GEOGRAPHIC VARIATION IN ARBOREAL SPIDER (ARANEAE) COMMUNITIES ON DOUGLAS-FIR IN WESTERN OREGON

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Abstract.—Relative abundance and community structure of arboreal spiders were estimated in sapling stands of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco. Samples were collected on two dates between June and August 1992 in three geographic provinces in western Oregon. A total of 7693 spiders of 15 families, 46 genera and at least 62 species were collected from lower crown branches. On both dates, mean spider density was significantly different among the provinces ($P < 0.0001$ and $P < 0.01$). Overall web-spinning spiders dominated in both collections, comprising 63 and 58% of the total spider fauna. The principal web-spinners were the Linyphiidae and Erigonidae, followed by the Araneidae, Theridiidae and Tetragnathidae. The spectrum of hunting families was dominated by the Salticidae and Philodromidae. Both families combined represented 79 and 78% of spiders in this guild for the two sampling dates. On both dates, the proportions of web-spinning to hunting spiders were significantly different among the provinces ($P < 0.001$ and $P < 0.0001$). Web-spinners were dominant in coastal areas, whereas hunters were a major group further inland. On both collecting dates, all geographic provinces were similar in terms of their species composition. A slightly greater similarity was detected between the two Coast Range provinces.

Key Words.—Arachnida, Douglas-fir, *Pseudotsuga menziesii,* spider community structure, geographic variation, western Oregon

The abundance, polyphagous habit, and widespread distribution of spiders make these predators well suited as potential natural controls of insect populations (Riechert 1974, Riechert & Lockley 1984). In forest ecosystems, spiders have been reported preying on various life stages of important forest insect pests including the Nantucket pine moth, *Rhyacionia frustrana* (Comstock), Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), and eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Turnbull 1956, Loughton et al. 1963, Eikenbary & Fox 1968, Dahlsten et al. 1977, Jennings & Houseweart 1978, Fichter 1984, Mason & Paul 1988, Jennings & Houseweart 1989).

Spiders in Pacific Northwest forests are poorly studied despite their abundance and potential roles in regulating insect pest populations. Turnbull (1956) studied spider predation on *C. fumiferana* in British Columbia, Canada. Moldenke et al. (1987) provide a list of species, key, and estimates of relative abundance for arboreal spiders in Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, and true fir, *Abies* spp., forests of the Pacific Northwest. Fichter (1984) documented the densities of arboreal spiders associated with early instar Douglas-fir tussock moth in *Abies concolor* (Gordon & Glendinning) Hildebrand, in central California.

Mason (1992) studied spider populations on Douglas-fir and true firs in eastern Oregon and Washington. He found a similar familial structure of spider com-

munities across the region, with the spectrum largely dominated by two families of hunting spiders. We hypothesized that spider abundance and community structure in the more mesic forests of western Oregon would differ from that in the dry eastern portions of the state. This study quantifies spider abundance and community structure on Douglas-fir canopies in three distinct geographic regions in western Oregon.

Materials and Methods

Geographic Provinces and Study Sites. — The study was conducted in three geographic provinces along an east-west transect in western Oregon. The provinces were the western Coast Range, the eastern Coast Range, and the western Cascade Range. Sites in the western Coast Range were located on the Siuslaw National Forest about 10 km east of Waldport, in Lincoln County, Oregon. Sites in the eastern Coast Range were located on the McDonald and Paul M. Dunn State Forests about 10 km northwest of Corvallis, in Benton County, Oregon. Sites in the western Cascade Range were located on the H. J. Andrews Experimental Forest within the Willamette National Forest about 15 km northeast of Blue River, in Lane and Linn Counties, Oregon. Mean elevations for sites within the three provinces were 228, 270, and 845 m, respectively. All three provinces are characterized by wet winters, warm dry summers and mild temperatures throughout the year. The annual precipitation values for the provinces moving from west to east are 228, 178 and 230 cm, respectively, with the majority of precipitation occurring between November and March. Mean annual temperatures for the provinces moving from west to east are 10.4, 9.8 and 7.9° C, respectively (Taylor & Bartlett 1993, 1994, 1995).

Study sites were mostly pure sapling stands of Douglas-fir (< 15-years-old) with occasional sparse components of western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, and western redcedar, *Thuja plicata* D. Don. The ground vegetation included dense patches of bracken fern, *Pteridium aquilinum* (Linnaeus) Kuhn in Decken, salmonberry, *Rubus spectabilis* Pursh, Gaultheria, *Gaultheria shallon* Pursh, fireweed, *Epilobium angustifolium* Linnaeus, and Pacific rhododendron, *Rhododendron macrophyllum* D. Don ex G. Don.

Sampling Methods. — Sampling procedures used in this study were similar to those of Mason (1992). A total of eight sites in each of the geographic provinces were sampled on two dates between Jun and Aug 1992 approximately one month apart. The timing of sampling was selected to coincide with the period of maximum density and diversity of spider populations (Uetz 1979, Hatley & MacMahon 1980, Döbel et al. 1990). On each collecting date, all provinces were sampled within a two-week period. A total of fifty sapling Douglas-fir trees were randomly selected for sampling at each of the sites. On each tree, 45-cm-long tips of three branches selected from the lower third of the canopy were sampled by beating over a hand-held drop cloth (Paul 1979). Sampling of the lower canopy was assumed to provide a good estimate of the structure of the spider community throughout the whole canopy. It has been shown that the relative abundance and density of spiders in Douglas-fir remains fairly constant in relation to the height of the canopy (Fichter 1984, Voegtlin 1982, Moldenke, unpublished data).

Spiders dislodged onto the drop cloth were collected using a portable vacuum (Paul & Mason 1985) and preserved in 75% ethanol. Ten trees were sampled

before emptying the vacuum, resulting in five 30-branch samples from each site. In the laboratory, spiders were sorted and identified. The identifications of specimens were based mostly on taxonomic keys in Roth (1985) and Moldenke et al. (1987). The densities of spiders were calculated as numbers of individuals per m^2 of branch area (Mason 1992).

Data Analyses.—Mean arthropod densities and ratios of web-spinning to hunting spider densities were compared among the three provinces by a one-way analysis of variance (ANOVA). Differences in spider densities and diversity between the two sampling dates were tested using a paired t-test. In order to satisfy the assumption of equal variance in ANOVA, mean arthropod densities and ratios of spider guilds were transformed to their natural logarithms (ln) before analyses. Back-transformed values and 95% CI are reported here. Means were compared and separated by Fisher's protected least significant difference (LSD) test (Steel & Torrie 1980). Diversity of spider populations was determined individually for each of the sites using the Shannon diversity index (H') (Pielou 1975). The parameter of evenness (J') of this index which measures the equitability of abundance of individual taxa in the sample was calculated. J' ranges between 0 and 1 with the value of 1 characteristic of hypothetical communities with an equal abundance of all taxa. Similarity of spider populations among the provinces was determined using the Sørensen similarity index (C_s) (Southwood 1992).

Differences in spider diversity and evenness among the provinces were tested by ANOVA and means were compared and separated by Fisher's protected LSD. All statistical analyses were performed using SAS computer programs (SAS Institute 1985).

RESULTS AND DISCUSSION

Absolute Densities of Spiders.—Statistical analyses revealed significant differences in mean spider densities (total) among the three provinces on both sampling dates ($F = 28.59$; df = 2, 21; $P < 0.0001$; and $F = 5.02$; df = 2, 21; $P < 0.01$). In June, mean spider densities were significantly higher in the eastern Coast Range compared with the other two regions which had similar densities (Fig. 1). In late July–early August, mean spider densities in both Coast Range regions were not significantly different and spider densities in the eastern Coast Range were significantly higher than those in the western Cascade Range (Fig. 1). Mean spider densities ranged from 4.6 to 16.7 individuals per m^2 of branch area similar to those found by Mason (1992) on true fir and Douglas-fir in eastern Oregon and by Jennings & Dimond (1988) on balsam fir, *Abies balsamea* (Linnaeus) Miller, and spruces, *Picea* spp., in east-central Maine. Some factors that may influence spider abundance include tree density, type and abundance of associated vegetation, abundance of potential prey organisms, patterns of air movement, and climate. Significant differences in spider densities among the provinces may have been caused by natural variation in the structure of branches and foliage (Gunnarsson 1988, 1990). In addition, we observed an increased abundance of herbaceous and shrub vegetation at the Coast Range sites in comparison with the Cascade Range sites. Further, the ground cover communities in the Coast Range sites were dominated by dense, structurally more complex, patches of salmonberry and Gaultheria, whereas the sites in the Cascade Range were mostly covered with patches of architecturally simpler bracken fern and rhododendron.
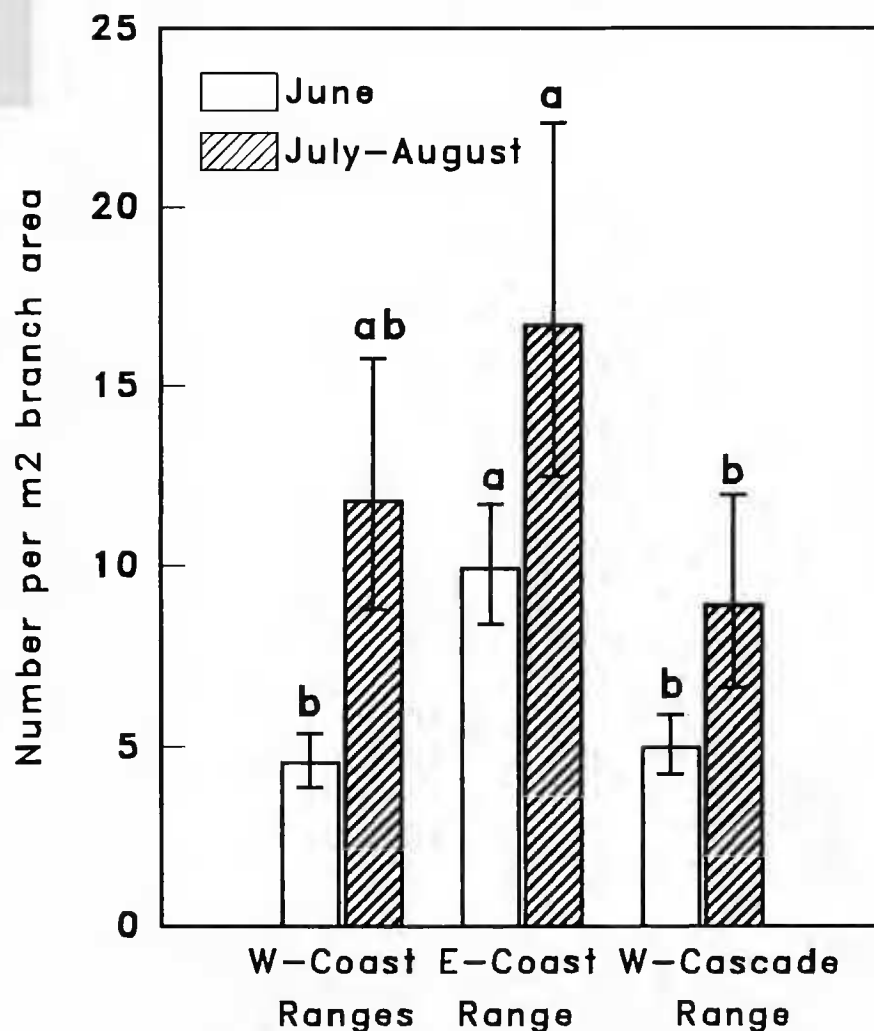
Figure 1. Mean spider densities ($\pm$ 95% CI) per m^2 of Douglas-fir branch area in three geographic provinces in western Oregon. Bars with the same letters are not significantly different ($P = 0.05$).

There was a significant increase in spider densities between the first and second sampling dates ($t = 7.53$; df = 23; $P < 0.0001$) (Fig. 1). Although the small number of collecting dates in our study limits temporal analysis of trends in the spider populations, we suspect that the increase in spider densities can be attributed to the hatch of eggs laid in the early summer by individuals overwintering as immatures (Loughton et al. 1963). This assumption is supported by an increased number of immature individuals (over 70% of total spiders) in the later samples.

Spider Diversity and Guild Composition. — A total of 7693 spiders of 15 families, 46 genera, and at least 62 species were collected from the foliage of Douglas-fir in western Oregon. Our data are comparable to those of Turnbull (1956) who collected 75 species of spiders representing 15 families from Douglas-fir foliage in British Columbia, Canada. Mason (1992) collected spiders from 11 families on Douglas-fir and true fir branches in interior Pacific Northwest forests. We recorded about twice the number of genera and species collected on balsam fir and spruces from east-central Maine (Jennings & Dimond 1988).

Analyses of variance indicated significant differences in spider diversity (H′) among the provinces in June reflecting a higher diversity in the western Coast Range and western Cascade Range provinces compared with the eastern Coast Range province ($F = 9.32$; df = 2,21; $P < 0.01$) (Table 1). No significant differences were detected in late July–early August ($F = 0.20$; df = 2,21; $P > 0.80$). There were significant differences in the evenness component of diversity (J′) among the provinces in June ($F = 9.86$; df = 2,21; $P < 0.01$), but not in late July–early August ($F = 0.06$; df = 2,21, $P > 0.90$) (Table 1).

Table 1. Mean values (SEM) of the Shannon diversity index (H') and evenness (J') for spider samples collected in western Oregon, 1992.

Province	n	June		Late July–early August	
		H'[a]	J'	H'	J'
W—Coast Range	8	2.43 (0.02)a	0.86 (0.01)a	2.28 (0.08)a	0.74 (0.02)a*
E—Coast Range	8	2.19 (0.10)b	0.71 (0.03)b	2.41 (0.04)a	0.77 (0.01)a
W—Cascade Range	8	2.32 (0.05)ab	0.83 (0.01)a	2.25 (0.06)a	0.75 (0.02)a*

[a] Means within a column followed by the same letter are not significantly different ($P = 0.05$).
* Denotes a significant difference between two collecting dates ($P = 0.05$).

Significant differences in the evenness (J') and diversity (H') among the provinces in June reflected a build up in the relative abundance of the Erigonidae detected in the eastern Coast Range. In addition, a significant drop in the evenness between June and late July–early August in the western Coast and Cascade Ranges ($t = 5.87$; df = 7; $P < 0.001$ and $t = 3.58$; df = 7; $P = 0.009$, respectively) can be attributed to an increase in the relative abundance of the Linyphiidae and Salticidae, respectively, in samples from these provinces. All three families were dominated by only a few species comprising over 95% of individuals (see below). Overall, relatively low values of evenness in our samples indicate an unequal abundance of species reflecting the presence of a few dominant species. These results are generally consistent with those of Mason (1992) who compared spider community structure at the family level among geographic regions of the interior Pacific Northwest. He found that a few families were dominant in each region, but individuals of most families were present in low numbers. Similarly, Turnbull (1966) recorded only a few spider species represented by a large number of individuals and the majority of species represented by a few individuals in a pasture community in Ontario, Canada.

On both collecting dates, all three provinces were similar in terms of their species composition. A slightly greater similarity was detected between both Coast Range provinces in June and late July–early August (0.70 and 0.80, respectively) (Table 2). In addition, relatively low values of C_s between the two collecting dates in each of the provinces (0.67, 0.75 and 0.69) indicate substantial temporal changes in the species composition of spider populations (Table 2).

Spiders were divided into two functional guilds based on their foraging strategies; web-spinners and hunters. Relative abundance of these two functional categories of spiders is often used to describe spider communities (Loughton et al. 1963, Fichter 1984, Jennings & Dimond 1988, Mason 1992). On both sampling dates, the ratios of web-spinning to hunting spiders differed significantly among the provinces ($F = 13.23$; df = 2,21; $P < 0.001$ and $F = 23.24$; df = 2,21; $P < 0.0001$, respectively). In general, the abundance of web-spinning spiders relative to hunting spiders declined with distance from the coast (Fig. 2). On both sampling dates, web-spinners were 1.4 to 2.3 times more abundant than hunters in both regions of the Coast Range. In contrast, hunters were more abundant than web-spinners in the western Cascade Range. Mason (1992) and Turnbull (1956) both reported a higher abundance of hunting spiders relative to web-spinners on Douglas-fir in interior Pacific Northwest forests.

Table 2. Values of the Sørensen similarity index (C_s) for spider samples collected in western Oregon, 1992.

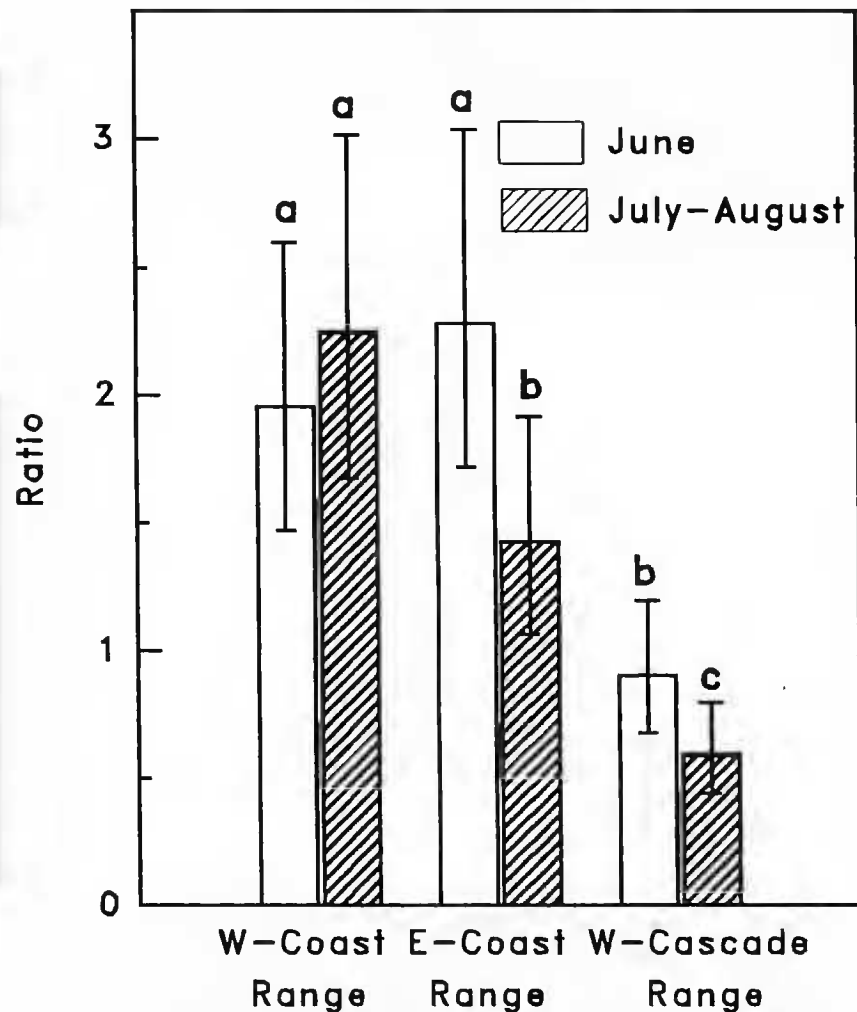| Province	June			Late July–early August		
	W–Coast Range	E–Coast Range	W–Cascade Range	W–Coast Range	E–Coast Range	W–Cascade Range
June						
W–Coast Range	1.00					
E–Coast Range	0.70	1.00				
W–Cascade Range	0.63	0.63	1.00			
July–August						
W–Coast Range	0.67	0.74	0.63	1.00		
E–Coast Range	0.63	0.75	0.65	0.80	1.00	
W–Cascade Range	0.55	0.69	0.69	0.74	0.78	1.00

Figure 2. Average ratios (± 95% CI) of web-spinning to hunting spiders in three geographic provinces in western Oregon. Bars with the same letters are not significantly different ($P = 0.05$).

Spider Families and Dominant Species.—Among the web-spinners, the Linyphiidae, Erigonidae and Araneidae combined were the principal families in all three provinces comprising over 74% of the spiders in this guild (Fig. 3). These were followed in abundance by the Theridiidae and Tetragnathidae. The Dictynidae and Uloboridae comprised <1% of all spiders collected in this guild. Compared with similar data from the interior Pacific Northwest (Mason 1992) the Linyphiidae and Erigonidae were much more abundant and the Dictynidae were much less abundant in our samples.

The Linyphiidae in all three provinces were dominated by *Pityohyphantes rubrofasciatus* Keyserling and *Pityohyphantes costatus* (Hentz); less abundant but fairly common was *Gnathantes ferosa* Chamberlin & Ivie. Among the erigonids, *Ceraticelus atriceps* (O. P.-Cambridge) and *Ceraticelus vesperus* Chamberlin & Ivie were the most common species. In addition, *Spirembolus mundus* Chamberlin & Ivie and *Erigone denticulata* Chamberlin & Ivie were frequently collected in the western Coast Range. The theridiids were dominated by *Dipoena nigra* (Emerton), *Theridion simile* C. L. Koch, *Theridion neomexicanum* Banks, *Theridion sexpunctatum* Emberton, and *Theridion differens* Emerton. *Araniella displicata* (Hentz) and *Cyclosa conica* (Pallas) were the most common araneid species.

The guild of hunting spiders was similar to that described by Turnbull (1956) and Mason (1992). The Salticidae and Philodromidae were dominant hunters composing over 75% of the spiders in this guild (Fig. 3). The salticids alone represented about 50% of hunting spiders (Fig. 3). *Metaphidippus aeneolus* Curtis, a species common throughout coniferous forests of the Pacific Northwest (Mol-
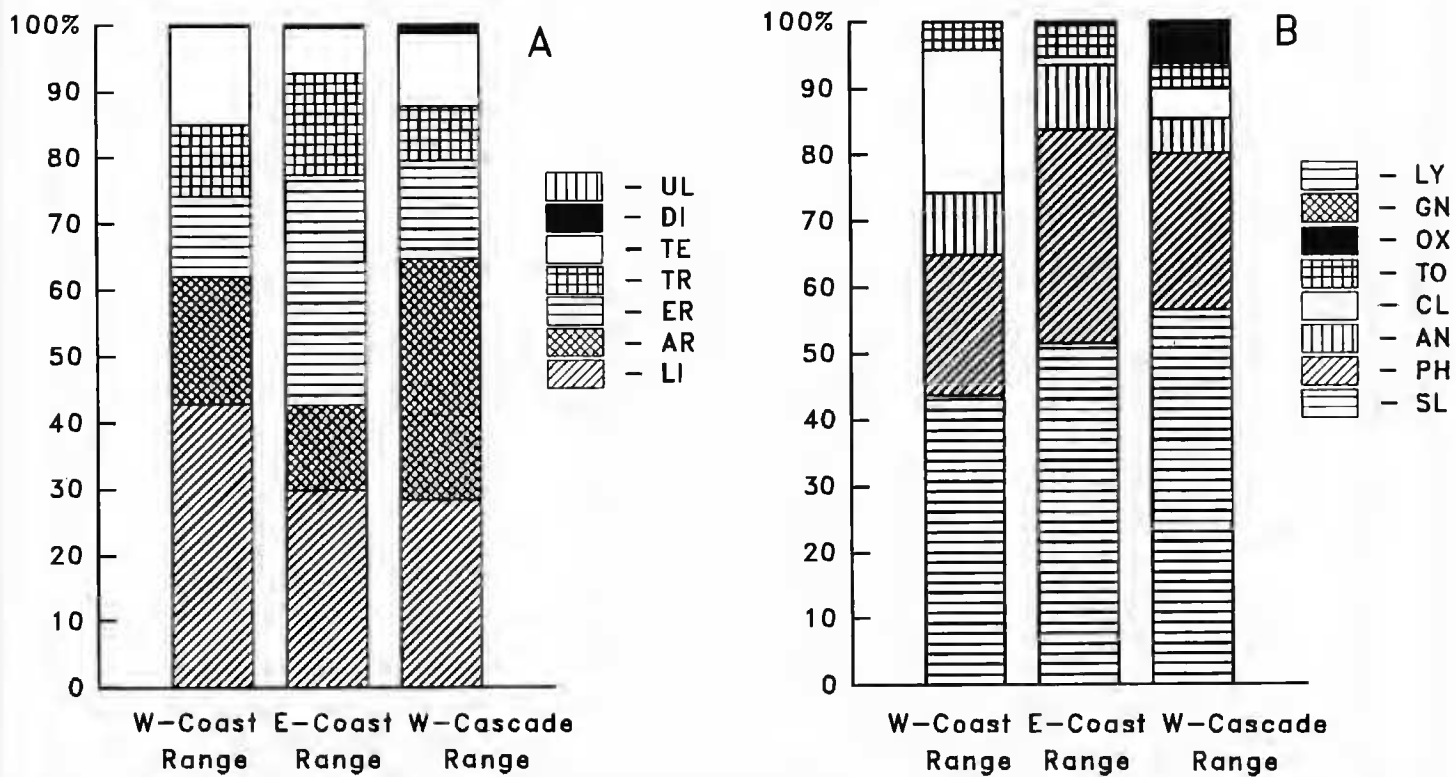
Figure 3. Relative abundance of individual spider families in the guild of web-spinners (A) and hunters (B) in combined samples from both collection dates in three geographic provinces. Family abbreviations are: ER, Erigonidae; SL, Salticidae; LI, Linyphiidae; AR, Araneidae; PH, Philodromidae; TR, Theridiidae; TE, Tetragnathidae; CL, Clubionidae; AN, Anyphaenidae; TO, Thomisidae; OX, Oxyopidae; DI, Dictynidae; GN, Gnaphosidae; UL, Uloboridae; LY, Lycosidae.

denke et al. 1987), was the most common jumping spider in our samples. The Philodromidae was dominated by *Philodromus rufus pacificus* Banks and *Philodromus spectabilis* Keyserling. In contrast to the previous studies in interior forests, our samples from western Oregon contained higher numbers of nocturnal hunters like the Clubionidae and Anyphaenidae. This was particularly true in the western Coast Range where clubionids alone comprised about 20% of the hunting spiders (Fig. 3). Both families include hunting spiders that forage at night, mostly on grasses and deciduous shrubs but which stray to tree canopies. The higher abundance of these spiders in western Oregon may reflect more diverse habitats with a rich layer of ground vegetation. The Oxyopidae, classified together with salticids as agile hunters, were primarily limited to the Cascade Range, almost completely lacking in samples from the Coast Range (Fig. 3).

The abundance of web-spinners in the Coast Range may be attributed to several factors. For sit-and-wait predators, such as web-spinning spiders, the location of a suitable site is critical to their success (Turnbull 1973, Riechert and Gillespie 1986). Robinson (1981) demonstrated experimentally that web-spinning spiders prefer more complex substrates that provide a greater number of points of attachment for web construction. Similarly, Chew (1961) postulated that a low density of shrubs providing less opportunities for web construction was among the factors responsible for under-representation of web-spinning spiders in a desert community. The abundance of a more diverse vegetation at the coast sites would add structural complexity to young conifer plantations possibly improving the habitat for web-spinning spiders. Further, Scheidler (1990) observed in Germany that about 70% of spiders inhabiting herbaceous vegetation in forest clearings were web-spinning spiders dominated by linyphiids. This might explain the dominance of this group in our samples.

In addition, the more consistent air movement near the coast may facilitate dispersal of these spiders and thus their movement from the herbaceous and shrub layers to tree canopies. Because of the sit-and-wait foraging strategy of these spiders, numbers of prey coming into contact with the web is a limiting factor. The regular air movements in coastal areas may increase the prey supply and, consequently, affect the suitability of the site.

In summary, our data show that spider communities of western Oregon are similar in terms of their species composition but significant differences exist in the absolute density and relative abundance of individual species and families. There is an increase in web-spinning spiders relative to hunters in forests closer to the coast. Climatically, all three provinces are very similar, with slightly lower annual temperatures in the western Cascades reflecting the higher elevation of the study sites in this province.

Our assessment of the habitat quality indicates that both coast provinces were characterized by denser and structurally more complex patches of ground vegetation which may be partly responsible for the observed differences. In addition, microclimate conditions at the site or local abundance of prey organisms may be equally important in determining the structure of spider communities. More research is needed to describe the composition and temporal changes of spider communities in this region and to experimentally assess the relative importance of the habitat structure, prey availability and climatic factors in the biology of these predators.

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