influencing the abundance and community composition of arboreal spiders in western Oregon.

In 1993, I compared the spider communities of several host-tree species which have different branch structure. I also assessed the importance of several habitat variables as predictors of spider abundance and diversity on and among individual tree species. The greatest abundance and species richness of spiders per 1-m-long branch tips were found on structurally more complex tree species, including Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco and noble fir, Abies procera Rehder. Spider densities, species richness and diversity positively correlated with the amount of foliage, branch twigs and prev densities on individual tree species. The amount of branch twigs alone explained almost 70% of the variation in the total spider abundance across five tree species.

In 1994, I experimentally tested the importance of needle density and branching complexity of Douglas-fir branches on the abundance and community structure of spiders and their potential prey organisms. This was accomplished by either removing needles, by thinning branches or by tying branches. Tying branches resulted in a significant increase in the abundance of spiders and their prey. Densities of spiders and their prey were reduced by removal of needles and thinning. The spider community of needle-sparse branches was dominated by orb weavers (Araneidae), whereas tied branches were preferably colonized by sheet-web weavers (Linyphiidae and Micryphantidae), and nocturnal hunting spiders

(Anyphaeñidae and Clubionidae). Spider species richness and diversity increased in structurally more complex habitats.

In 1994 and 1995, I excluded foraging *Camponotus* spp. ants from canopies of sapling Douglas-fir. Biomass of potential prey organisms, dominated by Psocoptera, increased significantly by 1.9 to 2.4-fold on the foliage following ant exclusion. Hunting spiders, dominated by the Salticidae, increased significantly by 1.5 to 1.8-fold in trees without ants in the late summer. The exclusion of ants did not affect the abundance of web-building spiders. Documented aggressive behavior of aphid-tending ants suggests interference competition between hunting spiders and ants.

Abundance and Community Composition of Arboreal Spiders: The Relative Importance of Habitat Structure, Prey Availability and Competition.

by

Juraj Halaj

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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CONTRIBUTION OF AUTHORS

Drs. Darrell W. Ross and Andrew R. Moldenke were involved in selecting the research topic, designing the experiments, and writing the manuscripts. Dr. Andrew R. Moldenke also assisted in identifications of selected arthropod groups collected throughout this study.

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DEDICATION

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I dedicate this work to my parents, Milan and Anna.

ABUNDANCE AND COMMUNITY COMPOSITION OF ARBOREAL SPIDERS: THE RELATIVE IMPORTANCE OF HABITAT STRUCTURE, PREY AVAILABILITY AND COMPETITION

1. INTRODUCTION

Spiders are among the most abundant and diverse terrestrial predators on earth (Coddington and Levi 1991). They rank seventh in global animal diversity after Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera and Acari (Parker 1982). There have been approximately 34,000 spider species described world-wide (Platnick 1989), with over 3,000 species in North America (Young and Edwards 1990). Despite this notability, only a limited amount of work has been done on the biology of these animals, and only recently, a popular trend to study spider ecology and behavior has emerged (e.g. see reviews in Turnbull 1973, Foelix 1982, Riechert and Lockley 1984, Nentwig 1987, Wise 1993). However, the biology of these animals and their role in natural communities remain largely unknown.

The physical structure of environments influences the habitat selection of spiders and ultimately the composition of spider communities (Uetz 1991, Wise 1993). The dependence of spiders on the physical structure of their habitat make them excellent model organisms; web-building spiders use different features of their habitat to anchor their webs, and all spiders use the habitat structure to perceive vibrations produced by their prey, mates, competitors or enemies (Uetz 1991). Not surprisingly then, the interplay between spiders and the structure of their habitat has been widely studied in various natural communities (Chew 1961, Duffey 1962, Riechert 1976, Riechert and Tracy 1975, Uetz 1976, Hatley and MacMahon 1980, Robinson 1981, Schoener and Toft 1983b, Greenstone 1984, Rypstra 1986).

Further, predation and competition are among the paramount forces regulating the distribution, affecting the behavior and shaping the community structure of animals in many terrestrial communities (e.g. reviews in Sih et al. 1985, Polis et al. 1989). Spiders, as generalist predators, share the same trophic level with other predators, providing

possibilities for competition, consumption of, or consumption by other generalist predators and competitors (Polis et al. 1989). For example, predation by scorpions reduces populations of spiders in a California desert (Polis and McCormick 1986), and spiders compete for food with and are consumed by *Anolis* lizards in the Caribbean (Pacala and Roughgarden 1984, Spiller and Schoener 1988, 1990).

Spiders are an important component of arboreal arthropod communities in temperate (Dahlsten et al. 1977, Moldenke et al. 1987, Schowalter 1989, 1995a, Halaj et al. 1996) and tropical forests (Stork 1991, Schowalter 1994, Russell-Smith and Stork 1995, Schowalter 1995b). For example, the abundance of spiders in young Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) plantations in western Oregon can reach 16.7 individuals per m² of branch area (Halaj et al. 1996). Jennings and Dimond (1988) estimate absolute populations of spiders in the forests of the northeastern United States to range from 35,000 to as many as 323,000 individuals per hectare. Spiders feed on a great variety of arthropods in arboreal communities (Turnbull 1956, Loughton et al. 1963, Eikenbary and Fox 1968, Dahlsten et al. 1977, Jennings and Houseweart 1978, Fichter 1984, Jennings and Houseweart 1989) and have the potential to limit populations of forest insect pests.

Despite the apparent importance of spiders in forest canopies, relatively few studies have investigated spider-habitat interactions in these systems. Stratton et al. (1979) and Jennings and Collins (1987) studied the spider fauna and habitat structure in several North American coniferous tree species. Eubanks and Miller (1992) investigated the habitat preference of a facultatively arboreal wolf spider in Mississippi. However, studies in which the spider habitat was experimentally altered to determine causal relationships are limited to those by Gunnarsson (1990, 1992) and Sundberg and Gunnarsson (1994). The authors studied populations of spruce-inhabiting spiders in southern Sweden and suggest that needle density is one of the factors limiting the abundance of spiders in this system.

Similarly, studies on the significance of predation or competition in limiting populations of arboreal spiders are essentially limited to those documenting negative

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effects of predation by passerine birds on spruce-inhabiting spiders in Sweden (Askenmo et al. 1977, Gunnarsson 1983).

Carpenter ants, *Camponotus* spp., are abundant foragers in Douglas-fir canopies in the northwestern United States (Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984). They share the arboreal habitat with spiders creating the possibility of negative interactions. However, the impact of ant foraging on arboreal spider communities has not been studied.

This work has been conducted at the H. J. Andrews Experimental Forest, a Long-Term Ecological Research Site (LTER), in the western Cascade Mountains of Oregon. This UNESCO Man and the Biosphere Program Reserve (MAB) has been the focus of intensive research on arthropod ecology for more than 40 years (Van Cleve and Martin 1991). As a result of this research, an extensive amount of information has been accumulated on the abundance and diversity of canopy-inhabiting arthropods in this system (Moldenke et al. 1987, Parsons et al. 1991, Lattin 1993, Schowalter 1989, 1995a). Spiders represent about 7.5% of the almost 300 arthropod species described from the H. J. Andrews Experimental Forest, ranking fifth in total arthropod diversity in this system (Parsons et al. 1991). The first data on the biology of spiders in this system were collected by Moldenke et al. (1987). Additional information has been provided by Parsons et al. (1991), Halaj et al. (1996), and other sources (Moldenke and Fichter, unpublished data).

The aim of this project was to further knowledge of the ecology and behavior of the arboreal spider community in this system. The overall objective of my research was to evaluate the relative importance of habitat structure, prey availability and natural enemies in determining the abundance and community composition of these predators. Three studies were designed to achieve the overall goal of this research. The objective of the first study was to identify habitat variables to predict the abundance and diversity of arboreal spiders (Chapter 2). In the summer of 1993, I collected spiders inhabiting several tree species, and measured selected characteristics of their habitat. In 1994, I experimentally tested the importance of several habitat variables that were identified as significant predictors of spider abundance and community structure in Douglas-fir (Chapter 3). Finally, in 1994 and 1995, I tested the importance of ant foraging on the spider abundance and community composition (Chapter 4). I experimentally excluded ants from Douglas-fir canopies to investigate the significance of ant foraging on local spider assemblages. I also recorded observations of the interactions between these two groups of predators.

2. Structural Complexity of Habitat and Prey Availability as Predictors of the Abundance and Diversity of Arboreal Spiders

Juraj Halaj, Darrell W. Ross and Andrew R. Moldenke

To be submitted to Environmental Entomology

2. STRUCTURAL COMPLEXITY OF HABITAT AND PREY AVAILABILITY AS PREDICTORS OF THE ABUNDANCE AND DIVERSITY OF ARBOREAL SPIDERS

Abstract

An observational study was conducted to investigate the importance of habitat structure and prey availability in determining the abundance and diversity of arboreal spiders in six forest stands. Assemblages of arthropods were collected by harvesting and bagging 1-m-long tips of lower crown branches of red alder, Almus rubra Bongard, western redcedar, Thuja plicata Donn ex D. Don, western hemlock, Tsuga heterophylla (Rafinesque) Sargent, noble fir, Abies procera Rehder, and Douglas-fir, Pseudotsuga menziesii (Mirbel) Franco. Several structural characteristics of arthropod habitats were measured. These included: tree diameter at breast height (d.b.h.), maximum horizontal and vertical spread of the branch, number of branching angles, total biomass of stems (branch twigs) and foliage. The abundance and diversity of spiders was significantly correlated with the selected habitat variables. The significance of individual habitat characteristics varied with individual spider functional groups, which may reflect specific habitat or prey requirements among these groups. The biomass of foliage and the availability of prey were the most common variables selected by stepwise procedures to predict spider abundance on individual host-tree species. Almost 70% of variation in spider densities among individual tree species can be explained by stem biomass of sample branches. The highest numbers of spiders per 1-m-long branch tip were collected from structurally more complex host-tree species including Douglas-fir (4.95 to 9.92 individuals) and noble-fir (7.33 to 9.65 individuals). These host-tree species also supported the greatest spider species richness (2.6 to 3.57 and 2.83 to 3.40 species. respectively). Spider community structure and species composition varied significantly among the tree species, which may reflect the quality of the habitat and specific requirements of individual spider groups. The greatest similarity in spider community structure was found among tree species with shared branch characteristics such as needles. The results of the study suggest that arboreal spider densities are under significant influence of the physical structure of their habitat, as has been suggested for other natural communities.

Introduction

The physical structure of the habitat is an important factor influencing the distribution and diversity of spiders. Many spider species construct webs to capture their prey, so the availability and quality of specific web-attachment sites is essential to their foraging success (Riechert and Gillespie 1986). The dependence of web-building spiders on the complexity of their habitat has been well documented in a number of observational and experimental studies (e.g. Robinson 1981, Greenstone 1984, Rypstra 1986, Uetz 1991).

Although hunting spiders do not construct webs to capture their prey, increased structural complexity of their habitat may provide a more favorable microclimate (Uetz 1979), with more suitable places for perching (Greenquist and Rovner 1976), hiding and constructing retreats (Hatley and MacMahon 1980, Duffey 1962). Increased structural complexity of habitat may also decrease rates of intraspecific predation among webbuilding (Rypstra 1983) and hunting spiders (Edgar 1969).

Further, growing evidence suggests that spiders are food-limited animals (Wise 1975, 1979, Spiller 1984), which tend to aggregate in patches of increased abundance of prey (Cherret 1964, Gillespie 1981, Rypstra 1985). Thus, non-random patch selection in spiders appears to be under strong influence of the structural complexity of their habitat and the availability of prey (Riechert and Gillespie 1986).

Spiders are extremely common predators within forest canopies (Dahlsten et al. 1977, Moldenke et al. 1987, Schowalter 1989, 1995a, Halaj et al. 1996), that prey on a number of forest insect pest species (Turnbull 1956, Loughton et al. 1963, Eikenbary and Fox 1968, Dahlsten et al. 1977, Jennings and Houseweart 1978, Fichter 1984, Jennings and Houseweart 1989). Despite the suggested role of spiders as natural controls in

arboreal communities, relatively little work has been done to understand their functioning, and to identify factors limiting their distribution in these systems.

Stratton et al. (1979) investigated spider assemblages associated with three tree species in northeastern Minnesota. These included red pine, Pinus resinosa Ait., white spruce, Picea glauca (Moench) and white cedar, Thuja occidentalis L. Tree species differed significantly in the abundance and community structure of the associated spider fauna. Although no habitat variables were measured and evaluated as predictors of spider densities, it was concluded that the observed differences were due mostly to differences among the tree species in the physical structure of branches. Jennings and Dimond (1988) and Jennings et al. (1990) found significantly higher densities of spiders on foliage of red spruce, *Picea rubens*, compared to balsam fir, *Abies balsamea*, in east-central Maine. They suggest that curved needles of red spruce provide a better habitat for spiders than flat needles of balsam fir. Perhaps the best documented significance of habitat structure on arboreal spiders has been demonstrated in a series of observational and experimental studies conducted in southern Sweden (Gunnarsson 1988, 1990, 1992, Sundberg and Gunnarsson 1994). The authors of those studies concluded that increased needle density of Norway spruce, Picea abies (L.), improves the habitat quality for spiders, possibly by providing increased protection against foliage-foraging birds (Askenmo et al. 1977, Gunnarsson 1983).

Spiders, as generalist predators, usually do not exhibit density-dependent response to prey. Therefore, it has been argued that individual spider species may not be very effective as insect pest regulators (Riechert and Lockley 1984). However, multi-species assemblages of spiders may act as density-independent mortality factors suppressing initial densities of insect pests below economic injury levels (Riechert and Lockley 1984, Wise 1993). For example, management practices aimed at enhancing densities and diversity of spiders through manipulations of their habitat appear to provide a measure of crop protection in some agricultural systems (Riechert and Bishop 1990, Carter and Rypstra 1995).

It has been suggested that similar spider-enhancing management may be feasible in forest ecosystems. By selecting and favoring tree species that harbor a high density and

diversity of spiders, one may increase natural resistance of stands to forest insect pests (Jennings et al. 1990). The first step to implementing such a plan, however, is to identify factors of spider habitat which affect their distribution and diversity in arboreal communities.

The objective of this study was to identify habitat variables that may influence the distribution and diversity of spiders on several host-tree species. I intended also to identify some factors of spider habitats which are common to several host-tree species with fundamentally different branch structure. If true, this would allow one to predict the distribution and diversity of one of the most abundant terrestrial predators across a wide range of arboreal habitats. The tree species selected for the study included: red alder, *Alnus rubra* Bongard, western redcedar, *Thuja plicata* Donn ex D. Don, western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, noble fir *Abies procera* Rehder, and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. These are common tree species found in western Oregon (Franklin and Dyrness 1988), and they differ substantially in branch structural complexity.

Materials and Methods

Study Sites and Experimental Design

This study was conducted on the H.J. Andrews Experimental Forest, within the Willamette National Forest in the western Cascade Range, Oregon. A total of six study sites were selected in March 1993. The main criterion for the selection of the study sites was the presence of at least 20 dominant or co-dominant trees (d.b.h. < 20cm) of each species at a particular site. Since I intended to sample all tree species at a particular site within a narrow range of time, observed differences in the abundance and community structure of spiders can be attributed directly to the habitat quality provided by individual tree species (Table 2.1). Three study sites were selected in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1988). The sites ranged in elevation from 597 to 768m, and tree

species sampled at these sites included red alder, western redcedar, western hemlock, and Douglas-fir. Since noble fir does not occur naturally at this elevation, three additional sites were selected in the *Abies amabilis* Zone (Franklin and Dyrness 1988), at elevations ranging from 1195 to 1292m. As a reference, Douglas-fir was also sampled at these high elevation sites.

The experimental design of the study was a randomized complete block. Tree species were considered treatments, and study sites served as blocks. The sampling units were defined as 1-m-long branch tips selected from the lower third of the tree canopy. Since a clustered, rather than random distribution of arthropods was expected, a total of four branches were sampled on each tree. The number of arthropods collected from all branches, as well as the habitat variables measured on a subset of branches (see below), were averaged for each tree (one data point). This estimate was used in all statistical analyses.

Field and Laboratory Procedures

At all sites, twenty dominant or co-dominant trees of each species were selected along a 10-m wide and 50-m long transect placed in the forest stand. This procedure was repeated (multiple transects were selected) until 20 trees of each species were designated. Thus, the size of the study site was determined by the number of sampled trees (n = 80). On each tree, four accessible non-interdigitated tips of branches of constant length (1m) were removed from the lower third of the tree canopy using a hand pruner. Each branch was quickly placed in a heavy-duty plastic bag, and transported to the laboratory. In order to prevent cannibalism in sample bags, and to facilitate the removal of arthropods from the branches, a three-second spray of insecticide (Hi-Power[®] Ant, Roach & Spider Spray Formula II; Ortho, San Ramon, California, USA) was applied into each bag before sealing it.

In the laboratory, each sample branch was shaken vigorously within the bag to remove arthropods. Dislodged arthropods were collected by washing the bag with tap water. Subsequently, the collected arthropods were preserved in specimen vials containing 75% ethyl-alcohol. Spiders were sorted and identified to the most feasible taxa. Spiders were further categorized into eight functional groups based on similarities in their foraging strategies. I used a modified classification proposed by Kaston (1948) and Gertsch (1979). Hunting spiders included: (1) agile hunters of the families Salticidae and Oxyopidae, a group of active foragers with keen vision; (2) ambushers of the family Thomisidae; (3) runners of the family Philodromidae, a group of spiders combining active search and ambush strategies; and (4) nocturnal hunters including Clubionidae, Anyphaenidae and Gnaphosidae, spiders actively searching foliage at night. Web-building spiders were divided into categories of spiders with similar web characteristics and included: (1) orb weavers of the families Araneidae, Tetragnathidae and Uloboridae; (2) cobweb spiders, family Theridiidae; (3) sheet-web weavers of the families Linyphiidae and Micryphantidae; and (4) hackled-band weavers, family Dictynidae. The rest of the arthropod community was sorted and identified to order. The abundance of all arthropods other than spiders was used as an estimate of the spider food resource (Uetz 1975, 1979, Rypstra 1986).

In the laboratory, three out of four branches harvested from each tree were randomly selected. I used this subgroup of branches to measure several characteristics of spider habitat. To assess arthropod-habitat relationships, only the arthropods collected from this subgroup of branches were used in correlation analyses. The habitat variables included:

1) Maximum horizontal and vertical branch spread (cm). These were defined as maximum distances across the branch measured horizontally and vertically, respectively. These measurements were taken with the branch positioned horizontally. I hypothesized that increased spread of branches would increase the probability of intercepting spiders during their dispersal by ballooning, and thus increase their densities on branches.

2) Total number of branching angles. These were defined as acute angles between two branch links. The number of branching angles was counted on branches of all tree species except for western hemlock. The number of branching angles reflects the architectural complexity of the branch, and thus may be related to the quantity and quality of the spider habitat. 3) The number of composite leaves. These were counted on each branch of western redcedar. I suspected that this variable might provide a better estimate of structural diversity of the branch than the number of branching angles, which is fairly constant among individuals of this tree species.

4) Total biomass of stems and foliage. Collected branches were oven-dried. Each branch was divided into two fractions, foliage and wooden stems, which were weighed separately. These variables are correlated with the total amount of available surface area on the branch, and may also reflect its structural complexity.

5) Diameter at breast height. One measurement of d.b.h. was taken on each tree. This measure is directly related to the tree size, and may provide an indirect measure of the total amount of spider habitat available on a particular tree.

Statistical Analyses

Differences in arthropod densities on individual tree species were assessed with multi-factor ANOVA, with tree species and sites as factors. All treatment means were compared and separated with the Fisher's protected least significant difference (LSD) test (Steel and Torrie 1980). In order to satisfy the assumption of homogeneous variance, variables were transformed to $\ln(Y)$, $\ln(Y+1)$ or $\ln(Y+0.01)$, as appropriate, prior to all analyses. In all cases, the original and adjusted means and their standard errors are reported here. Diversity of spider populations was determined with the Shannon diversity index (H') (Pielou 1975). I used the G-test of independence with the Williams' correction to determine similarities in the community organization of spiders among tree species (Sokal and Rohlf 1995). Overlap in the spider community structure, and species composition were determined with the formula in Schoener (1968), and with the Sørensen similarity index (C_s), respectively. Pearson correlation coefficients between densities of spiders and their prey, and the structural variables of their habitat were calculated: (1) individually for each tree species using samples pooled across all sites, (2) individually for lower elevation sites using samples pooled from all tree species, and (3) together using samples pooled from all tree species and sites. I used multiple regression analyses to select the best subset of independent variables to predict spider abundance and diversity.

Since I expected the group of predictor variables to be linearly related, I used the stepwise procedure to control for multicolinearity among the variables. All statistical analyses were performed with SAS computer programs (SAS Institute Inc. 1994).

Results

Arthropod Habitat Characteristics

Overall, individual tree species varied significantly in the quantity and quality of their branch habitat (Table 2.1). Branches of Douglas-fir, followed by redcedar, had the widest horizontal spread, whereas the branches of red alder were significantly slimmer. At all sites, the branches of redcedar typically had the greatest vertical spread reflecting the "hanging" arrangement of their foliage. Noble fir, Douglas-fir and redcedar provided the greatest amount of foliage biomass per branch tip. Douglas-fir had the highest amount of available wooden twigs at lower elevation sites. A higher structural complexity of Douglas-fir was also reflected by the number of branching angles. The branches of redcedar had generally the lowest number of branches angles. At all sites, noble fir was superior to Douglas-fir in terms of the availability of foliage and wooden twigs, and the complexity of their branches as measured by the number of branching angles (Table 2.1).

Abundance and Community Structure of Spiders

There were significant differences in the abundance of spiders (numbers/ branch tip) among the tree species at lower elevation sites (F = 108.23; df = 3,225; P < 0.001). The abundance of spiders varied with sites (F = 4.44; df = 2,225; P = 0.013). However, the differences among tree species were site independent (species*site interaction; F = 1.03; df = 6,225; P = 0.406). The highest total densities of spiders at low elevation sites were collected from Douglas-fir (mean ± SE; 5.36 ± 0.54), whereas red alder supported the lowest total spider abundance per branch tip (0.85 ± 0.14) (Fig. 2.1A). Similarly, significantly more spiders were collected from Douglas-fir branches compared

Site and tree		Elev.	Date	Trees	DBH	F(df)	Horiz. branch	F(df)	Vertical branch	F(df)
speci	species			sampled (n)	ст	Р	spread (cm)	Р	spread (cm)	Р
L106:	ALRU	597	26-Jun	20	5.28 (0.46)c	24.81 (3,74)	41.73 (2.46)c	44.96 (3,76)	25.37 (1.54)c	26.98 (3,76)
	THPL		28-Jun	20	10.92 (0.97)b	0.0001	72.75 (2.47)a	0.0001	45.70 (1.68)a	0.0001
	TSHE		29-Jun	20	14.25 (1.45)a		62.23 (1.89)b		29.45 (1.32)b	
	PSME		2-Jul	20	12.12 (0.64)ab		78.95 (2.94)a		31.02 (1.49)b	
L109A:	ALRU	805	30-Jun	20	3.45 (0.48)c	99.35 (3,75)	36.77 (2.87)c	54.38 (3,75)	23.67 (1.21)d	25.91 (3,75)
	THPL		10-Jun	20	18.97 (1.22)a	0.0001	72.48 (2.25)ab	0.0001	40.03 (1.57)a	0.0001
	TSHE		12-Jun	20	17.55 (1.12)ab		64.34 (2.65)b		28.82 (0.78)c	
	PSME		2-Jun	20	14.43 (0.91)b		79.33 (2.79)a		35.60 (1.99)b	
L112:	ALRU	768	13 -Jun	17	4.04 (0.46)c	78.14 (3,72)	38.97 (2.17)c	53.50 (3,73)	26.49 (1.65)b	4.96 (3,73)
	THPL		16-Jun	20	13.00 (0.66)b	0.0001	62.08 (1.34)b	0.0001	33.68 (1.30)a	0.0034
	TSHE		24-Jun	20	11.46 (0.84)b		63.33 (2.09)b		27.02 (1.13)b	
	PSME		17-Jun	20	17.70 (0.99)a		71.23 (2.03)a		29.51(1.57)b	
L707:	ABPR	1256	11-Jul	20	13.13 (0.51)	3.58 (1,37)	69.13 (1.94)	0.22 (1,38)	13.13 (0.38)b	235.84 (1.38)
	PSME		12-Jul	20	15.09 (0.84)	0.066	67.82 (1.95)	0.645	29.45 (1.25)a	0.0001
L210:	ABPR	1195	7-Jul	20	15.14 (0.86)	0.13 (1,38)	69,32 (1.95)	1.43 (1.38)	15.00 (0.77)b	107.48 (1.38)
	PSME	e	8-Jul	20	14.50 (0.61)	0.724	66.14 (1.59)	0.239	29.85 (1.31)a	0.0001
L211A:	ABPR	1292	3-Jul	20	12.75 (0.71)	1.98 (1.38)	69.19 (2.77)	0.02 (1.38)	18.70 (0.91)b	65.04 (1.38)
	PSME		4-Jul	20	14.40 (0.89)	0.167	69.20 (2.13)	0.897	30.02 (1.08)a	0.0001

Table 2.1. Summary of study site and spider habitat characteristics. Within a site, means (\pm SE) followed by different letters are different (LSD; P = 0.05). Statistics are results of one-way ANOVA tests for differences among tree species.

Site and tree species		Foliage biomass	F(df)	Wood biomass	F(df)	No. angles	F(df)
		g	Р	g	Р		Р
L106:	ALRU	24.28 (1.26)c	87.01 (3,76)	30.20 (1.30)b	27.18 (3,76)	32.17 (2.12)b	186.50 (2,57)
	THPL	112.68 (8.06)a	0.0001	51.24 (3.46)a	0.0001	16.07 (0.58)c	0.0001
	TSHE	74.13 (7.08)b		58.13 (3.15)a			
	PSME	85.32 (5.79)b		58.26 (3.23)a		96.93 (8.31)a	
L109A:	ALRU	19.28 (1.00)d	184.79 (3,76)	21.61 (1.27)c	59.57 (3,76)	19.48 (2.09)b	210.52 (2,57)
	THPL	112.83 (7.18)a	0.0001	46.48 (2.77)b	0.0001	16.45 (0.50)b	0.0001
	TSHE	76.38 (4.78)c		50.54 (3.86)b			
	PSME	91.54 (5.33)b		61.25 (3.26)a		152.20 (10.64)a	
L112:	ALRU	15.52 (0.81)c	293.22 (3,73)	22.25 (1.13)c	125.54 (3,73)	34.68 (2.16)b	466.27 (2,54)
	THPL	106.44 (4.23)a	0.0001	47.53 (1.55)b	0.0001	15.63 (0.46)c	0.0001
	TSHE	83.99 (5.08)b		53.69 (2.54)b			
	PSME	110.61 (5.78)a		77.51 (3.58)a		140.60 (7.98)a	
L707:	ABPR	204.68 (8.09)a	40.33 (1,38)	116.98 (4.13)a	17.12 (1,38)	250.30 (11.77)a	120.04 (1.38)
	PSME	137.17 (6.16)b	0.0001	93.59 (3.81)b	0.0002	122.90 (5.19)b	0.0001
L210:	ABPR	195.16 (9.41)a	44.73 (1,38)	116.95 (5.65)a	37.57 (1,38)	242.30 (14.17)a	99.48 (1.38)
	PSME	125.77 (5.75)b	0.0001	81.15 (2.94)b	0.0001	119.60 (5.12)b	0.0001
L211A:	ABPR	187.52 (11.57)a	15.20 (1,38)	120.93 (6.54)a	11.01 (1,38)	212.60 (15.04)a	13.66 (1.38)
	PSME	135.92 (8.66)b	0.0004	92.70 (5.29)b	0.002	145.30 (11.80)b	0.0007

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Table 2.1. Continued.



Figure 2.1. Mean densities (\pm SE) of spiders per 1-m-long branch tips of individual hosttree species in pooled samples from lower (A), and upper (B) elevation sites. Bars with the same letter are not significantly different (LSD, P < 0.05). ALRU, red alder; THPL, western redcedar; TSHE, western hemlock; PSME, Douglas-fir; ABPR, noble fir.

to noble fir at higher elevation sites (F = 3.16; df = 1,114; P = 0.012) (Fig 2.1B). Differences between these two species were the same regardless of the study sites (species*site interaction; F = 0.38; df = 2,114; P = 0.686).

Significantly more hunting spiders were collected from Douglas-fir compared to other tree species at lower and upper elevation sites (F = 52.55; df=3,225; P < 0.001; and F = 14.50; df = 1,114; P < 0.001, respectively) (Table 2.2). The species*site interaction was not significant at any elevation (F = 1.98; df = 6,225; P = 0.07; and F = 0.40; df = 2,114; P = 0.674, respectively). There was a significant species*site interaction term for the abundance of web-building spiders (F = 2.76; df = 6,225; P = 0.013). Therefore, individual study sites were analyzed separately (Table 2.2). Douglas-fir had the highest densities of web-building spiders at lower elevation sites. Douglas-fir and noble fir supported approximately the same densities of web-building spiders at all higher elevation sites (Table 2.2). Neither species, nor the species*site interaction terms, were significant (F = 0.35; df = 1,114; P = 0.556; and F = 0.20; df = 2,114; P = 0.820, respectively).

Table 2.2. Spider species richness (S), diversity (H'), and abundance of selected arthropod groups per 1-m-long branch tip. Within a site, means (\pm SE) followed by different letters are statistically different (LSD; P = 0.05). Statistics are results of one-way ANOVA tests for differences among tree species at individual sites.

Site a	nd tree	S	F(df)	H'	F(df)	Web-building	F(df)	Hunting	F(df)	Prey	F(df)
species			Р		Р	spiders	Р	spiders	Р	organisms	Р
L106:	ALRU THPL TSHE PSME	3.00 (0.38)d 4.10 (0.32)c 5.90 (0.46)b 7.80 (0.46)a	23.23 (3,76) 0.0001	0.90 (0.14)c 1.22 (0.08)b 1.54 (0.10)a 1.72 (0.06)a	13.61 (3,76) 0.0001	1.00 (0.19)c 1.05 (0.21)c 4.05 (0.68)b 7.45 (1.03)a	34.37 (3,76) 0.0001	1.75 (0.33)c 4.25 (0.45)b 4.05 (0.76)b 8.25 (1.24)a	12.75 (3,76) 0.0001	49.15 (5.32)a 25.95 (2.74)b 54.80 (10.44)a 50.05 (5.44)a	6.75 (3.76) 0.0004
L109A:	ALRU THPL TSHE PSME	2.60 (0.35)c 5.75 (0.46)b 5.40 (0.60)b 9.95 (0.61)a	29.60 (3,76) 0.0001	0.77 (0.13)c 1.51 (0.11)ab 1.40 (0.13)b 1.79 (0.06)a	14.88 (3,76) 0.0001	0.50 (0.17)c 2.65 (0.43)b 3.00 (0.38)b 6.30 (0.58)a	40.31 (3,76) 0.0001	2.40 (0.38)c 4.90 (0.62)b 4.70 (1.18)bc 11.3 (1.63)a	12.91 (3,76) 0.0001	52.30 (5.67)ab 33.75 (5.01)c 46.00 (6.28)bc 81.29 (16.10)a	6.19 (3,76) 0.0009
L112:	ALRU THPL TSHE PSME	1.35 (0.23)c 3.95 (0.33)b 5.25 (0.46)b 7.75 (0.45)a	51.19 (3,73) 0.0001	0.29 (0.11)c 1.20 (0.08)b 1.43 (0.11)ab 1.62 (0.09)a	31.43 (3,71) 0.0001	0.71 (0.24)b 1.15 (0.23)b 3.00 (0.66)a 4.75 (0.86)a	11.19 (3,73) 0.0001	1.00 (0.28)c 3.40 (0.44)b 4.25 (0.43)b 10.10 (1.35)a	39.73 (3,73) 0.0001	36.35 (5.12)b 22.55 (2.58)c 43.00 (8.51)b 65.85 (7.53)a	11.16 (3,73) 0.0001
L707:	ABPR PSME	10.20 (0.36) 10.00 (0.63)	0.34 (1,38) 0.564	1. 89 (0.05) 1. 75 (0.08)	2.37 (1,38) 0.132	6.95 (0.74) 7.70 (1.07)	0.02 (1,38) 0.888	15.40 (1.23)b 20.60 (1.76)a	6.44 (1,38) 0.015	67.35 (8.28)b 118.00 (14.09)a	12.03 (1,38) 0.0013
L210:	ABPR PSME	8.85 (0.44)b 10.70 (0.46)a	8.76 (1,38) 0.005	1.64 (0.05)b 1.90 (0.05)a	13.85 (1,38) 0.001	11.30 (1.27) 11.80 (1.23)	< 0.001 (1,38) 0.976	17.30 (1.24) 21.70 (1.89)	2.01 (1,38) 0.164	57.75 (7.10)b 90.65 (13.00)a	7.55 (1,38) 0.0091
L211A:	ABPR PSME	8.50 (0.37) 9.00 (0.49)	0.47 (1,38) 0.497	1.78 (0.06) 1.80 (0.05)	0.10 (1,38) 0.75	7.15 (0.80) 8.20 (0.80)	1.09 (1,38) 0.302	13.50 (1.26)b 19.20 (1.72)a	7.62 (1,38) 0.009	39.50 (4.79)b 119.05 (8.30)a	73.03 (1,38) 0.0001

There were significant differences in the abundance of spider prey among the tree species at lower elevation sites (F = 21.24; df = 3,219; P < 0.001). Since the species*site interaction term was not significant (F = 1.22; df = 6,219; P = 0.296), data for prey densities were pooled across sites to obtain a better estimate of species differences. In pooled samples, Douglas-fir had the highest densities of potential prey individuals per branch tip (21.33 ± 3.23). This was followed by western hemlock (15.98 ± 2.8) and red alder (15.48 ± 1.79), whose prey densities were not significantly different. Redcedar had the lowest prey abundance among the tree species (9.14 ± 1.15). Douglas-fir supported a greater abundance of prey than noble fir. However, the magnitude of the difference between these two species was dependent on the site (species*site interaction; F = 5.20; df = 2,114; P = 0.007) (Table 2.2).

Spider Community Structure

There were significant species*site interaction terms for spider species richness and diversity for lower and higher elevation sites. Therefore, tree species were compared separately at individual study sites (Table 2.2). Generally, Douglas-fir supported the greatest spider species richness (2.58 ± 0.15 to 3.32 ± 0.20 species) per branch tip at lower elevation sites. The lowest number of species was found on red alder (0.45 ± 0.08 to 1.00 ± 0.13). The Douglas-fir and noble fir were similar in terms of the spider species richness and supported from 2.83 (± 0.12) to $3.57 (\pm 0.15)$ spider species per branch tip (Table 2.2). Generally, spider diversity was highest in Douglas-fir, and tended to decrease with the structural complexity of host-tree species (Table 2.2).

There were significant differences in the community structure of spiders among individual tree species at all sites (Table 2.3). The community of spiders was dominated by hunting spiders for all tree species (Fig. 2.2, 2.3). The highest similarities in community structure were found between Douglas-fir and western hemlock, with an overlap ranging from 83 to 94%. However, with the exception of site L106, these pairwise comparisons were significantly different (Table 2.3). Significantly different communities of spiders were found on Douglas-fir and noble fir at higher elevation sites. The overlap, however, ranged from 81.2 to 90.9% (Fig. 2.3). A greater similarity in spider species composition

Species	L106				L109A				L112				
	ALRU	THPL	TSHE	PSME	ALRU	THPL	TSHE	PSME	ALRU	THPL	TSHE	PSME	
ALRU	1.00	0.74 ¹	0.57	0.58	1.00	0.71	0.77	0.67	1.00	0.71	0.62	0.67	
		28.8 ²	74.1	81.1		22.8	22.8	47.5		20.9	28.5	23.8	
THPL		1	0.65	0.7		1	0.71	0.58		1	0.62	0.753	
			63.7	56.5			37.3	121			71.6	53.02	
TSHE			1	0.94			1	0. 86			1	0.834	
				7.68 ^{ns}				17.7				17.28	
PSME				1				1				1	

Table 2.3. Similarity in the spider community structure in pairwise host-tree species comparisons.

¹ Schoener's (1968) Index of Overlap. ² The G-statistic value. ^m Non-significant difference (P = 0.263).

Table 2.4. Values of the Sørensen similarity index (C_s) for spider species composition in pairwise host-tree species comparisons.

	L106				L109A				L112			
Species	ALRU	THPL	TSHE	PSME	ALRU	THPL	TSHE	PSME	ALRU	THPL	TSHE	PSME
ALRU	1.00	0.60	0.50	0.56	1.00	0.56	0.51	0.51	1.00	0.50	0.50	0.41
THPL		1	0.6	0.7 8		1	0.6 8	0.74		1	0. 64	0.6
TSHE			1	0.79			1	0.74			1	0. 8
PSME		<u></u>		1				1				1


Figure 2.2. Relative abundance of dominant spider groups on individual host-tree species at lower elevation sites. The Gstatistics test the within-site similarities in the spider community structure among individual host-tree species. Numbers above columns indicate absolute densities of spiders collected from individual host trees. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups. Host-tree species abbreviations as in Fig. 2.1.





Figure 2.3. Relative abundance of dominant spider groups on individual host-tree species at upper elevation sites. The Gstatistics (G) test the within-site similarities in the spider community structure between the host-tree species. Overlaps in the spider community structure, and spider species composition are determined with the Schoener's Index of Overlap (D) (Schoener 1968), and the Sørensen similarity index (C_s), respectively. Numbers above columns indicate absolute densities of spiders collected from individual host trees. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups. Host-tree species abbreviations as in Fig. 2.1.

was detected between Douglas-fir and western hemlock (Table 2.4), and Douglas-fir and noble fir (Fig. 2.3). Across all sites, agile hunters and runners combined were the dominant spider groups in all tree species. The relative abundance of sheet-web spiders was higher in all coniferous species, whereas ambushers were more common in red alder.

Arthropod-Habitat Relationships

Red Alder (ALRU)—Total spider densities were positively correlated with the abundance of potential spider prey and the amount of foliage and wood biomass (Table 2.5). The number of branching angles and number of leaves were positively correlated with the abundance of web-building spiders, whereas the abundance of hunting spiders (especially runners) was positively correlated with the branch biomass. In contrast to web-building spiders, the abundance of prey was a significant predictor of spider densities for almost all groups of hunters (except for nocturnal hunters). The best model, combining the abundance of prey and the number of leaves, explained about 30% of the variation in the total spider densities in red alder (Table 2.6A). There were no significant correlations between the abundance of total spider prey and any of the habitat variables.

Spider species richness was positively associated with the biomass of branches and the abundance of prey (Table 2.5). Higher spider diversity was associated with increased biomass of branches. The biomass of foliage was selected as the best predictor of both spider species richness and diversity (Table 2.6B,C).

Western Redcedar (THPL)--Total spider densities were positively associated with the abundance of prey, number of composite leaves and the foliage biomass. There were significant positive correlations between the abundance of prey and web builders except for the cobweb spiders (Table 2.5). Among the hunting spiders, only the densities of agile hunters were positively correlated with the wood and foliage biomass. Tree d.b.h. was a significant predictor of the total abundance of spider prey. The leaf numbers and biomass were the best variables selected by the stepwise procedure as predictors of total spider densities (Table 2.6A). Both spider species richness and diversity were positively correlated with the abundance of arthropod prey, which was selected the best prediction variable for both parameters (Table 2.6B,C).

		Spider density											
Host-tree species and habitat variables	S	<i>H</i> ′	Total	WB	HU	OR	SH	СВ	AG	NT	RN	AM	Prey density
ALRU													
D.b.h.	0.063	0.155	0.047	0.124	0.013	0.096	-0.157	-0.007	-0.008	0.064	-0.044	0.143	-0.159
Horiz. branch spread	0.231	0.255	0.264	0.152	0.243	0.113	0.191	0.044	0.085	0.093	0.256*	0.075	0.154
Vertic. branch spread	0.076	0.095	0.080	0.086	0.051	0.135	0.223	-0.048	-0.220	0.191	0.232	0.188	0.028
Foliage biomass	0.404**	0.377**	0.350**	0.220	0.286*	0.097	0.036	0.027	0.067	0.040	0.400**	-0.008	0.195
Wood biomass	0.313*	0.273*	0.343**	0.245	0.260*	0.146	0.033	0.064	0.060	0.013	0.347**	0.052	0.110
No. branching angles	0.060	0.092	0.161	0.303*	0.039	0.241	0.082	0.019	0.131	-0.057	-0.100	0.045	-0.195
No. leaves	0.218	0.221	0.308*	0.336*	0.176	0.249	0.139	0.016	0.141	-0.038	0.124	0.034	-0.112
Prey density	0.263*	0.195	0.392**	-0.056	0.484**	-0.179	0.137	0.156	0.373**	-0.103	0.266*	0.320*	-
THPL									¥				
D.b.h.	0.257*	0.177	0.164	0.377**	-0.050	0.131	0.368**	0.330*	-0.240	-0.075	0.188	0.064	0.319*
Horiz. branch spread	0.200	0.128	0.200	0.249	0.013	0.017	0.195	0.353**	-0.066	-0.190	0.167	-0.215	0.135
Vertic. branch spread	0.219	0.201	0.146	0.235	-0.017	0.049	0.212	0.244	0.003	-0.095	0.008	0.050	0.218
Foliage biomass	0.154	0.090	0.260*	0.101	0.227	-0.034	0.163	0.124	0.377**	0.058	-0.133	0.109	0.232
Wood biomass	0.085	0.067	0.227	0.051	0.188	-0.058	0.116	0.082	0.402**	-0.061	-0.162	0.080	0.196
No. branching angles	0.016	-0.006	0.193	0.078	0.186	-0.015	0.066	0.089	0.138	0.089	0.056	0.030	0.125
No. leaves	0.156	0.094	0.298*	0.185	0.230	0.116	0.022	0.248	-0.016	0.131	0.259*	-0.052	0.068
Prey density	0.355**	0.319*	0.323*	0.497**	0.071	0.273*	0.534**	0.203	-0.214	-0.004	0.305*	0.068	•

Table 2.5. Pearson correlation coefficients for spider species richness (S), diversity (H'), and densities of spiders and their prey, and habitat variables on individual host-tree species.

Table 2.5. Continued.

	Spider density												
Host-tree species and habitat variables	S	H'	Total	WB	HU	OR	SH	СВ	AG	NT	RN	AM	Prey density
TSHE													
D.b.h.	0.090	0.041	0.140	0.105	0.114	0.040	0.080	0.183	0.182	-0.070	0.039	-0.162	0.432**
Horiz. branch spread	0.198	0.265*	0.096	0.172	0.011	-0.020	0.140	0.295*	0.004	0.041	0.017	-0.022	0.081
Vertic. branch spread	0.012	0.004	0.179	0.071	0.176	-0.102	0.198	-0.060	0.202	0.138	-0 129	0.083	-0 180
Foliage biomass	0.442**	0.328*	0.594**	0.256*	0.600**	0.013	0.431**	-0.012	0.670**	0.256*	-0.023	0.033	0 316*
Wood biomass	0.491**	0.414**	0.562**	0.178	0.611**	-0.018	0.333**	-0.098	0.650**	0.227	0.121	0.006	0.273*
Prey density	0.393**	0.337**	0.252*	0.285*	0.147	-0.039	0.321*	0.010	0.122	0.014	0.116	0.065	-
ABPR													
D.b.h.	-0.176	-0.333**	0.274*	0.166	0.264*	-0.060	0.188	-0.037	0.259*	-0.118	0.182	0.106	0.264*
Horiz. branch spread	-0.050	0.061	0.084	0.111	0.007	0.054	0.121	0.005	-0.046	0.013	0.082	-0.037	0.082
Vertic. branch spread	-0.255*	-0.111	0.062	0.010	0.046	0.163	0.003	-0.196	0.049	0.035	0.008	-0.110	-0.178
Foliage biomass	-0.070	-0.094	0.312*	-0.073	0.492**	0.051	-0.082	0.003	0.400**	-0.034	0.382**	-0.048	0 325*
Wood biomass	-0.093	-0.023	0.083	-0.130	0.209	0.146	-0.176	0.055	0.182	-0.242	0.312*	-0 144	0.038
No. branching angles	0.105	0.112	0.102	-0.123	0.275*	0.117	-0.171	0.153	0.162	-0.135	0.400**	-0.107	0.179
Prey density	0.162	-0.040	0.523**	0.331**	0.468**	-0.113	0.347**	-0.018	0.343**	0.251*	0.217	0.074	-

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Table 2.5. Continued.

	Spider density												
Host-tree species and habitat variables	S	H'	Total	WB	HU	OR	SH	СВ	AG	NT	RN	AM	Prey density
PSME lower elevation									•				
D.b.h.	0.046	0.026	-0.074	-0.016	-0.078	-0.053	-0.039	0.085	-0.101	0.111	0.016	0.032	0.232
Horiz. branch spread	0.084	0.200	0.070	0.130	0.004	-0.137	0.138	0.138	-0.008	-0.117	0.135	-0.036	0.043
Vertic. branch spread	0.123	-0.127	0.193	-0.024	0.233	-0.045	-0.068	0.275*	0.298*	-0.218	-0.093	-0.055	0.361**
Foliage biomass	0.213	-0.080	0.457**	0.186	0.408**	0.053	0.197	0.099	0.339**	0.240*	0.279*	-0.004	0.303*
Wood biomass	0.248	0.032	0.400**	0.107	0.394**	0.042	0.106	0.033	0.320*	0.236*	0.261*	0.112	0.242
No. branching angles	0.362**	0.069	0.376**	0.123	0.359**	-0.005	0.032	0.227	0.309*	0.169	0.217	0.017	0.359**
Prey density	0.405**	0.029	0.289*	0.096	0.274*	0.200	-0.049	0.326*	0.234	0.142	0.125	0.087	-
PSME upper elevation													
D.b.h.	0.237	0.117	0.005	-0.015	0.015	-0.196	0.058	0.081	-0.056	0.001	0.085	0.023	0 275*
Horiz. branch spread	0.178	0.272*	-0.015	0.128	-0.101	0.043	0.112	-0.034	-0.169	0.016	0.045	-0.060	0.102
Vertic. branch spread	0.115	0.058	0.051	-0.031	0.086	-0.075	-0.003	-0.175	0.054	0.009	0.083	-0 140	0.008
Foliage biomass	0.316*	0.081	0.344**	0.138	0.377**	-0.026	0.078	0.287*	0.251*	0.352**	0 149	0 152	0.000
Wood biomass	0.241	0.024	0.267*	0.110	0.289*	0.067	0.018	0.174	0.169	0 168	0 178	0 146	0.155
No. branching angles	0.347**	0.308*	0.284*	0.267*	0.213	0.382**	0.148	0.155	-0.095	0.227	0.364**	0.070	0.278*
Prey density	0.093	0.100	-0.133	-0.234	-0.037	-0.019	-0.214	-0.166	-0.071	0.050	0.009	-0.008	-

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Table 2.5. Continued.

			Spider density										
Host-tree species and habitat variables	S	H'	Total	WB	HU	OR	SH	СВ	AG	NT	RN	AM	Prey density
PSME both elevations													
D.b.h.	0.115	0.058	-0.037	-0.021	-0.039	-0.121	0.001	0.085	-0.084	0.021	0.028	0.026	0.208*
Horiz. branch spread	-0.001	0.136	-0.215*	-0.021	-0.265**	-0.187*	-0.018	0.126	-0.164	-0.177	-0.219*	-0.063	-0.114
Vertic. branch spread	0.066	-0.086	-0.011	-0.079	0.025	-0.114	-0.089	0.146	0.145	-0.123	-0.091	-0.097	0.075
Foliage biomass	0.365**	0.093	0.581**	0.302**	0.586**	0.208*	0.275**	0.076	0.373**	0.449**	0.454**	0.100	0.434**
Wood biomass	0.347**	0.117	0.538**	0.265**	0.550**	0.252**	0.220*	0.003	0.332**	0.351**	0.469**	0.139	0.367**
No. branching angles	0.367**	0.184*	0.311**	0.216*	0.285**	0.222*	0.116	0.182*	0.145	0.209*	0.271**	0.048	0.306**
Prey density	0.306**	0.137	0.247**	0.041	0.230**	0.202*	-0.001	0.014	0.140	0.219*	0.293**	0.043	-
All host-tree species													
D.b.h.	0.415**	0.427**	0.318**	0.298**	0.278**	0.136*	0.257**	0.204**	0.236**	0.142**	0.223**	0.006	0.247**
Horiz. branch spread	0.497**	0.545**	0.363**	0.363**	0.301**	0.165**	0.309**	0.256**	0.270**	0.170**	0.219**	0.004	0.136*
Vertic. branch spread	-0.128	-0.038	-0.198**	-0.208**	-0.157**	0.022	-0.259**	0.066	-0.120*	-0.187**	-0.102	-0.050	-0.039
Foliage biomass	0.608**	0.504**	0.658**	0.493**	0.636**	0.226**	0.486**	0.139**	0.556**	0.434**	0.455**	0.025	0.239**
Wood biomass	0.665**	0.536**	0.718**	0.558**	0.686**	0.269**	0.531**	0.156**	0.598**	0.415**	0.509**	0.069	0.300**
Prey density	0.452**	0.299**	0.456**	0.340**	0.465**	0.240**	0.286**	0.166**	0.362**	0.274**	0.400**	0.142**	•

WB, total web-building spider; HU, total hunting spiders; OR, orb weavers; SH, sheet-web weavers; CB, cobweb spiders; AG, agile hunters; NT, nocturnal hunters; RN, runners, AM, ambushers. *0.05 > P > 0.01; **P < 0.01.

Tree species	Best model	F(df)	Р	R ²
ALRU	$\ln(SPD) = +LF + PY$	11.46 (2,54)	0.0001	0.300
THPL	$\ln(SPD) = +\ln(FL) + \ln(LF)$	7.52 (2,55)	0.0013	0.210
TSHE	ln(SPD) = +ln(FL) + ln(PY)	22.98 (2,56)	0.0001	0.450
ABPR	$\ln(SPD) = +\ln(PY)$	25.28 (1,58)	0.0001	0.300
PSME lower elev.	$SPD = -\ln(DB) + \ln(VS) + \ln(FL) + \ln(AG)$	9.79 (4,57)	0.0001	0.454
PSME upper elev.	$\ln(SPD) = +FL -PY$	6.93 (2,56)	0.002	0.198
PSME all sites	$SPD = -\ln(DB) + \ln(FL)$	43.05 (2,108)	0.0001	0.444

Table 2.6. Best models to predict the abundance (A), species richness (B) and diversity (C) of spiders on individual host-tree species.

A. Spider abund:	ance
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B. Spider species richness

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Tree species	Best model	F(df)	Р	R ²
ALRU	$\ln(S) = +\ln(FL)$	13.51(1,56)	0.0005	0.200
THPL	$\ln(S) = +PY$	7.52 (1,56)	0.0082	0.120
TSHE	$\ln(S) = +\ln(WD) + \ln(PY)$	21.10 (2,56)	0.0001	0.430
ABPR	S = -VS	4.04 (1,58)	0.05	0.065
PSME lower elev.	S = +AG + PY	9.37 (2,49)	0.0004	0.277
PSME upper elev.	$\ln(S) = +\ln(AG)$	7.66 (1,57)	0.0076	0.120
PSME all sites	S = +AG + PY	13.36 (2,108)	0.0001	0.198

Table 2.6. Continued.

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				WALLEY.

Tree species	Best model	F(df)	Р	R ²
ALRU	H' = +FL	8.75 (1,53)	0.0046	0.142
THPL	$H' = +\mathbf{P}\mathbf{Y}$	6.49 (1,56)	0.0136	0.104
TSHE	$\ln(H') = +\ln(WD) + \ln(PY)$	15.20 (2,56)	0.0001	0.352
ABPR	$\ln(H') = -DB$	7.79 (1,58)	0.0071	0.118
PSME lower elev.	-	-	-	-
PSME upper elev.	$\ln(H') = -\ln(WD) + \ln(AG)$	7.34 (2,56)	0.0015	0.208
PSME all sites	H' = +AG	5.23 (2,108)	0.0241	0.050

AG, number branching angles; DB, diameter at breast height; FL, foliage biomass; VS, vertical branch spread; LF, number leaves; PY, abundance of prey; WD, wood biomass.

Western Hemlock (TSHE)--The biomass of foliage and wood were significantly correlated with total spider densities in western hemlock (Table 2.5). This relationship was fairly strong among hunting spiders. For example, the biomass of foliage and wood explained as much as 44.9 and 42.3% of the variation in the abundance of agile hunters, respectively (Table 2.5). The abundance of prey was a significant predictor of the abundance of total spiders and web-building spiders. A significant relationship was also detected between the densities of prey and d.b.h. and branch biomass. The foliage biomass and prey abundance combined (best model) explained about 45.0% of the variation in total spider abundance in this host-tree species (Table 2.6A). Higher spider species richness and diversity were associated with greater branch biomass (namely the biomass of wood) and abundance of prey (Table 2.5). The best prediction models for spider species richness and diversity included the biomass of wood and prey abundance,

and explained approximately 43.0 and 35.2% of the variation in these two variables, respectively (Table 2.6B,C).

Noble Fir (ABPR)—The abundance of prey, followed by the foliage biomass and tree d.b.h. were the best predictors of total spider densities in noble fir (Table 2.5). The same variables were good predictors of densities of hunting spiders and especially agile hunters. On the other hand, the abundance of web-building spiders and sheet-web spiders in particular, were positively correlated with the availability of prey. The abundance of prey was selected as the best prediction variable for the total spider abundance (R^2 = 0.30) (Table 2.6A). The abundance of other arthropods was positively correlated with the branch foliage biomass and tree d.b.h. The spider species richness and diversity were negatively correlated with the branch height (R^2 = 0.07) and tree d.b.h. (R^2 = 0.12), respectively (Table 2.6B,C).

Douglas-fir (PSME)--The branch foliage biomass was the best predictor of the total spider abundance in Douglas-fir at lower and upper elevation sites (Table 2.5). There was also a positive correlation between total spider densities and the biomass of wood, number of branching angles, and the abundance of prey at lower elevation sites. The abundance of prey was also significantly correlated with the biomass of foliage and number of branching angles at both elevations. The best model to predict the total abundance of spiders in Douglas-fir at lower elevation sites ($R^2 = 0.45$) combined the tree d.b.h., branch vertical spread, foliage biomass and the number of branching angles (Table 2.6A). The foliage biomass and the abundance of prey combined were the best predictors of spider densities at upper elevation sites. However, the model explained only a small portion of the variation in the spider abundance ($R^2 = 0.20$). The abundance of prey and the number of branching angles were the best variables selected by the stepwise procedures to predict spider species richness (Table 2.6B). There were no correlations between spider diversity and any of the habitat variables at the lower elevation sites. On the other hand, the biomass of wood and the number of branching angles were the best variables to predict the spider diversity at upper elevation ($R^2 = 0.21$) (Table 2.6C).

In combined samples from all sites, foliage and wood biomass were the best predictors of densities of almost all spider groups in Douglas-fir (except for cobweb spiders and ambushers) (Table 2.5). The best model to predict total spider abundance included tree d.b.h. and biomass of foliage ($R^2 = 0.44$). The best spider species richness model for Douglas-fir included the number of branching angles and the abundance of available prey ($R^2 = 0.20$) (Table 2.6B). Although the number of branching angles was positively correlated with the spider diversity, the best model with this variable explained only 5% of the variation in the response variable across all sites (Table 2.6C).

All Tree Species Pooled Together--With the exception of branch vertical spread. densities of all spider groups were significantly correlated with all of the habitat variables. Ambushers were the only group whose densities were correlated only with the abundance of available prey. The branch wood biomass alone was a good predictor of the total spider density across several tree species within, as well as across, individual study sites (Table 2.7A). For example, this variable alone explained almost 70% of the variation in the total spider abundance across five tree species (Fig. 2.4A). Total abundance of spiders was also strongly correlated with the foliage biomass ($R^2 = 0.59$), and to a lesser degree with the abundance of prey ($R^2 = 0.24$) (Fig. 2.4B.C). However, the addition of foliage biomass and the abundance of prey into the prediction model resulted in only a slight increase in its fit ($R^2 = 0.75$) (Table 2.7A). Similarly, models combining the biomass of wood, abundance of prey and the horizontal spread of branches explained from 53 to 69% of the variation in the total spider abundance across four tree species within lower elevation sites (Table 2.7A). Models combining the biomass of branch wood and foliage, branch horizontal spread and the abundance of prey explained 66 and 48% of the variation of spider species richness and diversity across all five tree species, respectively (Table 2.7B.C).

On the other hand, selected habitat variables did not appear to be good predictors of the total abundance of spider prey. The best model combining the biomass of wood and foliage explained only about 16% of the variation in the abundance of total arthropods other than spiders (Table 2.7A, Fig. 2.5A,B). Similarly, habit structure variables were poor predictors of densities of the most abundant arthropod groups on foliage, including Collembola, Psocoptera, Diptera and Aphidoidea (Table 2.7A).

A. Arthropod	abundance			
Site/Group	Best model	F(df)	Р	R ²
L106				
Araneae	$\ln(X) = +\ln(WD)$	84.04 (1,76)	0.0001	0.525
Total prey	$\ln(X) = +\ln(FL) + \ln(WD)$	11.28 (2,75)	0.0001	0.231
L109A				
Araneae Total prey	$\ln(X) = +\ln(HS) + \ln(WD) + \ln(PY)$	50.87 (3,68) -	0.0001 -	0.692 -
L112				
Araneae	$\ln(X) = +\ln(WD) + \ln(PY)$	77.27 (2,73)	0.0001	0.679
Total prey	$\ln(X) = -FL + WD$	9.40 (2,73)	0.0002	0.205
All sites				
Araneae	ln(X) = +ln(FL) + ln(WD) + ln(PY)	345.31 (3,341)	0.0001	0.752
Collembola	ln(X) = +ln(DB) + ln(FL) - ln(WD)	34.27 (3,341)	0.0001	0.232
Psocoptera	$\ln(X) = +\ln(DB) + \ln(HS) + \ln(FL) - \ln(WD)$	46.99 (4,340)	0.0001	0.356
Diptera	$\ln(X) = +\ln(VS) + \ln(WD)$	43.42 (2,342)	0.0001	0.203
Aphidoidea	$\ln(X) = -\ln(HS) - \ln(FL) + \ln(WD)$	18.90 (3,341)	0.0001	0.143
Total prey	$\ln(X) = -\ln(FL) + \ln(WD)$	31.38 (2,342)	0.0001	0.155

Table 2.7. Best models to predict the abundance of selected arthropod groups (A), spider species richness (B) and diversity (C) across all host-tree species at individual study sites.

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Site/Group	Best model	F(df)	Р	R ²
L106	$\ln(X) = +\ln(HS) - \ln(VS) + \ln(FL) + \ln(PY)$	20.42 (4,77)	0.0001	0.528
L109A	X = +HS +WD +PY	35.45 (3,68)	0.0001	0.610
L112	$\ln(X) = +\ln(FL) + \ln(WD) + \ln(PY)$	54.77 (3,72)	0.0001	0.695
All sites	$\ln(S) = +\ln(HS) + \ln(FL) + \ln(WD) + \ln(PY)$	164.23 (4,340)	0.0001	0.659

Table 2.7. Continued.

Site/Group	Best model	F(df)	P 0.0001	<i>R</i> ² 0.333
L106	$X = +\ln(WD)$	37.96 (1,76)		
L109A	$X = +\ln(HS) + \ln(WD)$	26.45 (2,69)	0.0001	0.434
L112	$\ln(X) = \ln(DB) + \ln(HS)$	52.37 (2,71)	0.0001	0.600
All sites	$\ln(X) = +\ln(HS) + \ln(FL) + \ln(PY)$	105.00 (3,339)	0.0001	0.483

C. Spider diversity

X, response variable; AG, number branching angles; DB, diameter at breast height; FL, foliage biomass; VS, vertical branch spread; LF, number leaves; PY, abundance of prey; HS, horizontal branch spread; WD, wood biomass.

Discussion

On all tree species, total spider densities correlated with structural variables of their habitat. This suggests that the habitat complexity may influence the abundance of these predators in tree canopies. With the exception of noble-fir, the number of leaves or the biomass of foliage consistently appeared in the best prediction models selected by stepwise procedures. This supports conclusions of other studies suggesting the importance of tree foliage as one of the determinants of the abundance of arboreal spiders (Gunnarsson 1988, 1990, Sundberg and Gunnarsson 1994). For example, Gunnarsson (1990) has shown experimentally that decreased density of needles has a negative effect on the abundance of spruce-inhabiting spiders in southern Sweden.

It has been suggested that structurally more complex habitats provide a wider selection of web-attachment sites and thus are more suitable for web-building spiders. Consequently the abundance of these spiders tend to increase in these habitat types (Robinson 1981, Rypstra 1983, 1986, Uetz 1991, Rypstra and Carter 1995). Significant positive correlations between some groups of web builders and structural features of habitat in this study partly support this hypothesis (Table 2.5).



Figure 2.4. The best prediction model for the total abundance of spiders in samples pooled across five host-tree species and six collecting sites. The model combines the branch wood biomass (A), branch foliage biomass (B), and the abundance of available prey (C). Data points represent pooled data from three branches harvested on each tree. The inserts in the right portion of the graph display site averages (n = 20) for each variable.



Figure 2.5. The best prediction model for the total abundance of spider prey in samples pooled across five host-tree species and six collecting sites. The model combines the branch wood (A) and foliage biomass (B). Data points represent pooled data from three branches harvested on each tree. The inserts in the right portion of the graph display site averages (n = 20) for each variable.

In addition, however, the abundance of hunting spiders was also correlated with the structure of their habitat. For example, the abundance of agile hunters was positively correlated with the amount of twigs and foliage in western redcedar, western hemlock and Douglas-fir. Similarly, higher densities of nocturnal hunters were collected from branches with a greater biomass of foliage in western hemlock and Douglas-fir (Table 2.5).

Although these spiders do not require web-attachment sites, increased structural complexity of habitat may provide a larger foraging area, or a greater availability of hiding places and retreat building sites. For example, Hatley and MacMahon (1980) suggest that increased densities of nocturnal hunters documented in structurally more complex *Artemisia* shrubs (manipulated by tying) reflected a greater availability of retreat-building sites in this habitat. The addition of substrate may also decrease the probability of aggressive encounters among spiders, and increase the carrying capacity of the habitat patch (Rypstra 1983, Uetz 1991).

Higher densities of total spiders were associated with increased densities of available prey organisms on branches. Correlative studies and field experiments have demonstrated that web-building and hunting spiders aggregate in patches of increased prey densities (Cherett 1964, Gillespie 1981, Olive 1982, Rypstra 1985, Weyman and Jepson 1994). The results of this study support these findings, and suggest that besides habitat complexity, increased abundance of available prey may also be an important factor affecting the abundance of spiders in arboreal habitats.

Significantly higher densities of spiders were collected from branches of structurally more complex tree species. Spider densities were significantly correlated with the habitat structure variables, and to a lesser degree with the abundance of potential prey on branches. The availability of wooden twigs (expressed as its biomass) alone, was a strong predictor of spider densities across the selected tree species. This pattern was consistent at all sites with four tree species, as well as in pooled samples comprising all tree species and sites. This supports the hypothesis that the plant size per se (as a unit of habitat, and one of the components of plant architecture) is a strong predictor of arthropod abundance and diversity in natural communities (Lawton 1978, 1983).

Rypstra (1986) has documented strong correlations between the abundance of web-building spiders found on the undergrowth vegetation and the amount of this vegetation. In addition, the abundance of flying insect prey and ambient temperature were also positively correlated with the spider abundance in her study. The amount of vegetation alone, however, explained from 41 to 98% of the variation in the density of web-building spiders. In addition, this pattern was consistent across three distinct communities, ranging from tropical Gabon, through subtropical Peru to temperate sites in the northeastern United States. Rypstra and Carter (1995) showed a strong positive correlation between the density of web-building spiders and the biomass of supportproviding vegetation in a soybean agroecosystem.

Structural complexity of habitat was also a significant predictor of the abundance of potential spider prey across several host-tree species. This relationship, however, was weak. Southwood et al. (1982) conclude that structural features of habitat (d.b.h., distance of the lowest branch from the ground, canopy volume and percentage cover of epiphytes) is not a good predictor of the abundance and biomass of several arthropod guilds on selected tree species native to Britain and South Africa. Spiders are generalist predators and the presence of specific features of habitat, or the habitat size per se, may be more critical to their distribution than the presence of a specific prey group. On the contrary, other groups of arthropods may have more specific requirements as to the quality of their habitat substrate. For example the nutritional quality of food or a presence of secondary metabolites limits the distribution of phytophagous insects (e.g. reviews in Schowalter et al. 1986, Perry 1994). This may also be true for such groups as Collembola or Psocoptera. Although these arthropods do not consume the tissue of the host-plant, the availability or quality of their food resource, including bacteria, algae and fungi, may be host-specific. Therefore, it is reasonable to suspect that a simple addition of habitat substrate, which is heterogeneous in nutritional quality (e.g. habitat transition from alder to western hemlock), may not be followed by a strong increase in the abundance of these arthropod groups.

The spider species richness and diversity were positively correlated with the structure of branch habitat and total availability of prey across the studied tree species. Greenstone (1984) has documented a strong positive relationship between the diversity of web-building spiders and the structural diversity of their habitat across several types of habitats ranging from tropical sites in Costa Rica to California scrub sites. Similarly, strong correlations between the species richness and the amount of habitat substrate (forest litter depth) have been uncovered in communities of wandering spiders (Uetz 1975, 1979). A greater species richness and diversity of spiders in structurally more complex

host-tree species may reflect a greater variety of available resources (types of hiding places, prey organisms or microclimate).

A significant portion of the variation in spider abundance and diversity was explained by the amount of available substrate (e.g. biomass of wood and branches), but the community structure of spiders differed significantly among the tree species. The results suggest, that although the abundance of spiders may simply reflect the availability of substrate, subtle changes in the structural quality of branches may be critical to individual spider groups. For example, the relative abundance of sheet-web spiders, a group requiring a more complex habitat to construct webs, was greater in structurally more complex tree species such as Douglas-fir and western hemlock as compared to red alder and redcedar. Similarly, Stratton et al. (1979) found a greater proportion of these spiders in red pine and white spruce in comparison with structurally simpler white cedar.

Conclusions

Overall, this study documented significant correlations between the complexity of branch microhabitat and the total abundance and diversity of spiders on individual hosttree species. The significance of individual prediction variables varied in relation to individual spider functional groups, which probably reflects specific habitat or prey requirements among these groups. The biomass of foliage and the availability of prey were most common among the variables selected by stepwise procedures to predict spider abundance on individual host-tree species. Almost 70% of variation in spider densities across individual host-tree species can be explained by the amount of wooden twigs provided by their branches. Due to the observational nature of the work, no cause-andeffect conclusions can be drawn. Nevertheless, the results of the study suggest that the densities of arboreal spiders are significantly influenced by the physical structure of their habitat, as has been suggested for other natural and agricultural communities. The relative importance of specific features of spider habitat and the availability of prey in determining the abundance and community structure of these predators in forest canopies requires experimental testing (see Chapter 3).

3. Changes in the Abundance and Community Organization of Spiders and Their Potential Prey Organisms Following Manipulations of Habitat Structure in Douglas-fir Canopies

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3. CHANGES IN THE ABUNDANCE AND COMMUNITY ORGANIZATION OF SPIDERS AND THEIR POTENTIAL PREY ORGANISMS FOLLOWING MANIPULATIONS OF HABITAT STRUCTURE IN DOUGLAS-FIR CANOPIES

Abstract

This study tested the importance of habitat structure on density and community structure of spiders and their potential prey organisms in Douglas-fir canopies. The habitat complexity, defined as needle density and branching complexity of Douglas-fir branches, was manipulated in a four-month experiment either by removing needles or by thinning and tying branches. The response to habitat perturbation of the entire arthropod community of Douglas-fir branches was monitored. Treatment effects on spiders were assessed in the context of tritrophic plant-herbivore-predator interactions, where the abundance of potential prey on foliage was used as a covariate. As indicated by sticky traps, habitat manipulations did not affect densities or biomass of potential flying spider prey in the vicinity of treatment branches. Removal of needles and thinning of branches, however, had a strong negative effect on the abundance of spider prey on foliage, dominated by Psocoptera and Collembola. Tying of branches resulted in a significant increase in the abundance of spider prey, namely Collembola. Even after accounting for the effect of prey density, significant changes in spider abundance resulted from changes in the complexity of their habitat. Densities of spiders were lower in treatments with lower density of needles. Thinning of branches resulted in decreased densities of spiders, and branch tying significantly increased spider abundance. The community structure of spiders changed as a result of habitat manipulations as well. The spider community of needlesparse branches was dominated by orb weavers (Araneidae), whereas tied branches were preferably colonized by sheet-web weavers (Linyphiidae and Micryphantidae), and nocturnal hunting spiders (Anyphaenidae and Clubionidae). Spider species richness and diversity increased in structurally more complex habitats. Increase in structural complexity of habitat had a slight positive effect on the average body size of spiders. It is suggested that observed changes in the spider community can be attributed to changes in

the structural complexity of their habitat, and to a lesser extent, to the availability of prey present on the foliage.

Introduction

The significance of habitat structure in the biology of spiders has been a topic of numerous ecological studies. This interest is undoubtedly due to the great abundance and diversity of spiders and the variety of ecological roles they play (Turnbull 1973, Foelix 1982, Wise 1993), as well as the intimate dependence of these predators on the physical structure of their habitat for foraging and perception of their surrounding environment (Foelix 1982, Riechert and Gillespie 1986, Uetz 1991).

The importance of habitat structure as one of the factors affecting the abundance and community structure of spiders has been documented in natural communities including deserts (Chew 1961, Riechert 1976, Riechert and Tracy 1975), grasslands and shrub communities (Duffey 1962, Colebourn 1974, Enders 1977, Schaefer 1978, Hatley and MacMahon 1980, Robinson 1981, Schoener and Toft 1983b, Greenstone 1984, Rypstra 1986, Rushton 1988, Scheidler 1990, Gibson et al. 1992), and forest floor and understory vegetation (Uetz 1976, 1979, Bultman and Uetz 1982, 1984, Waldorf 1976, Hodge 1987).

Trees are architecturally diverse habitats harboring an extraordinary species richness of arboreal communities (Lawton 1978, Southwood 1978, Moran and Southwood 1982, Strong et al. 1984). Spiders are an important component of arboreal arthropod communities in temperate (Dahlsten et al. 1977, Moldenke et al. 1987, Schowalter 1989, 1995a, Halaj et al. 1996) and tropical forests (Stork 1991, Schowalter 1994, Russell-Smith and Stork 1995, Schowalter 1995b), and their predatory role in these systems has been well documented (Turnbull 1956, Loughton et al. 1963, Eikenbary and Fox 1968, Dahlsten et al. 1977, Jennings and Houseweart 1978, Fichter 1984, Jennings and Houseweart 1989). Despite the apparent importance of spiders in forest canopies, relatively few studies have investigated spider-habitat interactions in these systems. Stratton et al. (1979) and Jennings and Collins (1987) studied the spider fauna and habitat structure in several North American coniferous tree species. Eubanks and Miller (1992) investigated the habitat preference of a facultatively arboreal wolf spider in Mississippi. However, studies in which the spider habitat was experimentally altered to determine causal relationships are limited to those by Gunnarsson (1990, 1992) and Sundberg and Gunnarsson (1994). The authors studied populations of spruce-inhabiting spiders in southern Sweden and suggest that needle density is one of the factors determining the abundance of these predators.

Further, it has been argued that studies of complex terrestrial communities should not be limited to investigations of simple pairwise trophic interactions without the consideration of additional trophic levels (Price et al. 1980, Kareiva and Sahakian 1990, Kareiva 1994). Commonly, observed changes in the structure of spider communities following manipulations of natural habitats are directly attributed to the physical alteration of the habitat (e.g. Hatley and MacMahon 1980, Rushton 1988, Gunnarsson 1990, Sundberg and Gunnarsson 1994), and only rarely is the effect of habitat perturbations on the intermediate trophic level monitored (e.g. Bultman and Uetz 1984, Gibson et al. 1992).

Herbivores require more than something to eat (Lawton 1983). Besides nutritional rewards, the host plant provides herbivores with places for oviposition, shelter or overwintering, all of which are qualities greatly determined by the architecture of the plant (Lawton 1983, Strong et al. 1984). Plant-inhabiting arthropods other than spiders respond to changes in the structure of their habitat (Denno 1977, Bach 1981, Lawton 1983, Leather 1986, Quinn and Walgenbach 1990). For example, Bach (1981) experimentally investigated the effect of growth form of cucumber (vertically vs. horizontally grown plants) on its herbivore, a chrysomelid beetle. She found significantly higher densities of beetles associated with vertically grown plants, a fact that she attributed to a simple effect of the growth form on the flight pattern of the beetle. In addition, one of the seven recognized guilds of tree-inhabiting arthropods are so-called "tourists" (Moran and Southwood 1982, Strong et al. 1984). These are non-predatory species

without any nutritional association with the plant. They colonize the plant for the purpose of seeking shelter, sun-basking or sexual display, and while at the plant they may be captured by local predators and thus become part of the community food web (Strong et al. 1984). Spiders have been shown to aggregate in habitats of increased prey densities (Gillespie 1981, Olive 1982, Rypstra 1985, Weyman and Jepson 1994, Halaj, unpublished data). Therefore, I argue that omission of prey monitoring in habitat manipulation studies conducted in natural communities may not provide a clear answer to the strength of spider-habitat interactions.

The objective of this study was to investigate experimentally the importance of habitat structure to arboreal spider communities. The structural complexity of spider microhabitat was defined as the needle density and branching complexity of Douglas-fir branches. I altered the habitat structure and measured responses of the local population of spiders and their potential prey to this perturbation. By monitoring the behavior of the whole arboreal community, I attempted to separate: (1) direct responses of spiders to the structure of their habitat, from (2) their indirect interactions with the habitat mediated through populations of their potential prey organisms (see below). This study tested the following hypotheses.

First (Hypothesis 1): a removal of needles and simplification of branch structure through thinning will have a negative effect on the abundance of phytophagous arthropods (potential spider prey) by decreasing the availability of food and heterogeneity of their habitat. Increase in habitat complexity through tying of branches will result in higher densities of arthropods. For example, effects of habitat structure on phytophagous insects have been experimentally documented in systems with chrysomelid beetles (Bach 1981) and sap-feeding homopterans (Denno 1977).

Second (Hypothesis 2): a removal of needles will result in reduced densities of spiders and changes in the community organization of these predators. This will be due to changes in their habitat as well as to a decreased abundance of potential prey. It has been suggested that needle density influences the abundance (Gunnarsson 1990, 1992, Sundberg and Gunnarsson 1994) and community structure (Gunnarsson 1988) of sprucedwelling spiders. Third (Hypothesis 3): a simplification of Douglas-fir branch structure will negatively affect the abundance and diversity of spiders. This will be due to both changes in their habitat and a lower abundance of the potential prey. For example, structural complexity of habitat has been shown to influence the abundance and community composition of shrub-dwelling spiders (Hatley and MacMahon 1980).

Materials and Methods

Site Location

This study was conducted between July and October 1994 at the H. J. Andrews Experimental Forest, within the Willamette National Forest about 15 km northeast of Blue River, in Lane and Linn Counties, Oregon. The region is characterized by wet winters, warm and dry summers and mild temperatures throughout the year. The annual precipitation averages about 230 cm, with the majority of precipitation occurring between November and March. Mean annual temperature for the region is 7.9 °C (Taylor and Bartlett 1993).

The study site was located in a young stand of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco. Occasional minor components included noble fir, *Abies procera* Rehder, and Pacific silver fir, *Abies amabilis* (Dougl.) Forbes. The ground-cover vegetation included bear-grass, *Xerophyllum tenax* (Pursh) Nutt., blueberry, *Vaccinium* spp., salal, *Gaultheria shallon* Pursh, and Pacific rhododendron, *Rhododendron macrophyllum* D. Don ex G. Don. The elevation of the site is 1,300 m.

Study Design and Treatments

The experiment was designed as a completely randomized block. Five treatments were randomly assigned to a total of 100 young Douglas-fir trees (< 15-years-old; < 10 m tall). The average trunk diameter measured at breast height was 16.5 cm (SE; \pm 0.8 cm). Treatment and sampling units in the study were defined as 1-m-long tips of branches randomly selected from the lower third of the tree canopy. One branch was treated on

each tree. Branches selected for sampling were permanently marked with a short strip of plastic ribbon.

The treatments were designed to partially mimic naturally occurring variations in the structure of Douglas-fir branches. This variation can be influenced by genetics (St. Clair 1994), or modified by growing conditions. Significant changes in needle density and morphology of branches may also result from insect herbivory (Mason and Wickman 1984), deer browsing (Black et al. 1979), or activity of pathogenic organisms (Filip and Schmitt 1990).

The first group of treatments was designed to investigate the importance of Douglasfir needle density (Fig. 3.1). The first treatment represented branches with completely removed needles (TOTAL). In the second treatment, the total length of branch, including the length of individual branchlets, was divided into sections of five centimeters. Starting at the tip of the branch, all needles from every other section were removed. This resulted in an approximately 50% reduction of needle density and a patchy appearance of the branch (PATCHY).

The second group of treatments tested the importance of Douglas-fir branching complexity. The first treatment represented branches from which about 50% of biomass was removed by pruning twigs to simplify their structure (THINNED). In the second treatment, 1-m-long tips of two adjacent branches were tied together to increase (approximately double) the complexity of the habitat (TIED). Finally, unmodified branches served as reference (CONTROL). The same control branches were used for both groups of treatments. In all treatments, 1-m-long sections (measured from the tip of the branch) plus a 50-cm-long buffer zone were treated similarly in the described way. All treatments were prepared July 1-9, 1994. Following the last sampling, all branches were harvested, oven-dried and weighed to estimate their biomass. For the purpose of this study, the unit of habitat was defined as a gram of plant material of treatment branches. To investigate the importance of needle density, the abundance of arthropods was standardized to numbers per gram of dry wood biomass (total branch biomass minus needle biomass) (Gunnarsson 1990, Sundberg and Gunnarsson 1994).

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Figure 3.1. Layout of treatment comparisons to test the importance of needle density (---) and branching complexity (---) of Douglas-fir branches in determining the abundance and community structure of canopy-dwelling spiders and their potential prey organisms.

Since, in the second group of treatments, I manipulated the availability of both wooden twigs and needles (thinning and tying), the densities of arthropods were expressed as numbers per gram of the total branch biomass (Schowalter 1989, 1995a,b).

Sampling of Arthropods

Spiders and other arthropods (here defined as potential prey organisms) were collected by beating 1-m-long tips of treatment branches (excluding the 50 cm buffer zone) over a hand-held drop cloth. Arthropods dislodged onto the drop cloth were quickly collected with a portable battery-powered vacuum collector (Paul and Mason 1985), and preserved in 75% ethanol. All treatment branches were sampled on August 6, September 5, October 2 and 22, 1994. Initial densities of spiders before the application of treatments were estimated, using the same techniques, on June 24-27, 1994. The abundance of potential actively flying or drifting spider prey organisms and their attraction to treatment branches were monitored with a series of sticky traps. Traps were constructed of sheets of a clear plastic craft canvas measuring 180×270 mm, with a grid of 2×2 mm. The traps were coated with a thin layer of Tanglefoot[®] (Tanglefoot Co., Grand Rapids, Michigan, USA). A total of fifteen branches in each treatment were randomly assigned one sticky trap. Each trap was attached to a vertical wooden stick with two push pins, and was positioned approximately 1 m from the branch tip. Orientation of the sticky trap was decided randomly with a table of random numbers. Sticky traps were exposed in the field for 24 hours during the course of each foliage sampling.

In the laboratory, collected arthropods were removed, sorted at the order level and the body length was measured on a stereo microscope. Spiders were identified to species whenever feasible, and were categorized into functional categories described above (Chapter 2; Materials and Methods). The body length of spiders was measured to the nearest 0.05 mm (excluding chelicerae and spinnerets); body length of other arthropods was measured to the nearest 0.5 mm. Oven-dry biomass of all arthropods collected in the course of the study was estimated with body-length based regression models. Biomass of spiders (at family level), Psocoptera, Collembola and Acari was estimated with regression models developed by Halaj and Moldenke (unpublished data). Biomass estimates of other insect orders were based upon regression models in Rogers et al. (1976, 1977).

Data Analyses

Since the same treatment branches were sampled over time, the data were analyzed with repeated-measures ANOVA. To investigate the effects of prey on spider abundance in this experiment, I regressed densities of spiders on total densities of their potential prey organisms on the foliage within individual treatment groups. In cases of a positive significant association, I assessed the preference of spiders for a particular habitat type with the analysis of covariance (ANCOVA). Before testing for homogeneity among the treatment groups, the group means of the dependent variable (spider density) were adjusted for the groups' differences in the covariate (prey density) with simple linear regression procedures (Sokal and Rohlf 1995). In other words, spider densities were

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compared at a constant level of prey densities (grand mean of covariate). With this adjustment, I attempted to separate the response of spiders to specific features of habitat from their numerical response to prey densities within a particular habitat type. In cases where there was no correlation between the covariate and the dependent variable in any of the treatment groups, the covariate was less likely to account for treatment differences in the dependent variable (Sokal and Rohlf 1995), and the original group means were tested for homogeneity with regular ANOVA. All treatment means were compared and separated with the Fisher's protected least significant difference (LSD) test (Steel and Torrie 1980). In order to satisfy the assumption of homogeneous variance, variables were transformed to $\ln(Y)$, $\ln(Y+1)$ or $\ln(Y+0.01)$, as appropriate, prior to all analyses. In all cases, the original and adjusted means and their standard errors are reported here. Diversity of spider populations was determined with the Shannon diversity index (H')(Pielou 1975). I used the G-test of independence with the Williams' correction to determine similarities in the community organization of spiders within both groups of treatments (Sokal and Rohlf 1995). All statistical analyses were performed with SAS computer programs (SAS Institute Inc. 1994).

Results

Abundance of Flying Insects

As indicated by sticky trap catches, there were no significant differences in the abundance of flying or drifting prey organisms in the vicinity of treatment branches (overall mean; F = 1.31; df = 4, 69; P = 0.276) (Fig. 3.2). The treatment * time interaction term was not significant (Wilk's lambda; F = 0.567; df = 12, 178; P = 0.866). The total biomass of trapped prey organisms was not significantly different among the treatments on any sample date (overall mean; F = 1.76; df = 4, 69; P = 0.147). The treatment * time interaction term was again not significant (Wilk's lambda; F = 0.372; df = 12, 178; P = 0.972). In terms of abundance, the majority of trapped arthropods were



Figure 3.2. Mean densities $(\pm SE)$ of potential spider prey organisms caught on sticky traps within one meter of treatment branches.

Diptera (54.9%), followed by Hymenoptera (23.8%) and Psocoptera (11.5%). In terms of biomass, the majority of trapped arthropods were Diptera (58.4%), followed by Coleoptera (15.0%) and Hymenoptera (13.0%). There were no significant differences in densities or biomass of any of the major insect groups among the treatments on any sample date (overall effect in all groups; P > 0.05; Wilk's lambda interaction in all groups; P > 0.05).

Abundance of Potential Prey on Foliage

Total abundance of arthropod prey on the foliage was positively correlated with needle abundance (Fig. 3.3). On all collecting dates, significantly lower densities of arthropods were collected from branches with reduced needle density compared with control branches (overall mean; F = 216.33; df = 2, 55; P = 0.0001). The magnitude of treatment differences varied with time (Wilk's lambda interaction term; F = 2.35; df = 6, 106; P = 0.0358). The spectrum of prey groups on foliage in the needle density treatments was dominated by Psocoptera (58.9%), Collembola (18.1%) and Aphidoidea (11.8%). In terms of biomass, Psocoptera (43.0%), Coleoptera (13.7%) and Lepidoptera



Figure 3.3 Mean densities (\pm SE) of potential spider prey organisms on Douglas-fir foliage in needle density treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.4. Mean densities (\pm SE) of potential spider prey organisms on Douglas-fir foliage in branching complexity treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).

(9.7%) were the dominant groups of potential prey on foliage. The highest densities of Psocoptera were associated with control branches (Fig. 3.3). Their abundance peaked in early September and declined in late October. Similarly, Collembola responded strongly to the removal of needles, and their densities decreased as much as 29-fold in patchy branches compared to control in late October (Fig. 3.3).

Arthropods responded strongly to the varying level of branching complexity (overall mean; F = 77.43; df = 2, 57; P = 0.0001). Significantly higher densities of total prey organisms per unit of habitat (gram of total plant material) were associated with tied branches in comparison with thinned and control branches (Fig. 3.4). In addition, thinning significantly reduced numbers of potential prey compared to control. The treatment differences were dependent on the sample date (Wilk's lambda interaction term; F = 17.62; df = 6, 110; P = 0.0001). In terms of abundance, the spectrum of prey in the branch complexity treatments was dominated by Collembola (42.9%), Psocoptera (40%) and Aphidoidea (9.5%). In terms of biomass, Psocoptera (35.9%), Coleoptera (18.3%) and Lepidoptera (10.2%) were the most common orders of arthropods on foliage. Psocoptera densities were not significantly different between control and tied branches, but their densities were significantly reduced by thinning. Similarly, Collembola avoided thinned branches but also responded strongly to the increased complexity of tied branches, and their abundance was as much as 7-fold higher in tied branches compared to control in late October (Fig. 3.4).

Abundance of Spiders

Estimates of total spider densities (numbers per branch) before the application of treatments were not significantly different among the treatment groups (F = 0.88; df = 4, 95; P = 0.482). After accounting for prey abundance, the densities of spiders varied significantly with the complexity of habitat (Table 3.1). The highest densities of web-building spiders were recorded in control branches, and their lowest densities were associated with needleless branches. Similar trends were detected in all major groups of web-building spiders (Fig. 3.5). Significantly fewer hunting spiders were collected from

Date	Parameter	Needle density		Branching complexity		Needle density		Branching complexity	
		<i>F</i> (df)	Р	<i>F</i> (df)	P	<i>F</i> (df)	Р	<i>F</i> (df)	Р
<u></u>		Hunting spiders			Web-building spiders				
6-Aug	Treatment ¹	48.28 (2,56)	< 0.001	19.75 (2,57)	< 0.001	24.59 (2,56)	< 0.001	6.80 (2,57)	0.002
	Prey	0.08 (1,55)	0.783	5.77 (1,56)	0.020	0.23 (1,55)	0.634	5.23 (1,56)	0.026
	Treatment adj ²	-	-	9.46 (2,56)	< 0.001	-	-	3.36 (2,56)	0.042
5-Sep	Treatment	38.43 (2,56)	< 0.001	22.48 (2,57)	< 0.001	32.33 (2,56)	< 0.001	9.47 (2,57)	< 0.001
	Prey	0.10 (1,55)	0.754	< 0.01 (1,56)	0.993	4.52 (1,55)	0.038	12.16 (1,56)	0.001
	Treatment adj	-	-	-	-	7.24 (2,55)	0.002	2.26 (2,56)	0.113
2-Oct	Treatment	20.16 (2,55)	< 0.001	21.42 (2,57)	< 0.001	35.85 (2,55)	< 0.001	9.25 (2,57)	< 0.001
	Prey	5.12 (1,54)	0.028	7.26 (1,56)	0.009	0.40 (1,54)	0.532	4.26 (1,56)	0.044
	Treatment adj	2.85 (2,54)	0.067	5.18 (2,56)	0.009	_	-	1.77 (2,56)	0.180
22-Oct	Treatment	18.60 (2,56)	< 0.001	3.93 (2,57)	0.025	23.20 (2,56)	< 0.001	12.39 (2,57)	< 0.001
	Prey	1.02 (1,55)	0.317	6.21 (1,56)	0.016	6.52 (1,55)	0.014	2.79 (1,56)	0.090
	Treatment adj	-	-	0.42 (2,56)	0.660	6.60 (2,55)	0.003	-	-

Table 3.1. ANOVA of the abundance of hunting and web-building spiders in needle density and branching complexity treatments

¹ Covariate. ² Treatment effects adjusted for the effect of covariate. - No adjustement of treatment effects (covariate; P > 0.05).



Figure 3.5. Mean densities $(\pm SE)$ of web-building spiders on Douglas-fir foliage in needle density treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.6. Mean densities (\pm SE) of hunting spiders on Douglas-fir foliage in needle density treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).


Figure 3.7. Mean densities (\pm SE) of web-building spiders on Douglas-fir foliage in branching complexity treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.8. Mean densities (\pm SE) of hunting spiders on Douglas-fir foliage in branching complexity treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).

branches with partial and total removal of needles if compared with control branches in early August and September (Fig. 3.6). This trend was similar for all major groups of hunting spiders.

Web-building spiders did not appear to be affected by the branch complexity early in the experiment. Significant differences, however, were recorded in late October (Fig. 3.7). This was mostly due to an increased abundance of theridiids and linyphiids in tied and control branches. These spiders also appeared to avoid thinned branches in the late season. On the other hand, densities of orb weavers decreased with increasing complexity of habitat towards the end of the season.

Densities of hunters increased in tied and control branches, whereas fewer spiders were collected from thinned branches (Fig. 3.8). Nocturnal hunters did not discriminate between control and thinned branches but appeared to prefer tied branches.

Spider Diversity and Community Structure

The removal of needles had a strong negative effect on spider species richness (Table 3.2). On all collecting dates, the highest number of species (mean \pm SE; 3.30 ± 0.33 to 5.55 ± 0.49) was recorded in control branches, whereas only $0.65 (\pm 0.18)$ to $1.2 (\pm 0.22)$ species were found on branches with a complete removal of needles (Fig. 3.9). Similarly, significantly lower species diversity was recorded in branches with patchy and complete removal of needles. Significantly more species of spiders colonized the more complex tied branches and significantly fewer species were collected from thinned branches when compared with the control (Table 3.2, Fig. 3.10). Similarly, on all collecting dates, the spider diversity was positively correlated with the complexity of the habitat. On the other hand, evenness followed a reversed trend; its values tended to decrease with the increasing complexity of habitat (Fig. 3.9, 3.10). There were no significant correlations between any of the parameters of spider diversity and the abundance of prey on foliage within individual treatments on any sample date (P > 0.05).

Spider community structure was significantly affected by changes in the habitat structure in both groups of treatments (Table 3.3). There was a gradual decrease in the relative abundance of web-building spiders with increasing complexity of habitat structure

Date		Needle d	lensity	Branching complexity			
	Parameter	F (df)	Р	<i>F</i> (df)	Р		
6-Aug	S	46.23 (2, 57)	< 0.001	80.47 (2, 57)	< 0.001		
_	H'	11.81 (2, 39)	< 0.001	24.18 (2, 52)	< 0.001		
	Ε	3.91 (2, 39)	0.028	11.53 (2, 52)	< 0.001		
5-Sep	S	35.84 (2, 57)	< 0.001	51.96 (2, 57)	< 0.001		
	H'	8.46 (2, 40)	0.001	19.35 (2, 54)	< 0.001		
	Ε	5.64 (2, 40)	0.007	17.28 (2, 54)	< 0.001		
2-Oct	S	33.51 (2, 57)	< 0.001	41.94 (2, 57)	< 0.001		
	H'	16.73 (2, 38)	< 0.001	38.19 (2, 54)	< 0.001		
	Ε	0.95 (2, 38)	0.396	6.92 (2, 54)	0.002		
22-Oct	S	32.57 (2, 57)	< 0.001	36.97 (2, 57)	< 0.001		
	H'	4.27 (2, 21)	0.028	15.56 (2, 45)	< 0.001		
	Ε	0.68 (2, 21)	0.516	10.66 (2, 45)	< 0.001		

Table 3.2. ANOVA of spider species richness (S), diversity (H') and evenness (E) in needle density and branching complexity treatments.

Table 3.3. G-test analysis of the similarity in the community structure of spiders in needle density and branching complexity treatments.

	Needle de	nsity	Branch complexity			
Date	G (df)	P	G (df)	Р		
6-Aug	25.77 (8)	0.002	18.14 (10)	0.070		
5-Sep	21.37 (10)	0.023	48.98 (12)	< 0.001		
2-Oct	29.99 (8)	< 0.001	57.91 (12)	< 0.001		
22-Oct	17.91 (6)	0.010	18.73 (8)	0.020		



Figure 3.9. Mean parameters of spider diversity (\pm SE) on Douglas-fir foliage in needle density treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.10. Mean parameters of spider diversity (\pm SE) on Douglas-fir foliage in branching complexity treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.11. Relative abundance of spider groups on Douglas-fir foliage in needle density and branching complexity treatments. Numbers above columns indicate absolute densities of spiders collected in individual treatments. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups. Data from all collecting dates are plotted together.

(Fig. 3.11). Almost 80% of spiders colonizing needleless branches were orb weavers. Their relative abundance gradually declined in patchy and control branches. The community of spiders in control branches was dominated by sheet-web weavers of the families Linyphiidae and Micryphantidae. Among hunting spiders, total removal of needles led to a decline in the representation of agile hunters and nocturnal hunters dominated by the Clubionidae. Similar changes in the community structure of webbuilding spiders resulted from thinning and tying of treatment branches. Araneidae and Tetragnathidae dominated the spectrum of web-building spiders in thinned branches but were gradually replaced by sheet-web weavers in control and tied branches. Changes in the branching complexity of habitat did not appear to have a strong effect on the community structure of hunting spiders. One exception was a significant increase in the representation of nocturnal spiders in structurally complex tied branches (Fig. 3.11).

		Needle de	ensity	Branching complexity		
Date	Group	F (df)	Р	<i>F</i> (df)	Р	
6-Aug	Agile hunters	1.22 (3,20)	0.310	9.50 (2,49)	0.0003	
	Sheet-web spiders	0.07 (2,26)	0.928	4.48 (2,44)	0.017	
	Total spiders	1.67 (2,51)	0.198	2.75 (2,56)	0.070	
5-Sep	Agile hunters	4.24 (2,27)	0.025	0.94 (2,41)	0.399	
-	Sheet-web spiders	3.73 (2,27)	0.037	3.04 (2,47)	0.057	
	Total spiders	3.29 (2,51)	0.045	3.56 (2,56)	0.035	
2-Oct	Agile hunters	. 0.24 (2,16)	0.791	3.92 (2,32)	0.030	
	Sheet-web spiders	0.33 (2,28)	0.722	4.20 (2,44)	0.021	
	Total spiders	0.48 (2,47)	0.620	4.06 (2,57)	0.023	
22-Oct	Agile hunters	0.66 (1,5)	0.453	0.84 (1,9)	0.385	
	Sheet-web spiders	0.93 (2,22)	0.408	6.12 (2,39)	0.005	
	Total spiders	0.67 (2,39)	0.515	0.48 (2,54)	0.622	

Table 3.4. ANOVA of the mean body length of spiders in needle density and branching complexity treatments.

There was no clear effect of needle density on the average body size of total spiders (Table 3.4). As an exception, significantly larger spiders were collected in control than in patchy branches in early September. Needle density did have a slight effect on body size of the two most abundant spider groups (Fig. 3.12). Significantly larger agile hunters colonized needleless branches as compared with patchy branches, but larger sheet-web spiders were collected in control branches as compared with patchy branches in early September. Branching complexity appeared to have a stronger effect on body size of spiders than needle density (Table 3.4). Smaller spiders colonized thinned branches in early September, and larger spiders were found in tied branches than in control in early October (Fig. 3.13). After each sampling, significantly larger agile hunters tended to



Figure 3.12. Mean body length (\pm SE) of spiders on Douglas-fir foliage in needle density treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).



Figure 3.13. Mean body length (\pm SE) of spiders on Douglas-fir foliage in branching complexity treatments. Bars within a day followed by the same letter are not significantly different (LSD; P < 0.05).

recolonize more complex tied branches, and this trend was significant in early August and October. Similarly, the average body size of sheet-web spiders was positively affected by the increasing complexity of tied branches (Fig. 3.13).

Discussion

Abundance of Potential Prey

As indicated by sticky trap catches, the densities and biomass of flying insects were not significantly different among the treatments on any sample date. This suggests that alterations of habitat structure did not result in significant changes of the visual or olfactory attractiveness of foliage to flying organisms. Consequently, the availability of potential spider prey in the air volume enveloping the foliage was the same regardless of the treatment. This suggests that observed changes in the abundance of spiders reflected changes either in their habitat or changes in the availability of prey on the foliage, or both.

The term "plant architecture" was originally proposed by Lawton (1978) and Lawton and Schröder (1977) to cover a wide array of plant attributes such as size, design and structural complexity. Two main components of plant architecture include the size and the variety of above-ground parts (Lawton 1983). The size hypothesis predicts that larger plants (or habitats) are more likely to be discovered and colonized by arthropods, and consequently they support larger populations and a greater diversity of species (Lawton 1978, 1983). In addition, generally larger habitats have higher colonization and lower extinction rates (MacArthur and Wilson 1967). The resource diversity hypothesis predicts that plants (or habitats) with a greater variety of structural or resource types (e.g. resting, sexual display, escape and feeding sites) are more superior habitats supporting a greater abundance and diversity of arthropods (Lawton 1978, 1983).

The removal of needles resulted in a loss of feeding substrate and altered the microhabitat of branches and their attractiveness to arthropods. Lower densities of prey per gram of wood biomass indicate that the density of needles was a major determinant of their abundance on foliage. Since the abundance of potential flying colonizers did not vary

significantly among the treatments, differences in the abundance of arthropod prey on foliage may reflect differences in their retention rates among individual habitat types.

Abundance of arthropods was expressed as numbers per gram of wood biomass, a part of the habitat which was left unaltered in this group of treatments. Although this approach allows a test of the significance of the presence or absence of needles to arthropods, it poses a problem in ferreting out the possible mechanism. For example, higher densities of arthropods in control branches, if compared to patchy branches, may reflect the disparity in the amount of surface area sampled between the two treatments (size per se hypothesis). On the other hand, the presence of needles may affect the branch microclimate, provide food and shelter and thus improve the quality of the habitat (resource diversity hypothesis). The presence of some habitat features such as dead thatch has been implicated as an important factor affecting the quality of habitat for arthropods in salt marsh grass systems (Davis and Gray 1966, Denno 1977, Döbel et al. 1990). For example, Denno (1977) found lower abundance and diversity of some species of sapfeeding insects in the thatch-free grass Spartina alternifolia in comparison with thatchforming grass S. patens, which he attributes to the availability of suitable feeding, oviposition and hiding sites provided by the thatch. Similarly, an experimental removal of thatch from plots with S. patens led to a decrease in the abundance and diversity of resident sap-feeders (Denno 1977).

Densities of prey per gram of total branch biomass were lower in thinned branches but increased in tied branches when compared with control. This strongly suggests that the quality of habitat was influenced by simply decreasing or increasing its structural complexity. For example, the abundance of Collembola was almost 8-fold higher in tied branches compared with control (Fig. 3.4). This suggests that a simple doubling of the habitat size (tying two branches together) had a profound effect on its quality. Similar to needle density, increased complexity of habitat may provide a more favorable microclimate and a greater protection from natural enemies. It may also indirectly affect the availability of food resources for those organisms that do not feed directly on the plant tissue. For example, Halaj and Moldenke (unpublished data) have documented fall migrations of Collembola from forest litter into Douglas-fir canopies. Similarly, in this study there was a

dramatic increase in the abundance of these organisms in control branches in October (Fig. 3.4). Collembola may have responded to a greater availability of algae and bacteria growing on needles during the wet fall and winter months. It is plausible that tying two branches together may increase the humidity of the habitat, enhance the growth of algae and bacteria and, consequently, attract a greater abundance of grazers.

Abundance of Spiders

Spiders responded negatively to the removal of needles. This trend was similar for all major spider groups (Fig. 3.5, 3.6). The treatment effects were generally significant even after adjusting for the presence of arthropod prey on the foliage. This adjustment, however, lowered the treatment differences, and in some cases resulted in non-significant treatment effects (Table 3.1). This result underscores the importance of monitoring the second trophic level when studying spider-habitat interactions.

The results of this experiment are similar to studies conducted with Norway spruce suggesting the importance of needle density as an important factor affecting the abundance of arboreal spiders (Gunnarsson 1988, 1990, Sundberg and Gunnarsson 1994). Gunnarsson (1988) compared densities of foliage-dwelling spiders between two spruce stands of different needle densities. He found lower abundance of larger spiders (>2.5mm) on needle-sparse branches. However, the total densities of spiders and densities of dominant spider groups were not affected by the loss of needles. As an exception, densities of orb weavers were higher on branches with lower density of needles, which is not paralleled by my findings (Fig. 3.5). Subsequent studies in natural communities involving experimental removal of needles revealed negative effects of low needle density on the total abundance of spiders (Gunnarsson 1990, Sundberg and Gunnarsson 1994). Unfortunately, possible effects of habitat manipulations on potential spider prey were not monitored in these studies.

It has been suggested that lower abundance of spiders in needle-sparse branches can be due to a greater exposure of these predators to their natural enemies such as birds (Gunnarsson 1988, 1990, Sundberg and Gunnarsson 1994). It is a plausible hypothesis in light of the fact that Askenmo et al. (1977) and Gunnarsson (1983) experimentally documented the importance of bird predation as a significant mortality factor in spruceinhabiting spiders. The importance of bird foraging on arboreal spiders, and the importance of habitat structure as a mediator of these interactions in Douglas-fir, remains to be tested.

The removal of needles simplified the complexity of habitat and presumably altered its microclimate. It is plausible that spiders responded negatively to these changes. In a series of choice tests, Gunnarsson (1990) demonstrated a preference of several spider families for branches with regular needle density over needle-sparse branches. The experiments were performed under controlled laboratory conditions (plastic terraria) with the absence of natural prey and enemies. The outcome of that experiment supports the hypothesis that spiders prefer regular branches due to their more favorable microclimatic conditions. On the other hand, the preference for unaltered branches may have represented an innate or learned response of spiders to a habitat type offering increased densities of prey or providing a greater protection from natural enemies.

One of the qualitative attributes of needle density is the provision of sites for construction of retreats. All groups of hunting spiders in this study construct retreats, which they use for resting, molting or deposition of egg sacs (Halaj, personal observation). The removal of needles and a patchy appearance of branches may decrease the availability of suitable sites for retreat construction. This suggested function of foliage may also account for the presence of positive significant correlations between the biomass of needles and the abundance of agile and nocturnal hunters in western hemlock and Douglas-fir (Table 2.5, Chapter 2). Similarly, Döbel et al. (1990) suggest that the presence of grass thatch provides suitable retreat-building sites and thus increases the habitat quality for a gnaphosid, *Zelotes pullis*.

Spider densities increased in structurally more complex tied branches but decreased in simpler thinned branches when compared with the control. These effects, however, were not as pronounced as those resulting from the reduction of needle density. Web-building spiders as a group avoided thinned branches but the addition of structural complexity (tied branches) generally did not significantly increase their densities (Fig. 3.7). The exception was a high density of web-builders in tied branches in late October. This was mostly due

to an increase in the abundance of theridiids in the sample. However, the adjustment for the effect of prey eliminated treatment effects detected in early September and October (Fig. 3.7, Table 3.1). Despite a trend indicating higher densities of some spider groups in tied branches, increased variability of the data did not allow detection of a significant difference. Hatley and MacMahon (1980) documented increased densities of web-building spiders in structurally more complex tied *Artemisia* shrubs. The preference of tied shrubs by web-builders in their study may have reflected the functional composition of this group. Over 50% of their web-builders were cobweb spiders of the genus *Theridion*, spiders that require structurally more complex environment for the construction of their irregular mesh webs. Similarly Robinson (1981) documented a preference of *Theridion* species for experimental modules with a high density of jute strands. Web-building spiders in this study were dominated by orb weavers and sheet-web spiders. These spiders construct simpler webs, and additional habitat complexity may not be critical for their web construction, and in fact may impede it. In October, orb weavers even tended to prefer structurally simpler thinned branches (Fig. 3.7).

Thinning had a negative effect on the total abundance of hunting spiders in early August and September. On the other hand, hunting spiders were generally more numerous in tied branches. This trend was especially pronounced in early September and October (Fig. 3.8). Densities of agile hunters tended to be higher in this habitat type, although this increase was not significant, likely due to high variability of the data. There was, however, a significant increase in the number of nocturnal hunters in tied branches (Fig. 3.8). This supports findings of Hatley and MacMahon (1980) who reported higher densities of these spiders in tied *Artemisia* shrubs. Hatley and MacMahon (1980) suggest that clubionids select structurally more complex tied shrubs because of a greater availability of retreat-building sites in this habitat. It appears then that an increased needle density and branching complexity may be important in the selection of suitable retreatbuilding sites in nocturnal hunting spiders.

Similar to needle density, increased branching complexity may also provide better protection for spiders against natural enemies or competitors. Contrary to trends displayed by web-builders, hunting spiders appeared to respond more strongly to the increased complexity of tied branches. Hunters actively search the foliage for food and may be more susceptible to detection by their natural enemies. For example, in Douglasfir canopies hunting spiders are more likely to suffer from interference competition with ants than web-building spiders (Chapter 4).

Spider Diversity and Community Structure

The removal of needles resulted in significant changes in the community composition of spiders. The community in needleless branches was skewed towards web-building spiders (78%), and orb weavers alone accounted for 60% of all spiders in this habitat type (Fig. 3.11). It has been suggested that provision of web-building sites is one of the critical factors responsible for higher abundance of spiders in structurally more complex habitats (Hatley and MacMahon 1980, Robinson 1981). These data suggest that even structurally simple habitats can be colonized by web-building spiders. For example, orb weavers dominated the spider community in needleless branches (Fig. 3.11), but absolute density of orb weavers decreased with decreasing density of needles (Fig. 3.5). Therefore, the dominance of this spider group in needleless branches should be interpreted as a tolerance of, rather than preference for, this habitat type. On several occasions, I also commonly observed small orb weavers colonizing needleless branches of dead trees at the study site. There are several reasons why this group of spiders may be well-suited for colonizing needleless branches. First, the quality of a branch to anchor a simple orb web does not appear to bear any strong relationship to the presence or absence of needles. The removal of needles leaves the basic structure (branching complexity) of the branch unaltered. providing sufficient substrate for the construction of their webs. On the other hand, I had observed that juvenile linyphilds and theridiids used needles as a support for their webs. Second, a great majority of orb weavers colonizing needleless branches were immature Araniella displicata (Hentz), with web diameters less than 7 cm. I observed that small orb weavers were foraging in their typical sit-and-wait position in the center of the web, and used short remains of needles on twigs for concealment. Due to their small size, this group of spiders was probably able to tolerate the reduction in the number and size of hiding places, and consequent exposure to natural enemies following the removal of

needles. Finally, orb weavers are more active foragers than other groups of web-building spiders. Due to their ability to ingest their old webs, they invest less energy per mg body weight to construct a new web (Janetos 1982a,b). Consequently, this flexibility may allow them to temporarily exploit even less suitable foraging sites.

In contrast, the relative abundance of sheet-web spiders and theridiids decreased in needleless branches and addition of needles resulted in an increase in the relative and absolute abundance of these spiders on the foliage (Fig. 3.5, 3.11). These spiders construct more complex webs, and their preference for more complex habitat may reflect this requirement. Lower density of needles leads to a decrease in the relative abundance of agile and nocturnal hunters on foliage. I have observed that both groups of spiders construct retreats among needles. In addition, their active foraging mode can make them more conspicuous to visual predators such as birds in needleless branches.

Alterations of branching complexity resulted in similar changes in spider community structure. Orb weavers dominated the community of spiders in thinned branches, which may again reflect their ability to tolerate structurally simpler habitats. Addition of branching angles (tied branches) led to an increase in dominance of sheet-web spiders, and agile and nocturnal hunters.

Spider species richness and diversity were positively correlated with increasing needle density and branching complexity. Interestingly, the evenness component of diversity was negatively correlated, with more complex habitats having the lowest equality of species abundance (Fig. 3.9, 3.10). The high evenness detected in simple habitat types such as needleless and thinned branches was mostly due to the low densities of individuals in these treatments, and the fact that the number of individuals was usually equal to the number of species. On the other hand, although control and tied branches contained a greater number of species including a jumping spider, *Metaphidippus aeneolus* Curtis, and two linyphiids, *Pityohyphantes rubrofasciatus* Keyserling and *P. costatus* (Hentz). A greater species richness and diversity detected in structurally more complex treatments may have reflected a greater variety of available resources (types of feeding sites, heterogeneity of oviposition and hiding places) and/or a more suitable microclimate (temperature.

humidity) in these habitats. However, a greater number of species in more complex habitat may also be interpreted as a species-area relationship, reflecting the inequality in the sample size of individuals collected in different treatments. Another explanation for the increase in spider diversity in a more complex environment could be the increased abundance of prey. However, although the abundance of prey increased with the complexity of habitat, the analyses did not detect any significant correlations between spider diversity and prey densities within individual treatment groups. This suggests that the prey abundance was not likely to be responsible for observed differences between individual treatments (Sokal and Rohlf 1995). These findings support the conclusions of Greenstone (1984) that the role of vegetation structural heterogeneity is the main determinant of web spider species richness and diversity. Greenstone (1984) detected high correlations between the spider species richness and diversity, and vegetation tip height diversity at several sites in California and Costa Rica. Similar to my results, the abundance of available prey in his study did not prove to be a significant predictor of spiders species richness or diversity. Uetz (1975) found significant correlations between the species richness and diversity of litter-dwelling spiders and some structural aspects of their habitat (litter depth and a measure of habitat space). Spatially, the abundance of prey, moisture and temperature were not correlated with the parameters of spider diversity in his study. Abraham (1983) found strong correlations between spider species richness and various measures of herb stratum habitat diversity, but the abundance of prey was not monitored in this study.

With the exception of samples collected in early September, there were no significant differences in the average body size of spiders between the treatments (Fig. 3.12). Similarly the needle density in spruce does not appear to affect the body size of spiders (Gunnarsson 1988, 1990, Sundberg and Gunnarsson 1994). But it was found that larger spiders did tend to be associated with more complex tied branches (Fig. 3.13). Spider mortality due to bird predation has been shown to be body-size dependent (Askenmo et al. 1977, Gunnarsson 1983). In both studies, the experimental exclusion of foraging birds had a greater positive effect on the survival of larger (> 2.5 mm) than smaller spiders. If one of the factors affecting the habitat selection of spiders in Douglas-fir canopies is the

protection against their natural enemies, one might expect larger spiders in habitats providing the greatest protection. The results of this study indirectly support this hypothesis.

Conclusions

This study experimentally demonstrated the importance of needle density and branching complexity of Douglas-fir foliage on the abundance and community organization of arboreal spiders. Since the availability of potential flying prey in the vicinity of treatment branches was the same regardless of the treatment, it appears that observed changes in the spider population can be attributed to changes in the complexity of their habitat and/or the availability of prey present on the foliage. Both spiders and their prey positively responded to the increasing complexity of their habitat. Significant correlations between the densities of spiders and potential prey on foliage suggested that spiders responded to an increased availability of prey on the foliage. Nevertheless, the overall response of spiders to habitat alterations remained significant even after adjusting for the presence of their prey. 4. Negative Effects of Ant Foraging on Spiders in Douglas-fir Canopies

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Submitted to Oecologia

4. NEGATIVE EFFECTS OF ANT FORAGING ON SPIDERS IN DOUGLAS-FIR CANOPIES

Abstract

This study tested the effect of foraging by *Camponotus* spp. ants on spider assemblages in Douglas-fir canopies in a 5-month exclusion experiment. Ants were excluded from canopies with sticky bands applied to tree trunks. Biomass of potential prey organisms, dominated by Psocoptera, increased significantly by 1.9 to 2.4-fold on the foliage following ant exclusion. The removal of ants did not affect the abundance of flying arthropods in the vicinity of tree canopies as indicated by sticky trap catches. Hunting spiders increased significantly by 1.5 to 1.8-fold in trees without ants in the late summer. The exclusion of ants did not affect the abundance of web-building spiders, nor did it significantly influence spider species richness and diversity. Ant removal had a slight effect on the spider guild structure; the relative abundance of hunting spiders in ant-free canopies increased by 8.0 and 9.3% in late August and September, respectively. The majority of prey captured by ants were Aphidoidea (48.1%) and Psocoptera (12.5%); spiders represented only 1.4% of the ants' diet. The dominant prey groups of webbuilding spiders were Psocoptera (41.4%) and adult Diptera (31.3%). Diets of ants and web-building spiders overlapped substantially. About 40% of observed ants were tending Cinara spp. aphids. Foraging ants behaved aggressively toward other arthropods on foliage. It is suggested that treatment differences may be due to interference competition between hunting spiders and ants resulting from ant foraging and aphid-tending activities. Direct predation of spiders by ants appeared to be of minor importance in this study system.

Introduction

Ants and spiders are among the most ubiquitous and diverse predators in terrestrial ecosystems. Many species share the same trophic level and can potentially compete with and prey upon each other (Wise 1993).

Although high rates of predation by ants upon ground-dwelling spiders have been reported (Petal and Breymeyer 1969, Kajak et al. 1972), most observational studies have found no significant differences in densities of spiders between areas of high and low ant foraging activity (Otto 1965, van der Aart and de Wit 1971, Brüning 1991). As an exception, Cherix and Bourne (1980) reported lower densities of wolf spiders and a lower spider species richness within a super-colony of *Formica lugubris* Zett. Exclusion experiments in pastures with red imported fire ants, *Solenopsis invicta* Buren, revealed only slight negative effects of ant foraging on two species of hunting spiders (Lycosidae and Clubionidae) (Howard and Oliver 1978). Similar experiments with the same species of fire ants conducted in a cotton field in Texas failed to detect any changes in spider densities in ant-removal plots (Sterling et al. 1979). At present, clear experimental evidence on the significance of competition and direct predation between spiders and ants is lacking (Wise 1993).

Spiders and ants are the most abundant predatory arthropods in the canopies of coniferous forests in the northwestern United States (Dahlsten et al. 1977, Campbell et al. 1983, Moldenke et al. 1987, Schowalter 1989). Carpenter ants, *Camponotus* spp., which are abundant and widespread foragers in Douglas-fir canopies, prey on a number of insect defoliators (Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984). Research conducted in 1992 in western Oregon showed lower densities of arboreal spiders at sites which had higher densities of foliage-foraging *Camponotus* ants (Halaj, unpublished data). However, the impact of ant foraging on arboreal spider communities remains unknown.

The objective of this study was to determine whether or not exclusion of ants affected spider assemblages in Douglas-fir canopies. In view of the documented impact of ant foraging on some insects in Douglas-fir canopies (Campbell and Torgersen 1982,

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Campbell et al. 1983), I hypothesized that removing ants would have a positive effect on the abundance of spiders in the canopy.

Materials and Methods

Study Area

The study was conducted at the H. J. Andrews Experimental Forest, within the Willamette National Forest in the Western Cascade Province of Oregon, USA. This province is characterized by wet winters, warm and dry summers, and mild temperatures throughout the year. The annual precipitation is approximately 230 cm, with the majority of precipitation occurring between November and March. Mean annual temperature for the province is 7.9 °C (Taylor and Bartlett 1993).

The study site was in a young plantation of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, with occasional western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, and western redcedar, *Thuja plicata* D. Don., at an elevation of 800 m. The ground vegetation included dense patches of bracken fern, *Pteridium aquilinum* (L.) Kuhn in Decken, salal, *Gaultheria shallon* Pursh, fireweed, *Epilobium angustifolium* L., and Pacific rhododendron, *Rhododendron macrophyllum* D. Don ex G. Don. The site contained large amounts of coarse woody debris, which provided excellent nesting sites for carpenter ants.

Study Design

The study design was a completely randomized block, with two treatments randomly assigned to a total of 30 young Douglas-fir trees (< 15-years-old; < 10 m tall). Ants were excluded from 15 trees with 50-cm-wide sticky barriers of Tanglefoot[®] (Tanglefoot Co., Grand Rapids, Michigan, USA) applied to the base of tree trunks on May 15, 1994 (hereafter referred to as "ant-free" trees). The vegetation that was surrounding trees was cleared to prevent dispersal of ants into the canopies. An equal number of trees was left untreated to serve as controls.

Arthropod Sampling

Within each tree, 1-m-long tips of three randomly selected branches from the lower third of the canopy were sampled. Branches selected for sampling were permanently marked with a short strip of plastic ribbon. Arthropods were sampled by beating branches with a plastic rod over a hand-held drop cloth. All arthropods dislodged onto the drop cloth were collected with a portable battery-powered vacuum collector (Paul and Mason 1985) and preserved in 75% ethanol. To assess the initial conditions in the study system (Hairston 1989), all trees were sampled on May 12, 1994, before the exclusion of ants. Beginning six weeks after the exclusion of ants, trees were sampled five times at 1-month intervals.

The abundance of actively flying and drifting arthropod prey at the study site was determined with a series of sticky traps. Traps were Tanglefoot[©]-coated sheets (180 x 270 mm) constructed of a clear, rigid plastic mesh, with a grid size of 2×2 mm. In each treatment, traps were assigned to ten randomly selected trees. Each trap was attached to a wooden stick using two push pins and was positioned vertically at a height of 170 cm above ground, approximately 1 m from the tree canopy. The cardinal direction from the tree at which the trap was positioned and the orientation of the trap were determined randomly. The traps were exposed in the field for 48 hours during each monthly sampling period.

In the laboratory, captured arthropods other than spiders were sorted to order, and spiders were sorted and identified to species when possible. The body length of spiders was measured to the nearest 0.05 mm (excluding chelicerae and spinnerets); body length of other arthropods was measured to the nearest 0.5 mm. The biomass of all arthropods was estimated with body-length based regression models developed by Rogers et al. (1976, 1977) and Halaj and Moldenke (unpublished data). To describe the spider community structure, hunting and web-building spiders were further divided into categories based on their foraging strategies (Chapter 2; Materials and Methods).

Predator Foraging and Diets

Foraging behavior of predators was observed on treatment branches at three to four week intervals between June and October 1994. On each date, between 8:00 and 17:00, approximately 2 minutes were spent observing each branch. The species of foraging ants and spiders, their prey organisms, their mutual interactions and frequencies of aphid-tending by ants were recorded. Prey-carrying ants and spiders were collected and preserved in 75% ethanol.

Additional behavioral and dietary data on ants and spiders were collected at the same site at two to three week intervals between June and September 1995. The foliage and trunks of young Douglas-fir trees selected haphazardly along 100-m-long transects were searched for predators. Data were collected as in 1994. In addition, the composition of the diet of web-building spiders was assessed. All trapped insects and the resident spiders were removed from webs located in the lower third of Douglas-fir canopies and preserved in 75% ethanol.

Due to low frequencies of prey-carrying ants in the canopy in 1994, additional information on the ants' diet was collected by observing them at their nests. Three colonies (built in old tree stumps) were sampled of the most common canopy forager, *Camponotus laevigatus* (Smith). Workers carrying prey organisms to the nest were collected with an aspirator and preserved in 75% alcohol. Nests were monitored for a total of 14.1 hours on ten dates between July 4 and September 14, 1995.

Data Analyses

Data obtained from individual branches of each treatment tree were averaged before analyses. Treatments were compared using estimates of arthropod densities per branch. Since the same trees and branches were sampled over time, the data were analyzed with repeated-measures ANOVA. Means were compared and separated by Fisher's protected least significant difference (LSD) test (Steel and Torrie 1980). In order to satisfy the assumption of homogeneous variance in ANOVA, variables were transformed to $\ln(Y)$, $\ln(Y+1)$ or $\ln(Y+0.01)$ as appropriate prior to all analyses. In all cases, original means and standard errors are reported. Diversity of spider populations was defined by the Shannon diversity index (H') (Pielou 1975). Body-size frequency distributions of arthropods were compared with the Kolmogorov-Smirnov two-sample test. The G-test of independence with the Williams' correction was used to determine similarities in the community structure of spiders and similarities in taxonomic composition of arthropod diets (Sokal and Rohlf 1995). Taxonomic and body-size overlap between diets of spiders and ants was calculated with the formula in Schoener (1968). All statistical analyses were performed with SAS computer programs (SAS Institute Inc. 1994).

Results

Abundance of Potential Prey

The biomass of arthropod prey on foliage did not differ between the two groups of trees in pretreatment samples (F = 0.01; df = 1,27; P = 0.91). Following the exclusion of ants, the biomass of prey in ant-free trees was significantly higher than in the controls, (overall mean; F = 22.98; df = 1,27; P < 0.001), reaching a 2.4-fold difference between the treatments in late August (F = 18.56; df = 1,27; P < 0.001) (Fig. 4.1A). Differences between the treatments were dependent on sample dates (interaction effect; F = 9.52; df = 4,108; P < 0.001). The increase in number of prey was mostly due to an increase in the abundance of barklice, Psocoptera, which were the most common arthropods on foliage, accounting for about 56.7% and 66.5% of biomass of prey in control and ant-free trees, respectively. The most abundant psocid species were *Teliapsocus conterminus* (Walsh) and *Caecilius* spp. Also a significantly larger biomass of arthropod prey was recorded in control trees in late October (F = 7.56; df = 1,27; P = 0.011). This was largely due to a substantial increase in the number of Collembola migrating from the forest litter into the tree canopies. Their low numbers in ant-free trees were likely due to the presence of sticky barriers on tree trunks.

There were no differences in the biomass of flying arthropods in the vicinity of control vs. ant-free trees (overall mean; F = 0.001; df = 1,18; P = 0.97). The abundance



Figure 4.1. Biomass of potential insect prey organisms collected (A) in foliage-beating samples and (B) on sticky traps. Bars indicate standard errors; *P < 0.05; **P < 0.01.

of flying arthropods peaked in late July and gradually declined (Fig 4.1B). The majority of trapped prey were Diptera, accounting for about 63% of the total biomass of flying insects.

Abundance and Diversity of Spiders

Densities of hunting and web-building spiders did not differ between treatments prior to exclusion of ants (F = 0.26; df = 1,27; P = 0.61, and F = 0.01; df = 1,27; P = 0.91, respectively). Following the exclusion of ants, the abundance of hunting spiders was significantly higher on ant-free trees (overall mean; F = 7.91; df = 1,28; P = 0.009). There was a significant interaction between treatment and sample date (F = 6.08; df = 4, 112; P = 0.001). Although the densities of hunting spiders increased steadily from late July, significantly higher densities in ant-free trees were recorded only in late August and September (F = 8.00; df = 1,28; P = 0.009, and F = 9.95; df = 1,28; P = 0.004, respectively) (Fig. 4.2A). Following subzero temperatures in early October, densities of hunters abruptly declined. Densities of web-building spiders were not significantly different between treatments on any sample date (overall mean; F = 0.11; df = 1,28; P = 0.748) (Fig. 4.2B).

As indicated by the Shannon index, there were no significant differences in spider species richness or diversity between control and ant-free trees on any sample date (Table 4.1). Ant removal had a slight effect on the spider guild structure; the relative abundance of hunting spiders in ant-free canopies increased by 8.0 and 9.3% in late August and September, respectively (Fig. 4.3). However, G-test analyses did not detect any significant differences in the spider community structure between the treatments (Table 4.2). The spider community was dominated by hunting spiders representing 59.6 and 65.3% of all spiders in pooled samples from control and ant-free trees, respectively (Fig. 4.3). About 70% of hunting spiders were agile hunters, the majority being jumping spiders *Metaphidippus aeneolus* Curtis. The majority of web-building spiders were sheetweb weavers of the families Linyphiidae and Micryphantidae. In addition, the exclusion of ants did not appear to have a strong effect on the body length of spiders (Table 4.3).



Figure 4.2. Number of (A) hunting spiders and (B) web-building spiders per 1-m branch tip collected in foliage-beating samples. Bars indicate standard errors; ** P < 0.01.

Ň		S			H'			E		
Date	Treatment	X (SE)	F (df)	P	X (SE)	F (df)	Р	X (SE)	F (df)	Р
28-Jun	Control Ant-free	4.53 (0.48) 4.53 (0.52)	< 0.01 (1,28)	1	1.24 (0.10) 1.19 (0.13)	0.08 (1,28)	0.782	0.86 (0.02) 0.80 (0.06)	0.70 (1,28)	0.410
30-Jul	Control Ant-free	4.60 (0.41) 4.73 (0.46)	0.05 (1,28)	0.831	1.31 (0.09) 1.27 (0.11)	0.07 (1,28)	0.794	0.90 (0.02) 0.86 (0.03)	0.79 (1,28)	0.380
27-Aug	Control Ant-free	5.13 (0.49) 5.87 (0.36)	1.46 (1,28)	0.237	1.42 (0.10) 1.51 (0.07)	0.62 (1,28)	0.437	0.89 (0.02) 0.87 (0.02)	1.17 (1,28)	0.289
24-Sept	Control Ant-free	4.87 (0.57) 6.00 (0.58)	1.96 (1,28)	0.173	1.27 (0.15) 1.49 (0.10)	1.48 (1,28)	0.233	0.77 (0.08) 0.86 (0.02)	1.29 (1,28)	0.267
29-Oct	Control Ant-free	3.00 (0.38) 2.53 (0.53)	0.51 (1,28)	0.481	0.93 (0.15) 0.93 (0.21)	< 0.01 (1,25)	0.9 8 6	0.77 (0.10) 0.66 (0.14)	0.45 (1,25)	0.506

Table 4.1. Mean values (\pm SE) for spider species richness (S), diversity (H'), and evenness (E) in control and ant-free trees. Statistics are results of one-way ANOVA tests for treatment differences on individual sampling dates.

	Guild con	position	Bod	Body size			
Date	G (df) ¹	Р	DN ²	Р			
28-Jun	10.24 (7)	0.18	0.28	0.28			
30-Jul	6.92 (6)	0.33	0.34	0.11			
27-Aug	9.40 (6)	0.15	0.32	0.16			
24-Sep	9.70 (5)	0.08	0.36	0.08			
29-Oct	8.14 (5)	0.15	0.5	0.003			
Pooled data	9.34 (7)	0.23	0.28	0.29			

Table 4.2. Similarities in the community structure and body size frequency distributions of spiders in control and ant-free trees.

¹ G-test of independence; ² Kolmogorov-Smirnov two-sample test.

One exception was a significantly smaller body size of hunting spiders in ant-free trees in late September. The body-size frequency distributions between the pooled specimens of control and ant-free trees were similar (Table 4.2). A suggestive difference (P = 0.08) in late September was due mostly to a greater abundance of spiders less than 2 mm long (66%) in ant-free trees. Larger spiders, measuring more than 3 mm, constituted only 10% of individuals in this treatment. On the other hand, the body-size distribution in control trees was bimodal, with only 53% of spiders measuring less than 2mm. Larger spiders (> 3mm) accounted for more than 20% of all individuals in this treatment. In late October, over 63% of spiders collected in control trees were less than 2 mm in length.



Figure 4.3. Relative abundance of spider groups on Douglas-fir foliage in control and ant-free trees. Numbers above columns indicate absolute densities of spiders collected in individual treatments. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups.

Diet Composition of Spiders and Ants

Out of 723 ants observed in the canopy over the two seasons, only 11 individuals were found carrying prey organisms (Table 4.4). One worker of *Camponotus modoc* Wheeler was observed carrying a fresh body of a male jumping spider, *M. aeneolus*.

Based on canopy observations, the most abundant foraging ant species was C. laevigatus (72.0%), followed by C. novaeboracensis (Fitch) (16.3%), Formica spp. (8.3%) and C. modoc (3.4%). About 40% of all ants were involved in aphid-tending activities with Cinara spp. The proportion of aphid-tending individuals was high in C. novaeboracensis (66.3%) and C. modoc (76.2%). On the other hand, workers of C. laevigatus and Formica spp. were more frequently observed actively foraging and fewer individuals were found tending aphids (31.2% and 33.3%, respectively).

A total of 216 prey organisms was collected from ant workers returning to the nests (Table 4.4). Despite the use of an aspirator in collecting ants, I was only 80 to 90% successful in removing the prey from the ants. The ants were very cautious and agile, and even a slight disturbance caused them to drop their prey and hide in the nearby vegetation. The most abundant prey organisms brought to the nest were Aphidoidea (48.1%), followed by Psocoptera (12.5%) and Lepidoptera larvae (6.0%) (Table 4.4). Only three spiders (two lycosids and one salticid) were brought to the nests. The most common prey organism in the samples was a bracken-fern feeding aphid, *Sitobion rhamni* (Clarke) (Jensen et al. 1993).

I observed 196 hunting spiders, mostly salticids and philodromids, on foliage in the course of the study. The low number of observations was mostly due to the tendency of these spiders to hide within the Douglas-fir foliage upon a slight disturbance. Only a small proportion of observed hunting spiders was consuming prey (Table 4.4). I surveyed a total of 215 webs. The majority of the webs was built by sheet-web weavers (53.0%) and orb weavers (40.5%). The dominant prey groups captured by web spiders were Psocoptera (41.4%) and adult Diptera (31.3%) (Table 4.4).

The taxonomic composition of prey in spider webs differed significantly from the composition of prey on foliage (G = 384.60; df = 9; P < 0.001), and sticky traps (G = 326.50; df = 9; P < 0.001). Nevertheless, they overlapped substantially (55% and 48%,

Date		Hu	unting spiders		Web-building spiders				
	Treatment	X (SE)	F (df)	Р	X (SE)	F (df)	Р		
28-Jun	Control	2.66 (0.09)	0.05 (1,28)	0.823	1.80 (0.13)	3.67 (1,24)	0.070		
	Ant-free	2.63 (0.05)			1.52 (0.06)				
30-Jul	Control	2.96 (0.14)	0.002 (1,27)	0.966	1.71 (0.08)	2.25 (1,26)	0.146		
	Ant-free	2.96 (0.11)			1.54 (0.08)				
27-Aug	Control	2.28 (0.11)	0.36 (1,28)	0.556	1.73 (0.09)	3.09 (1,26)	0.091		
	Ant-free	2.19 (0.10)			1.51 (0.09)				
24-Sept	Control	2.42 (0.13)	6.03 (1,28)	0.020	1.84 (0.14)	3.04 (1,25)	0.094		
-	Ant-free	2.07 (0.05)			1.56 (0.08)				
29-Oct	Control	2.69 (0.31)	0.03 (1,21)	0.868	1.64 (0.14)	0.38 (1,21)	0.547		
	Ant-free	2.74 (0.28)			1.75 (0.07)				

Table 4.3. Mean values $(\pm SE)$ for the body length of spiders collected in control and ant-free trees. Statistics are results of one-way ANOVA tests for treatment differences on individual sampling dates.

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	Ant nests ¹		Ants on foliage		Hunting spiders		Web-building spiders	
Prey group	n	mg	n	mg	n	mg	n	mg
Diplopoda	2	-						
Araneae	3	16.7	1	3.6	1	3.27		
Acari	2	0.06						
Collembola					2	0.06	2	0.06
Psocoptera	27	4	3	0.29	2	0.39	94	8.69
Thysanoptera							1	0.07
Hemiptera	4	3.08	1	0.62			4	2.09
Homoptera Aphidoidea Other	104 5	17.48 12.9	1	0.13	1	0.4	21 7	1. 82 13
Neuroptera ²	2	2.28						
Coleoptera Larvae (Coccinellidae) Adults	3 2	1.7 11.9	1 1	1.81 3.6			1 2	0.42 2.87
Lepidoptera ²	13	35.62						
Diptera Larvae Adults	11 11	2.63 7.76	2	0.28	2	0.85	71	15.17
Hymenoptera Larvae (Symphyta) Adults Formicidae	4 5 9	5.28 30.51 5.18					8 5 ³	0.61 18.2
Unidentified	9	21.18	1	0.34	1	0.56	11	1. 48

Table 4.4. Diet composition of ants, hunting and web-building spiders.

¹ Pooled data from three nests of *Camponotus laevigatus*. ² Larvae only. ³ Three *Camponotus* sp. workers captured by ant specialists *Dipoena nigra* (Em.); two winged females found in orb webs.

respectively). Although the taxonomic composition of the diets of web spiders and ants was significantly different (G = 135.47; df = 9; P < 0.005), the overlap in their diets was almost 50%. Both web spiders and ants were capturing prey of similar size distribution (DN = 0.26; P = 0.41), with diets overlapping 69%. The limited information on the diet of hunting spiders does not allow to make meaningful comparisons of their diet with ants.

Discussion

Ant Foraging

The use of sticky barriers was not expected to significantly limit the dispersal of spiders into the canopy because of their well-developed ability to balloon (Duffey 1956, Greenstone et al. 1987, Bishop and Riechert 1990) and to disperse on silken bridges among tree canopies (Turnbull 1973). Further, elimination of ground dispersal does not appear to have significant effects on densities (Bishop and Riechert 1990) or community structure (Ehmann 1994) of newly formed spider assemblages. I observed that ants were by far the major walking arthropod predators found dispersing on tree trunks.

The increased abundance of arthropod prey in the canopies of ant-free trees suggests that ant foraging had a significant impact on the foliage-dwelling arthropod community. The importance of ant foraging in Douglas-fir canopies was also indirectly supported by the composition of the prey sample collected at ant nests. After the bracken-fern feeding aphids, the second most abundant prey organism brought to the nests was a psocid, *Teliapsocus conterminus*, a species commonly found in Douglas-fir canopies.

Only a small percentage of the ants was observed carrying visible prey. Low frequencies of workers carrying visible particles in their mandibles (1 to 6%) have been reported also for *Camponotus pennsylvanicus* (DeGeer) (Sanders 1972, Fowler and Roberts 1980). It has been suggested that, besides honeydew, part of the captured prey is transported to the nest in the ant's crop in the form of haemolymph and water-soluble proteins (Ayre 1963). Consequently, observations of ants would underestimate the level of foraging based on the presence of visible prey. In addition, the foraging activity of
some *Camponotus* species can shift seasonally into night hours, with some species becoming largely nocturnal (Sanders 1972, Fowler and Roberts 1980). Since the foliage observations were limited to daytime, I cannot evaluate the frequency of nocturnal ant foraging.

There were no differences in the abundance of flying organisms between the treatments during the study. An increased abundance of psocids in ant-free canopies was not reflected in significantly higher sticky-trap catches. This may be due to their limited ability and tendency to fly (Broadhead and Thornton 1955, Halaj, personal observation). The results suggest that the observed increase in the density of hunting spiders can be attributed either to increased densities of the psocid-dominated prey complex on the foliage or to an absence of antagonistic spider-ant interactions.

Exploitative Competition for Prey Between Spiders and Ants

The first alternative suggests the presence of exploitative competition for a common resource between hunting spiders and ants. Several studies indicate that spiders are foodlimited animals (see review in Wise 1993), which tend to aggregate in patches of increased prey densities (Gillespie 1981, Olive 1982, Rypstra 1985, Weyman and Jepson 1994). The abundance of additional prey in ant-free trees should be reflected by one of the following: (1) increased densities of spiders; (2) increased feeding rates; (3) larger body sizes and (4) increased reproduction rates. The abundance of hunting spiders appeared to respond to a build-up of the prey population on foliage and subsequently increased spider densities appeared to suppress prey populations to the control level by late September. The abundance of available prey, however, did not translate into an increased body size of hunting spiders. On the contrary, the average body size of hunters was even smaller on ant-free trees in late September (Table 4.3). This probably reflected slightly higher densities of small spiders (< 2mm) in this treatment. It is unclear whether these spiders represented the progeny of females colonizing the ant-free trees in the early season. One hypothesis would be that the abundance of food and relative protection on foliage resulting from the absence of ants might have "attracted" gravid females to these patches and increased their production of eggs. On the other hand, accumulation of small spiders

in ant-free trees may have been the result of increased retention rates of immature spiders in a habitat of increased prey densities. Weyman and Jepson (1994) have experimentally demonstrated that immature linyphild spiders exhibited higher retention rates in patches of barley infested with aphids, and were responsible for increased densities of the total number of spiders in this treatment.

Based on a limited amount of dietary information, it appears that both ants and web-spiders were consuming prey of similar size and taxonomic composition. Psocoptera, Homoptera and Diptera were especially represented in the diets of both groups of predators. Despite the increase in the availability of prey on foliage resulting from the removal of ants, the densities of web-building spiders remained the same in both treatments. This finding contradicts results of other studies with web-building spiders. For example, experimental removals of *Anolis* lizards led to increased densities of available prey and a significantly higher abundance of web spiders in the Caribbean (Pacala and Roughgarden 1984, Spiller and Schoener 1990).

It is possible that factors other than food limited the abundance of web spiders (see also below). Several studies have demonstrated that besides food, web-building spiders are limited by the availability of substrate providing web-attachment sites (e.g. Schaefer 1978, Rypstra 1983). It is plausible to suggest that perhaps competition for web-building sites was more critical than food in limiting the densities of these spiders.

Direct Spider-Ant Interactions

The results of my field observations suggest that ants were not able to capture a substantial number of spiders in tree canopies. This was also supported indirectly by relatively low numbers of spiders in the ant diet (1.4%). Similarly, Brüning (1991) concluded that predation by *Formica polyctena* Först. on ground-dwelling spiders was "relatively ineffective". Spiders represented only 4.6% of all prey organisms brought to the nest of this ant species. On the other hand, Petal and Breymeyer (1969) estimated that spiders constituted 11-38% of prey captured by meadow-inhabiting *Myrmica* ants. The authors, however, did not provide any direct evidence on the impact of ant foraging on the local spider fauna.

I commonly observed aggressive behavior of ants towards other arthropods on foliage. Twice I observed ants attacking much larger bald-faced hornets, *Dolichovespula maculata* (L.), that collected honeydew on the foliage. The hostility of ants towards other arthropods generally results from their natural predatory behavior and from their mutualistic interactions with homopteran insects (Way 1963). Numerous studies have documented aggressive behavior of homoptera-tending ants towards other predators (e.g. El-Ziady and Kennedy 1956, Bristow 1984, Bach 1991). I observed that about 40% of all ants on the foliage were tending aphids, which may partly account for the aggressive behavior of ants in the canopy.

Both hunting and web-building spiders share the foliage microhabitat with ants. However, the active foraging of hunting spiders makes them more likely to interact directly with ants. On several occasions, I observed encounters between foraging ants and hunting spiders. Visually oriented jumping spiders actively avoided an approaching ant by backing up and rapidly moving away to the opposite side of the twig. If the ant continued in the direction of the escaping spider, the spider dropped on a silken line and ballooned away from the canopy. It appears that hunting spiders use an effective escape mechanism to avoid predation by foraging *Camponotus* ants. However, escaping spiders usually initiated dispersal, an activity which represents considerable risk for the spider (Wise 1993).

The situation may be different for web-building spiders. The web spiders construct webs and are typically sit-and-wait predators. Brüning (1991) observed that foraging *Formica polyctena* Först. workers are not able to recognize spiders sitting motionless in webs as potential prey. On the other hand, this behavior does not appear to provide protection against predators such as lizards (Schoener and Toft 1983a). It appears that the foraging strategy of web-building spiders may provide a selective protection against ants.

Foraging ants did not have a significant effect on overall spider community structure. Spider species richness and diversity did not differ between the treatments. Similar results have been reported by van der Art and de Wit (1971). The authors did not find any differences in the number of total spider species between two parts of a meadow, one of which had a great abundance of foraging *Formica rufa*. On the other hand, Cherix and Bourne (1980) reported higher spider species richness outside a super-colony of *Formica lugubris*. It is unclear, however, whether this was a result of ant foraging. Unfortunately, observational nature of both studies and a lack of replication make interpretation of these results difficult.

Conclusions

This study demonstrated that excluding ants resulted in a significant increase in the biomass of potential foliage-dwelling prey organisms. This may have been a result of direct predation by ants or disturbance resulting from aphid-tending activities of ants. Consequently, the density of hunting spiders increased significantly in ant-free trees. This supports the food-competition hypothesis. However, the average size of hunters did not increase, and since other indicators of spider performance were not monitored, it is unclear how the abundance of food affected the fitness of these animals. Increased abundance of food also did not affect densities of web-building spiders suggesting that factors other than food were limiting the abundance of spiders in the canopies.

On the other hand, aggressive behavior of foraging ants appeared to be a source of disturbance to hunting spiders. Disturbed spiders usually initiated dispersal, which may have been a reason for their lower densities in control trees. Direct predation of ants on spiders appeared to be of minor importance in this canopy system. I suggest that this is mostly due to an efficient escape mechanism of hunting spiders (dropping on silken lines), and a unique foraging strategy of web-building spiders (protection provided by webs). This is supported by my observations and a low frequency of spiders in the ant diet.

Polis and McCormick (1986) emphasize the role of direct predation by scorpions in reducing spider densities in a California desert. Similarly, predation by *Anolis* lizards is assumed to be more important than competition for food in reducing the abundance of webbuilding spiders in the Caribbean (Spiller and Schoener 1988, 1990). Results of this study suggest that interference and possibly exploitative competition for food is more important than direct predation by ants on spiders in young Douglas-fir canopies. This study partly supports conclusions of several observational studies suggesting negative impacts of ant foraging on spider populations. To my knowledge, this study provides the first experimental evidence for the existence of competitive interactions between two of the most abundant terrestrial predators. To clarify the mechanisms of competition between spiders and ants, and its occurrence in other terrestrial communities, requires further testing.

5. CONCLUSIONS

Summary

Spiders are the most common arboreal predators of forest systems in the Pacific Northwest. Despite this fact, not much is known about what limits their abundance and diversity in these systems. This work examined the importance of structural complexity of habitat, availability of prey and competition with ants as factors influencing the abundance and community composition of these predators in western Oregon.

In an observational study conducted in 1993, I found the greatest abundance and species richness of spiders per 1-m-long tips of branches on structurally more complex tree species, including Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco (4.95 to 9.92 individuals, and 2.6 to 3.57 species) and noble fir *Abies procera* Rehder (7.33 to 9.65 individuals, and 2.83 to 3.40 species). Spider densities, species richness and diversity positively correlated with the amount of foliage, wooden twigs and prey densities on individual tree species. The amount of branch wooden twigs alone explained almost 70% of the variation in the total spider abundance across five tree species. This finding allows with fair accuracy the prediction of spider abundance across several host-tree species with significantly different branch structure. The results of this study suggest that the structure of habitat and, to a lesser degree, the availability of prey were significant factors determining spider densities and diversity.

In 1994, I selected Douglas-fir as a model host-tree species to test the significance of specific structural variables of spider habitat. I experimentally tested the importance of needle density and branching complexity of Douglas-fir branches on the abundance and community structure of spiders and their potential prey organisms. This was done by either removing needles, or thinning and tying branches. Tying of branches resulted in a significant increase in the abundance of Collembola. Densities of spiders and their prey were reduced by removal of needles and thinning. Branch tying significantly increased spider abundance. Orb weavers (Araneidae and Tetragnathidae) dominated the spider community of needle-sparse branches, whereas the control and tied branches were preferably colonized by sheet-web weavers (Linyphiidae and Erigonidae) and nocturnal hunting spiders (Clubionidae). Spider species richness and diversity increased in structurally more complex habitats. This study experimentally demonstrated the importance of habitat structure in shaping the community structure and abundance of Douglas-fir dwelling spiders.

In 1994 and 1995, I excluded foraging *Camponotus* spp. ants from sapling Douglas-fir to test the effect of their foraging on the local spider fauna. Biomass of potential prey organisms, dominated by Psocoptera, increased significantly by 1.9 to 2.4fold on the foliage following ant exclusion. Hunting spiders, dominated by the Salticidae, increased significantly by 1.5 to 1.8-fold in trees without ants in the late summer. The exclusion of ants did not affect the abundance of web-building spiders. Ant removal resulted in a slight increase (8.0 - 9.0%) in the relative abundance of hunting spiders in ant-free canopies, however, there was no significant difference in spider species richness and diversity between control and ant-free trees. Through a series of observations, I documented aggressive behavior of aphid-tending ants towards hunting spiders, which suggests the presence of interference competition between these groups of predators.

Recommendations for Future Research

Increased complexity of habitat structure has been shown to reduce severity of intraspecific predation among spiders (Edgar 1969, Rypstra 1983). In my work, both the structural complexity of habitat and foraging of ants have been shown to be significant factors affecting spider abundance. Unfortunately, however, the impact of both variables were investigated independently. I believe that by combining these two variables in a factorial study, which would involve alterations of habitat structure and ant exclusion, the interplay between spiders, the structure of their habitat, and their competitors could be better understood.

There is limited evidence suggesting that predation by some bird species including *Parus* spp., *Certhia familiaris* L. and *Regulus regulus* L. has a significant negative effect on densities of spruce-dwelling spiders in southern Sweden (Askenmo et al. 1977, Gunnarsson 1983). Gunnarsson (1988, 1990) further suggests that simplification of branch habitat structure increases the pressure of predation by birds on spiders by exposing spiders to their natural enemies. In my study, the abundance and diversity of spiders declined on needle-sparse and thinned branches. On the contrary, significantly higher densities of some spider groups, namely nocturnal hunters, were found in structurally more complex tied branches. In addition, significantly higher densities and spider species richness were found on structurally more complex host-tree species such as Douglas-fir and noble fir. How important are birds as predators of arboreal spiders in western Oregon? I believe it would be worthwhile to investigate: (1) the significance of bird predation as a mortality factor of arboreal spiders in these systems, and (2) to test whether or not this process is dependent on the complexity of spider habitat.

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APPENDICES

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APPENDIX A

۰.

Arthropod Biomass Models

Table A.1. Oven-dry biomass models for major arthropod groups.

Group	n	Model *	R ²	Source
Araneae				
Salticidae, Oxyopidae	162	$Y = 0.026X^{3.115}$	0.980	Halaj, unpubl. data
Philodromidae	44	$Y = 0.048X^{2.910}$	0.986	Halaj, unpubl. data
Clubionidae, Anyphaenidae, Gnaphosidae	16	$Y = 0.034 X^{2.837}$	0.991	Halaj, unpubl. data
Thomisidae	19	$Y = 0.053 X^{2.968}$	0.989	Halaj, unpubl. data
Araneidae, Tetragnathidae, Uloboridae	79	$Y = 0.056X^{2.716}$	0.945	Halaj, unpubl. data
Linyphiidae, Micryphantidae, Dictynidae	62	$Y = 0.038X^{3.012}$	0.912	Halaj, unpubl. data
Theridiidae	26	$Y = 0.053 X^{3.019}$	0.964	Halaj, unpubl. data
All Araneae (Phalangida) ^b	408	$Y = 0.042 X^{2.878}$	0.947	Halaj, unpubl. data
Acari ·	32	$Y = 0.040 X^{2.761}$	0.723	Rogers et al. 1977
Collembola				•
Sminthuridae	-	~ 0.010 mg/individual °	-	Moldenke, unpubl. data
Entomobryidae	-	~ 0.032 mg/individual °	-	Moldenke, unpubl. data
Orthoptera	35	$Y = 0.049 X^{2.515}$	0.941	Rogers et al. 1977

Table A.1. Continued.

Group	n	Model	R ²	Source
Psocoptera	88	$Y = 0.013 X^{2.952}$	0.936	Halaj, unpubl. data
Thysanoptera	-	~ 0.074mg/individual °	-	Moldenke, unpubl. data
Hemiptera	34	$Y = 0.050 X^{2.270}$	0.960	Rogers et al. 1977
Homoptera	59	$Y = 0.037 X^{2.696}$	0.980	Rogers et al. 1977
Coleoptera				
Larvae (Neuroptera larvae)	63	Y = -0.792 + 0.571X	0.640	Rogers et al. 1977
Adults	151	Y = 0.031X2.790	0.960	Rogers et al. 1977
Lepidoptera				
Larvae (Hymenoptera-Symphyta larvae)	28	Y = 0.006X2.809	0.941	Rogers et al. 1977
Adults (Ephemeroptera, Plecoptera and Neuroptera adults)	22	Y = 0.018X2.903	0.980	Rogers et al. 1977
Diptera				-
Larvae	18	Y = 0.024e0.356X	0.757	Rogers et al. 1977
Adults	84	Y = 0.037X2.366	0.922	Rogers et al. 1977
Hymenoptera				•
Adults	97	Y = 0.021X2.407	0.941	Rogers et al. 1977
Formicidae	34	Y = 0.018X2.572	0.960	Rogers et al. 1977

^a Body length (X) expressed in mm; body weight (Y) expressed as mg dry biomass. ^b Body weight of the group(s) in parentheses estimated with the model developed for the original group. ^o Fresh body weight converted to dry biomass with a factor of 0.32 (Edwards 1967).

APPENDIX B

Arboreal Arthropod Community Structure

Table B.1. Arthropod community structure on individual host-tree species and study sites.

<u></u>		ALRU			THPL	<u> </u>		TSHE	
Group	L106	L109A	L112	L106	L109A	L112	L106	L109A	L112
	n (mg) ¹	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)
Apterygota					2(-)	1(-)			
Diplopoda							1(-)		
Araneae ²	77 (147.32)	72 (151.77)	30 (62.05)	145 (151.35)	208 (156.35)	120 (117.16)	219 (195.58)	194 (173.49)	191(146.75)
Phalangida		. ,		1 (1.43)	1 (0.45)	· · ·		· · ·	. ,
Acari	4 (0.09)		3 (0.80)	51 (1.52)	2 (0.03)	21 (0.60)	617 (15.66)	145 (4.47)	374 (10.38)
Collembola	1 (0.02)	12 (0.25)	10 (0.20)	46 (0.96)	273 (5.68)	152 (3.16)	16 (0.33)	319 (6.63)	22 (0.44)
Ephemeroptera		3 (33.85)		11 (50.78)	2 (7.45)		7 (33.03)		3 (4.84)
Orthoptera			1 (5.98)					1 (4.02)	
Plecoptera		1 (10.80)							
Psocoptera	2 (0.23)	5 (0.67)	1 (0.13)	158 (40.56)	228 (16.48)	164 (9.38)	136 (31.94)	169 (12.60)	217 (32.52)
Thysanoptera	37 (2.72)	14 (1.03)	69 (5.08)	1 (0.07)					1 (0.07)
Hemiptera	47 (82.18)	13 (1.35)	16 (38.20)	6 (27.69)	16 (19.18)	9 (16.15)	6 (20.94)	19 (25.73)	8 (23.63)
Homoptera									
Aphidoidea	377 (26.66)	606 (45.50)	170 (9.06)		11 (1.83)	8 (2.38)		26 (5.05)	81 (42.30)
Other	335 (228.45)	217 (116.01)	254 (65.57)	24 (16.97)	10 (19.77)	9 (14.90)	76 (91.11)	53 (124.08)	6 (8.61)
Neuroptera									
Larvae	3 (2.83)			5 (6.32)	2 (3.32)		3 (1.18)	1 (0.94)	3 (0.53)
Adults	1 (2.87)			2 (0.27)		1 (3.97)	2 (2.17)	· · · ·	

		ALRU			THPL			TSHE	
Group	L106	L109A	L112	L106	L109A	L112	L106	L109A	L112
	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	L109A n (mg) 2 (0.46) 22 (367.32) 18 (12.63) 101 (24.83)	n (mg)
Coleoptera									
Larvae	2 (0.22)			2 (1.19)		1 (0.03)		2 (0.46)	1 (1.59)
Adults	26 (131.19)	20 (31.46)	12 (169.40)	8 (73.16)	26 (175.11)	7 (62.67)	20 (218.90)	22 (367.32)	18 (76.81)
Lepidoptera		、			. ,				
Larvae	39 (104.50)	22 (17.35)	14 (4.26)	7 (43.22)	13 (34.60)	7 (34.53)	5 (16.38)	18 (12.63)	24 (25.17)
Adults			1 (0.38)		1 (12.16)	. ,	. ,		1 (12.45)
Diptera					. ,				
Larvae	1 (0.11)	1 (0.14)		2 (0.22)		1 (0.71)	38 (1.91)		12 (0.62)
Adults	63 (12.97)	76 (14.48)	38 (8.77)	176 (33.45)	73 (54.77)	53 (36.45)	97 (13.47)	101 (24.83)	45 (11.71)
Hymenoptera						. ,			
Larvae		5 (1.10)	1 (0.25)	1 (0.05)	2 (1.87)		13 (28.69)	9 (5.84)	16 (49.62)
Adults	8 (0.55)	22 (2.45)	8 (3.21)	16 (1.72)	11 (4.41)	11 (1.08)	35 (1.79)	24 (4.67)	10 (0.76)
Formicidae	37 (100.84)	29 (69.05)	20 (30.69)	2 (4.16)	2 (0.40)	6 (5.20)	24 (54.71)	11 (31.45)	18 (53.31)

Table B.1. Continued.

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			F	PSME				ABPR	
Group	L106	L109A	L112	L707	L210	L211A	L707	L210	L211A
	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)
Apterygota									
Diplopoda					1(-)	5(-)		5(-)	16 (-)
Araneae	421 (418.78)	631 (604.69)	376 (298.67)	729 (715.00)	950 (559.20)	742 (521.72)	605 (329.08)	743 (278.93)	593 (239.8)
Phalangida	. ,				· · ·			,	···· (-···)
Acari	131 (4.01)	46 (1.95)	37 (0.60)	24 (0.42)	5 (0.12)	6 (0.34)	74 (1.79)	90 (4.85)	50 (1.84)
Collembola	14 (0.29)	97 (2.00)	44 (0.92)	28 (0.58)	23 (0.48)	58 (1.21)	30 (0.62)	30 (0.62)	70 (1.45)
Ephemeroptera	15 (51.11)		1 (0.06)	5 (14.30)	1 (9.55)	1 (0.19)	1 (15.21)		3 (8.39)
Orthoptera	. ,	16 (6.67)		1 (11.64)		- ()	6 (74.62)	1 (12.67)	- ()
Plecoptera									
Psocoptera	209 (65.68)	194 (12.49)	547 (64.28)	217 (35.09)	98 (12.19)	32 (2.53)	221 (34.04)	220 (20.46)	54 (3.61)
Thysanoptera		2 (0.15)	. ,		1 (0.07)	12 (0.88)	~ ~ ~	3 (0.22)	3 (0.22)
Hemiptera	4 (0.63)	11 (13.60)	19 (28.87)	104 (51.76)	58 (22.65)	160 (80.81)	25 (9.00)	22 (8.23)	38 (26.94)
Homoptera		. ,							
Aphidoidea	88 (25.10)	417 (84.51)	378 (66.10)	1077 (318.13)	694 (175.01)	1156 (252.39)	406 (212.51)	309 (217,45)	162 (67.31)
Other	56 (99.43)	44 (80.84)	10 (17.99)	5 (2.82)	14 (13.07)	7 (7.03)	3 (2.84)	6 (5.39)	15 (10.12)
Neuroptera									
Larvae	8 (6.34)	7 (15.16)	4 (3.47)	23 (33.30)	11 (14.33)	19 (22.23)	4 (3.82)	1 (1.59)	2 (2.76)
Adults	1 (0.19)	1 (0.85)	1 (12.16)	14 (61.11)	1 (2.45)	14 (37.32)	5 (12.62)	5 (15.76)	13 (72.76)
Coleoptera						. ,			. ,
Larvae		1 (0.16)	1 (1.59)	1 (2.46)	7 (3.35)	2 (1.41)		7 (7.95)	
Adults	53 (224.49)	31 (186.22)	31 (232.37)	157 (423.95)	124 (709.16)	100 (497.11)	117 (559.40)	65 (501.14)	66 (588.57)

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Table	B.1 .	Continu	ed.

]	PSME				ABPR	
Group	L106	L109A	L112	L707	L210	L211A	L707	L210	L211A
	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)	n (mg)
Lepidoptera									
Larvae	2 (8.36)	8 (75.52)	17 (13.56)	89 (347.61)	78 (259.14)	54 (87.63)	38 (150,58)	21 (65.85)	28 (158.02)
Adults	3 (21.72)	1 (19.09)		7 (4.94)	1 (0.36)	6 (28.83)	5 (7.82)	1 (10.80)	6 (7.22)
Diptera						· · ·			
Larvae	4 (1.29)	3 (0.44)	14 (3.67)	5 (1.02)	4 (1.44)	2 (1.03)	3 (1.59)	1 (1.06)	3 (0.45)
Adults	313 (83.27)	91 (31.47)	99 (22.09)	329 (190.27)	174 (90.17)	336 (142.34)	130 (107.03)	89 (43.75)	144 (78.03)
Hymenoptera		. ,							
Larvae	34 (200.60)	135 (56.05)	54 (64.11)	137 (466.81)	445 (1495.49)	135 (259.14)	200 (1073.17)	236 (797.07)	67 (136.71)
Adults	27 (3.97)	12 (6.54)	26 (2.22)	42 (32.88)	44 (15.90)	124 (21.19)	26 (14.72)	20 (4.66)	32 (18.63)
Formicidae	39 (76.99)	21 (52.00)	34 (78.51)	95 (304.32)	29 (86.59)	152 (294.37)	53 (124.70)	23 (61.17)	18 (28.37)

¹ Densities and dry body weight of arthropods collected from three 1-m-long branch tips on each of 20 host trees (60 branches) sampled at the study site.

² Densities and dry body weight of spiders collected from four 1-m-long branch tips on each of 20 host trees (80 branches) sampled at the study site.

					Tre	atment				
	Co	ntrol ¹	Т	otal	Pa	atchy	Th	inned	Т	'ied
Group	n	mg	n	mg	n	mg	n	mg	n	mg
Diplopoda									2	-
Chilopoda									1	-
Araneae	625	550.62	91	46.98	262	164.46	249	165.35	1360	1465.63
Phalangida	4	15.09							30	104.76
Acari	91	3.66	11	0.28	44	1.53	41	2.53	292	13.60
Collembola	1063	32.05	19	0.56	119	3.54	123	3.76	8855	274.06
Ephemeroptera	1	0.14								
Psocoptera	2857	574.68	165	27.26	893	194.99	1176	245.96	5321	1008.30
Thysanoptera	1	0.07			1	0.07	1	0.07	2	0.15
Hemiptera	32	42.90	2	6.45	17	20.61	12	12.27	46	67.91
Homoptera										
Aphidoidea	578	93.64	18	3.83	188	29.72	211	40.23	1434	275.59
Other	18	13.62	3	3.10	6	6.48	7	7.00	31	27.82
Neuroptera						-				
Larvae	63	99.67	2	2.28	14	14.43	16	21.61	112	176.75
Adults	15	42.78	4	12.94	8	17.73	7	18.78	13	34.71
Coleoptera										
Larvae	5	13.88	. 1	2.90	4	13.02	4	10.94	19	78.95
Adults	39	140.92	7	18.11	18	64.67	20	66.13	82	621.62
Lepidoptera										
Larvae	34	144.54			8	20.18	11	72.60	42	242.88
Adults	2	9.23			1	5.32			9	47.73

Table B.2. Arthropod community structure on Douglas-fir foliage in the spider habitat structure experiment.

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Table B.2. Continued.

					Tre	atment				
	C	ontrol	Total		Pa	Patchy		inned	Tied	
Group	n	mg	n	mg	n	mg	n	mg	n	mg
Diptera										
Larvae	8	2.59			3	0.75	3	0.30	13	6.86
Adults	96	51.49	12	8.51	49	25.53	45	19.63	209	97.72
Hymenoptera										
Larvae										
Adults	68	20.91	15	3.05	27	16.96	39	7.61	129	38.53
Formicidae	11	23.36			4	1.97	4	6.62	56	115.23

¹ Densities and dry body weight of arthropods collected from a 1-m-long branch tip of 20 treatment trees. Data from four collecting dates are pooled together.

					Treatment					
	Ca	ontrol ¹	1	Fotal	Pa	itchy	Th	inned	1	Fied
Group	n	mg	n	mg	n	mg	n	mg	n	mg
Araneae	33	17.22	33	14.69	26	13.02	31	7.65	38	20.06
Phalangida							1	0.21		
Acari	1	0.01	2	0.04	2	0.02	1	0.01	1	0.07
Collembola	6	0.19	2	0.06	6	0.19	6	0.19	6	0.19
Ephemeroptera			1	6.36						
Isoptera	1	0.04			2	25.65				
Psocoptera	184	11.41	203	13.78	206	12.26	193	12.81	205	12.67
Thysanoptera	14	1.03	17	1.25	17	1.25	13	0.96	12	0.88
Hemiptera	19	24.71	42	53.08	23	27.61	33	38.01	12	17.35
Homoptera										
Aphidoidea	18	1.97	17	2.18	21	1.71	13	1.46	25	2.72
Other	20	15.50	32	19.83	25	19.63	18	11.69	19	10.81
Neuroptera										
Larvae			1	0.08						
Adults			1	1.82	2	2.62	4	5.24	1	2.76
Coleoptera ²	44	118.81	43	91.20	52	144.06	35	122.68	34	95.06
Lepidoptera ²	3	13.54	1	5.48	1	12.16	3	6.22		
Diptera ²	821	443.41	1043	485.93	1030	494.42	1066	472.32	776	327.13

Table B.3. Community structure of arthropods collected on sticky traps in the spider habitat structure experiment.

Table B.3. Continued.

					Treatment				_	
	Co	ontrol]	Fotal	Pa	tchy	Thi	nned	Tied	
Group	n	mg	n	mg	n	mg	n	mg	n	mg
Hymenoptera Adults Formicidae	407 2	94.40 0.86	393 3	121.76 13.34	428 4	, 87.85 9.28	389 6	83.26 24.39	434 1	106.56 0.09

¹ Densities and dry body weight of arthropods collected from 15 sticky traps (850.50 cm²/trap) during a 24-hour sampling period. Data from four collecting dates are pooled together. ² Adults only.

		Fo	liage ¹		Sticky traps ²								
Group	Co	ntrol	An	t-free	Co	ntrol	Ant-free						
	n	mg	n	mg	n	mg	n	mg					
Araneae	579	388.53	713	383.94	14	2.45	31	10.05					
Acari	261	6.75	57	1.47			1	0.023					
Collembola	1137	20.61	6	0.17	7	0.272	1	0.032					
Ephemeroptera							1	0.45					
Isoptera					4	28.18	5	73.23					
Plecoptera	5	0.73	11	1.52			1	.0.03					
Psocoptera	2975	775.8	5385	1376.61	166	18.48	163	20.67					
Thysanoptera	7	0.52	5	0.37	49	3.61	41	3.02					
Hemiptera	23	29.41	30	20.39	8	5.95	3	3.11					
Homoptera													
Aphidoidea	75	31.58	225	45.68	29	2.05	19	1.33					
Other	5	8.15	4	11.68	21	30.39	17	26.12					
Neuroptera													
Larvae	88	121.94	110	148.73									
Adults	10	25.85	5	19.09	7	22.3	5	15.55					
Coleoptera													
Larvae	5	7.76	20	33.11									
Adults	64	114.81	129	237.41	27	53.86	34	90.08					
Lepidoptera													
Larvae	21	71.93	24	80.26									
Adults					1	0.51	1	0.36					
Diptera					_								
Larvae	58	29.77	70	38.15									
Adults	50	9.8	75	25.26	1737	421.41	1669	391.83					
Hymenoptera					_ / _ ·								
Larvae	2	9.48	1	10.01									
Adults	18	2.46	24	5.23	306	23.37	289	28.13					
Formicidae	47	101.57	5	14.56	25	13.63	29	11.5					

Table B.4. Arthropod community structure on Douglas-fir foliage and sticky traps in control and ant-free trees.

¹ Densities and dry body weight of arthropods collected from three 1-m-long branch tips of 15 treatment trees (45 branches). Data from five collecting dates are pooled together. ² Densities and dry body weight of arthropods collected from 10 sticky traps (850.50 cm²/trap) during a 48-hour sampling period. Data from four collecting dates are pooled together.

APPENDIX C

Arboreal Spider Species List

Table C.1. Spider community structure on individual host-tree species and study sites.

	ALRU		THPL		TSHE		PSME					ABPR						
Group	L106 ¹	L109	L112	L106	L109	L112	L106	L109	L112	L106	L109	L112	L 7 07	L210	L211A	L707	L210	L211A
AGILE HUNTERS																		
Oxyopidae																		
Oxyopes scalaris Hentz			2	3	3	9	16	12	9	8	47	16	1	2			1	
Salticidae																		
Eris marginata (Walckenaer)						1	1											
Habrocestum sp.		1				1	1					1						
Metaphidippus aeneolus Curtis	22	26	10	57	34	48	56	54	60	143	243	156	330	292	214	238	272	197
Metaphidippus albeolus Maddison							1		1									
Metaphidippus sp.	2	1		2									1					1
Phidippus johnsoni (G.& E.Peckham)				1														
AMBUSHERS																		
Thomisidae																		
Coriarachne versicolor (Keyserling)	1																	
Misumena vatia (Clerck)	2	4	2				5	4	7	3	3	5	6	4	5	2	2	1
Misumenops celer (Hentz)	3		1	1		1	2		2	1			1					1
Xysticus gosiutus Gertsch					1					2	1	2	2	2	5	3	4	1

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Table C.1. Continued.

		ALR	U		THP	L		TSH	E			PSN	мЕ			4	ABPI	2
Group	L106	L109	L112	L106	L109	L112	L106	L109	L112	L106	L109	L112	L <i>7</i> 07	L210	L211A	L 7 07	L210	L211A
NOCTURNAL HUNTERS																		
Anyphaenidae																		
Anyphaena pacifica (Banks) Clubionidae		2		4	6	2	2	4	4	4	14	7	7	18	11	7	6	2
Clubiona moesta Banks								1								1	1	7
Clubiona trivialis C.L.Koch	1	2	1	4	7	8	7	5	15	11	4	23	37	32	46	38	35	52
Gnaphosidae Sergialus montanus (Emerton)																	2	
																	-	
RUNNERS																		
Philodromidae																		
Apollophanes margareta Lowrie & Gertsch Philodromus oneida Levi						2	1	5	3	4	9 3	4 2	9	23	8	22 1	20	14
Philodromus rufus pacificus Banks Philodromus speciosus Gertsch	7	14		27	64 1	12	10	22	5	35	39 4	21	69 3	87	67	45 1	34	27
Philodromus spectabilis Keyserling	11	9	1	5	13	1	2	4	4	7	12	12	63	151	161	52	58	61
Tibellus oblongus (Walckenaer)					4				1			1						1
COBWEB SPIDERS																		
Theridiidae							-											
Argyrodes fictilium (Hentz) Dipoena nigra (Emerton)				1	1		1		1	6	20	5	2			1		
Euryopis formosa Banks	1																	
Theridion aurantium Emerton							1											

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Table C.1. Continued.

		ALR	U		THP	L	·	TSH	E			PSN	Æ				ABPI	R
Group	L106	L109	L112	L 7 07	L210	L211A	L707	L210	L211A									
Theridion differens Emerton				1	3					1	23		4	9	6	1		2
Theridion lawrencei (Gertsch & Archer)				2	9		3	10	6	1	45	10	10	24	8	9	15	
Theridion melanurum Hahn																	1	
Theridion neomexicanum Banks	2	1	1		1							1	2	2	3	2		
Theridion sexpunctatum Emerton			3		4			1	1									1
Theridion simile C. L. Koch	1							1		1	1	2				1	1	
Theridion varians Hahn								1								1		1
Theridion sp.	2	4		2	3		1	4	1		3	3			1	1	1	
HACKLED-BAND WEAVERS																		
Dictynidae																		
Dictyna olympiana Chamberlin	10			2			9	11	5	12	25	16	24	8	1	7	10	12
ORB WEAVERS																		
Araneidae																		
Araneus gemma (McCook)										3	2		4	4	2		1	
Araniella displicata (Hentz)	7	4	8	3	9	10	5	8	3	13	20	17	26	54	60	18	18	21
Cyclosa conica (Pallas)				2	3	3	1	3	1	1	5	1	1	1		1		1
Undetermined genus, sp. 1	2	2		1	3	2	3	1	1	2	1					3		3
Tetragnathidae																		
Metellina curtisi (McCook)				1	3	4					1							
Tetragnatha laboriosa Hentz												1	6	1				
Tetragnatha versicolor (Walckenaer)	1	1		1	3				1	8	4	5	4	2	6	2	1	1
Uloboridae																		
Hyptiotes gertschi Chamberlin & Ivie				5	4	6	6	6	3	4		2						

Table C.1. Continued.

	A	LRU		T	HPI	Ĺ		TSH	E			PSN	Æ				ABPI	2
Group	L106 L1	109 L11	2 LI	06 L1	09	L112	L106	L109	L112	L106	L109	L112	L707	L210	L211A	L 7 07	L210	L211A
SHEET-WEB WEAVERS																		
Linyphiidae Pityohyphantes costatus (Hentz) Pityohyphantes rubrofasciatus Keyserling Prolinyphia litigiosa (Keyserling) Undetermined genus, sp. 1 Undetermined genus, sp. 2		1	2	2 · 5 1	7 10 3	1 2	19 6 19′	19 6 2	19 2 9	40 10 50	1 39 12 38	2 27 3 6	25 37 40	7 26 180	24 99	8 28 36	5 12 35	3 4 29
Micryphantidae Ceraticelus atriceps (O. PCambridge) Undetermined genus, sp. 1							35	1 2	22	49	11	24	12 3	20 1	7 4	33 27	199 1	113 1
OTHER	2	1	1	2	9	7	5	7	5	2	1	1			3	16	10	36

¹ Densities of spiders collected from four 1-m-long branch tips of 20 host trees (80 branches) at one study site.

 Table C.2. Spider community structure on Douglas-fir foliage in the spider habitat structure experiment.

									Trea	tmen	t								
	<u></u>	Co	ntro	l ¹		Т	otal		Pa	tchy			Thi	inned			Т	ied	
Group	8/6	9/5	10/2	10/22	8/6	9/5	10/2 10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22
AGILE HUNTERS																			
Salticidae Habrocestum sp. Metaphidippus aeneolus Curtis Phidippus johnsoni (G.& E.Peckham)	53	48	21	6	4	2	1	17	20 1	9	1	21	7	6	0	2 109 1	107	59	6
AMBUSHERS																			
Thomisidae Misumena vatia (Clerck) Xysticus gosiutus Gertsch	1 1					1	1	1	1	2		1	1			1 3	1		
NOCTURNAL HUNTERS																			
Anyphaenidae Anyphaena pacifica (Banks) Chibionidae	1	2						1	1							3	7	7	2
Clubiona trivialis C.L.Koch Clubiona pacifica Banks Clubiona sp.	5	11	6 1	2		1		3	2	2			6	3	3	40	78	46 1 1	15
RUNNERS																			
Philodromidae Apollophanes margareta Lowrie & Gertsch Philodromus oneida Levi	2	1						2	1							4	3 1	4	22

Table C.2. Continued.

										Trea	tmer	ıt			<u></u>					
		Co	ntrol	l		Т	otal			Pa	tchy			Thi	inned			Т	ied	
Group	8/6	9/5	10/2	10/22	8/6	9/5	1 0/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22
Philodromus rufus pacificus Banks Philodromus spectabilis Keyserling	17 9	16 7	16 3	6	1 5	2 1	1		2 7	12 2	5 1	2	8 2	6 5	6 1	5	27 23	18 17	20 11	10
COBWEB SPIDERS																				
Theridiidae Dipoena nigra (Emerton) Theridion differens Emerton Theridion lawrencei (Gertsch & Archer) Theridion sexpunctatum Emerton Theridion sp. Theridion sp. 1 HACKLED-BAND WEAVERS Dictynidae Dictyna peragrata (Bishop & Ruderman)	1 6 4	6 4 3	14 3 8	3 12 4 1	1	1	1	1	4 1	5 3 1	2 3 4 2	5 1 1	2 4 1	1 2 5 3	4 2 1	8	2 19 7 3	1 1 11 14 7	2 15 5 7	1 2 53 5
ORB WEAVERS																				
Araneidae Araneus gemma (McCook) Araniella displicata (Hentz) Cyclosa conica (Pallas) Undetermined genus, sp. 1 Undetermined genus, sp. 2	8 19	6 17 1	4 19	2 6	8 4 2	2 8	11 3	3 2	11 6 1 1	1 17 1	20	4	2 8	2 9	2 23	7 1	7 10 1	2 19 1	5 27 1	3 7 1

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Table C.2. Continued.

										Trea	tmen	ıt								
		Co	ntrol			Т	otal			Pa	tchy			Thi	nnec	1		Т	ied	
Group	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22	8/6	9/5	10/2	10/22
Tetragnathidae				·																
Metellina sp.				1		1		2						1		1		1		
Tetragnatha versicolor (Walckenaer)	7	4	12		· 2	1	5	1	4	4	3		2	1	9	3	11	9	24	10
Zygiella sp.																1	1	1	1	
SHEET-WEB WEAVERS																				
Linyphiidae																				
Pityohyphantes costatus (Hentz)	3	1	7	9			1	1			1	1			1	2	14	9	16	38
Pityohyphantes rubrofasciatus Keyserling	32	37	42	26		2	1	2	9	12	12	8	6	9	3	5	61	58	74	54
Undetermined genus, sp. 1	17	9	3		1	1			6	4	2		13	3	6		21	19	9	
Undetermined genus, sp. 2	1	1							1				1				5		1	
Undetermined genus, sp. 3		5	3	1						1				2	2			6	2	
Undetermined genus, sp. 4		3								1				2	1			7	6	
Undetermined genus, sp. 5				1															2	1
Micryphantidae																				
Ceraticelus atriceps (O. PCambridge)	1		1	3			1					1	1		1		5	5	3	2
Undetermined genus, sp. 1									1										3	
Undetermined genus, sp. 2																	1			
Undetermined genus, sp. 3						1														
Undetermined genus, sp. 4																1				
OTHER			1									1		1	1		3	1	2	1

¹ Spider densities collected from one 1-m-long branch tip of 20 treatment trees.

			Control	L				Ant-free	:	
Group	6/28	7/30	8/27	9/24	10/29	6/28	7/30	8/27	9/24	10/29
AGILE HUNTERS										
Oxyopidae										
Oxyopes scalaris Hentz	3	4	7	6	9	3	6	22	15	5
Salticidae										
Habrocestum sp.						1				
Metaphidippus aeneolus Curtis	64	39	49	56	3	51	49	67	88	3
Phidippus johnsoni (G.& E.Peckham)	1	1	2					1	2	
AMBUSHERS										
Thomisidae										
Misumena vatia (Clerck)			1			2			1	
Misumenops celer (Hentz)			1			•			1	
Tmarus angulatus (Walckenaer)										1
Xysticus gosiutus Gertsch	1	2	1		1			2	1	
Xysticus locuples Keyserling	1	1				1	1			
NOCTURNAL HUNTERS										
Anyphaenidae										
Anyphaena pacifica (Banks)	1	2	6	7	4	6	5	11	24	3
Clubionidae										-
Clubiona trivialis C.L.Koch	1	7	15	3		1	7	14	2	
Gnaphosidae										
Undetermined genus, sp.1		1					1	1		

 Table C.3. Spider community structure on Douglas-fir foliage in control and ant-free trees.

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Table C.3. Continued.

			Control					Ant-free	;	
Group	6/28	7/30	8/27	9/24	10/29	6/28	7/30	8/27	9/24	10/29
RUNNERS										
Philodromidae										
Apollophanes margareta Lowrie & Gertsch			1	1		2		3	2	
Philodromus rufus pacificus Banks	7	2	5	9	6	3	5	11	14	6
Philodromus spectabilis Keyserling	9	1	2	2	1	6	4	5	5	1
COBWEB SPIDERS										
Theridiidae										
Dipoena nigra (Emerton)	2	1	2	2		1		3	4	2
Euryopis formosa Banks	1		1							
Theridion differens Emerton	2		1	3	3	1	3	7	6	3
Theridion intervallatum			2	3	1			5	9	
Theridion lawrencei (Gertsch & Archer)	2	3	1	9	2	1	1		4	6
Theridion neomexicanum Banks	2	1				1				
Theridion simile C. L. Koch			1							
Theridion tinctum (Walckenaer)				1			1	1		
Theridion sp.		3	1	1			5	2		1
Theridion sp. 1									1	
HACKLED-BAND WEAVERS										
Dictynidae										
Dictyna olympiana Chamberlin	1					1		1		

Table C.3. Continued.

			Control					Ant-free	;	
Group	6/28	7/30	8/27	9/24	10/29	6/28	7/30	8/27	9/24	10/29
ORB WEAVERS										
Araneidae										
Araneus gemma (McCook)	1	3	1			1	2			1
Araniella displicata (Hentz)	3	3	2	7	1	4	1	3	14	3
Cyclosa conica (Pallas)		1					1	2		
Undetermined genus, sp. 1										1
Tetragnathidae										
Tetragnatha versicolor (Walckenaer)		4	3	1	6	3	2		4	4
Zygiella sp.		1			1					
Uloboridae										
Hyptiotes gertschi Chamberlin & Ivie									1	
SHEET-WEB WEAVERS										
Linyphiidae										
Pityohyphantes costatus (Hentz)	1			1					1	
Pityohyphantes rubrofasciatus Keyserling	2	1	1	2	3	1	4	1	2	2
Undetermined genus, sp. 1	27	33	11	6	1	43	32	10	1	
Undetermined genus, sp. 2							1			
Undetermined genus, sp. 3			9	4	3			5	1	
Micryphantidae										
Ceraticelus atriceps (O. PCambridge)	11	9	7	4	7	8	7	4	5	2
Undetermined genus, sp. 1						1				
OTHER							1	5		

¹ Spider densities collected from three 1-m-long branch tip of 20 treatment trees (60 branches).

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APPENDIX D

Ambient Temperature Records



Figure D.1. Study site ambient temperature records in the spider habitat structure experiment. Arrows indicate sampling dates.



Figure D.2. Study site ambient temperature records in the ant-exclusion experiment. Arrows indicate sampling dates.