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Source: Journal of Arachnology, 42(1):34-43. 2014.
Published By: American Arachnological Society
DOI: http://dx.doi.org/10.1636/P13-73.1
URL: http://www.bioone.org/doi/full/10.1636/P13-73.1

2014. The Journal of Arachnology 42:34–43

Vertical stratification of spider assemblages in two conifer plantations in central Japan

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Abstract. We compared the structure of spider assemblages between the upper and lower canopy layers, and between the canopy and forest floor, in plantations of evergreen cedar (*Cryptomeria japonica*) and deciduous larch (*Larix kaempferi*). The estimated number of species was similar between the upper and lower canopy layers (49.0 *vs* 45.1) in *C. japonica*, but was noticeably smaller in the upper canopy layer (11.3) than in the lower layer (36.9) in *L. kaempferi*. Arboreal spider assemblages in the canopy differed significantly between the upper and lower layers in both *C. japonica* and *L. kaempferi* stands, based on an abundance-based measure. However, based on an incidence-based measure, they only differed significantly between layers in the *L. kaempferi* stand. The spider assemblages also differed distinctly between the canopy and the forest floor in both stands. Wandering spiders and orb-web builders were dominant in the canopy, while space-web builders dominated the forest floor in the *C. japonica* stand. In the *L. kaempferi* stand, wandering spiders dominated both the canopy and the forest floor. Our results suggested that spider assemblages in conifer plantations were distinctive among strata because of differences in such factors as resource quality (i.e., living or dead foliage) and association with adjacent layers along the vertical gradient of the forests.

Keywords: Community composition, forest canopy, forest floor, functional groups

Vertical stratification in forests both above ground and at ground level is attributed to the variability of the three-dimensional spatial arrangement of trees and other structural elements (Ishii et al. 2004). Forest canopies provide various food resources such as leaves, fruits, and seeds and diversified microhabitats based on the structural complexity of foliage and twigs, resulting in a high abundance and diversity of arthropods (Lawton 1983; Basset et al. 2003). The forest floor also contains a mixture of organic resources such as leaf litter, fungi, and dead wood, with a continuous stratum packed into a thin layer (Lavelle & Spain 2005). Spiders (Arachnida: Araneae) are one of the most prevalent groups of predatory arthropods in species diversity and biomass, both in the canopy and on the forest floor (Moulder & Reichle 1972; Basset 1991; Wise 1993). These groups occupy a highly diversified set of habitats, ranging from various plants to the soil itself, construct a variety of web structures (or no web for many forest-floor species) and exhibit broad feeding behaviors.

The canopy and forest floor have different architectures derived from the substrates that exist in each stratum, which could be a determining factor of the structure of spider assemblages. Previous studies have revealed that the foliage structural complexity of the canopy and vegetation, such as foliage density and number of leaves and branchlets, affected spider species composition (Gunnarsson 1988, 1990; Sundberg & Gunnarsson 1994; Halaj et al. 2000; De Souza & Martins 2005; Corcuera et al. 2008). Likewise, the structural complexity of forest-floor litter and understory vegetation, such as litter depth, litter shape, interstitial space/volume, and ground cover by plants, can influence spider assemblages on the forest floor (e.g., Uetz 1975, 1979; Bultman & Uetz 1982; Docherty & Leather 1997; Bultman & Dewitt 2008). The canopy and forest-floor strata can provide different microhabitats for arthropods, presumably leading to different spider assemblages among the strata.

Even-aged and monoculture forest plantations usually have simple architecture compared to natural forests, and thus they are good model systems for examining the effects of the vertical structure of forests on biological communities. Japanese cedar *Cryptomeria japonica* D. Don and Japanese larch *Larix kaempferi* [Lamb.] Carrière, two endemic coniferous species in Japan, are general tree plantation species that provide different microhabitats for forest arthropods. For example, the seasonal stability of microhabitats differs between the two species: *C. japonica* is an evergreen species, whereas *L. kaempferi* is deciduous. *Cryptomeria japonica* trees usually have a large amount of dead foliage attached to their trunks in the lower part of the canopy (Yoshida & Hijii 2006), whereas in *L. kaempferi* forests, most of the foliage is alive in both the upper and lower layers until the period of leaf fall in late autumn (from October to November: Miyaura & Hozumi 1988). The structural complexity of foliage also differs greatly; thicker, harder, and more complex foliage forming needle-like leaves in *C. japonica*, compared to the soft and clumped needles of *L. kaempferi*. These differences in spatial and temporal traits between habitats and between tree species should affect the composition of spider assemblages in the canopy and on the forest floor.

In the present study, we investigated the community structures of arboreal and ground-dwelling spiders in *C. japonica* and *L. kaempferi* plantations to test two hypotheses: 1) compositions of arboreal spider species differ between the upper (living foliage) and lower (dead foliage) layers of the *C. japonica* canopy, but not of *L. kaempferi* due to its similarities

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between upper and lower layers; and 2) spiders have different community structures in the canopy and on the forest floor due to the difference of habitat resources, such as elongate foliage and accumulated litter.

METHODS

Study site.—The study was carried out in a 38-year-old (as of 2008) *C. japonica* plantation and a 15-year-old *L. kaempferi* plantation in the Experimental Forest of Nagoya University, in central Japan (35°11′N, 137°33′E; 980 to 1000 m a.s.l.). Annual rainfall at this site averages 2100 mm, and the mean annual air temperature is 9.7 °C (2008). Both stands are embedded in a forested area and are more than 1000 m from each other. Tree height and height at the lower edge of the canopy are 24 m and 7 m in the *C. japonica* stand, and 10 m and 2 m in the *L. kaempferi* stand, respectively. In the *C. japonica* stand, the canopy is almost closed due to more densely packed and elongated, thickened branches in the upper layer and large numbers of dead leaves and branches remaining attached to the trunk of each tree in the lower layer (Yoshida & Hijii 2006). Thus the lower layer is similar in overall architecture to the upper layer. In the *L. kaempferi* stand, the canopy is more open due to less crowding of branches mixed in with some young broadleaf trees in the understory. The canopy of each stand was divided into upper and lower layers at the following points: in *C. japonica* at the uppermost height of dead leaves and branches attached to the tree stems (ca. 15 m above the ground), and in *L. kaempferi* at half the length of the canopy (ca. 6 m above the ground). The vertical lengths of the upper and lower layers of the canopy are 9 m and 8 m in *C. japonica*, 4 m and 4 m in *L. kaempferi*, respectively. Five trees of each species were selected for sampling of the spider assemblages. The sampled *C. japonica* trees were located near a 20-m tower and had a mean height (± SD) of 22.6 ± 0.4 m and a mean diameter at breast height of 23.9 ± 1.8 cm. The *L. kaempferi* trees sampled have a mean height of 9.1 ± 0.9 m and mean diameter of 10.1 ± 1.4 cm. The average thickness of the litter layer on the forest floor is less in the *C. japonica* stand (0.9 ± 0.4 cm) than in the *L. kaempferi* stand (3.4 ± 0.8 cm). However, many dead branches with foliage had accumulated on the ground in some parts of the *C. japonica* stand, increasing the local thickness of the litter layer (~ 6.8 cm) and thus causing a greater habitat heterogeneity on the forest floor than in the *L. kaempferi* stand (T. Yoshida, unpubl. data).

Spider sampling.—Spiders were collected from three habitats (upper and lower layers of canopies, and forest floor) in each tree stand at one-month intervals from 10 July to 19 December 2008. We accessed the canopies by using a 20-m tower in the *C. japonica* stand and by climbing on a connectable tube ladder on the trunks of *L. kaempferi* trees. Three branches in each layer were randomly selected for spider collection. Spiders were dislodged by beating the branches with a 1.8-m bamboo stick and were trapped with a fine net (0.2-mm mesh size; 60 cm in aperture diameter of a round frame). The spiders were quickly collected with a vacuum sampler and preserved in 70% ethanol. Spiders on the forest floor were collected using pitfall traps, which consisted of 400-cm^3 plastic cups with openings 7.5 cm in diameter. Each trap contained 100 ml of water, with small amounts of detergent to prevent the animals from floating, and one to two grams of sorbic acid for preservation. Ten traps were set at least 5 m apart from each other in a transect on the forest floor of each stand, the openings level with the ground surface (not with the top of the litter layer), and collected after a week.

Spiders were first sorted to genus, and then morphospecies or identified to described species according to the keys and descriptions of Chikuni (1989) and Ono (2009). We recorded the number of individuals in each species for each habitat, each forest stand, and each month. Voucher specimens were deposited in the Laboratory of Forest Protection, Nagoya University, Japan. Using the information in Shinkai (2006) and Ono (2009), we divided these species into four functional groups, which included the guilds reported by Halaj et al. (1998, 2000), Hatley & MacMahon (1980), Uetz et al. (1999) and Cardoso et al. (2011): 1) space-web builders, including hackled-band weavers (Dictynidae), sheet-web weavers (Cybaeidae, Agelenidae, and Linyphiidae) and cobweb spiders (Theridiidae); 2) orb-web weavers (Uloboridae, Araneidae and Tetragnathidae); 3) wandering spiders, including jumping spiders (Salticidae), ambushers (Thomisidae) and running spiders (Philodromidae and Lycosidae), nocturnal hunters (Clubionidae, Anyphaenidae and Gnaphosidae), and a part of Theridiidae and Araneidae that have wandering foraging strategies (Shinkai 2006); and 4) edaphic spiders (Antrodiaetidae).

Data analysis.—We excluded juveniles and unidentified individuals prior to the analyses. Spiders collected from each habitat (i.e., upper canopy, lower canopy and forest floor from both tree species) were pooled for each month; hence, all analyses were based on six monthly samples within each habitat. We quantified the diversity of spider assemblages in each habitat using EstimateS 8.2 (Colwell 2009). With a bootstrap estimator, we randomized the data 100 times and calculated the estimated number of species (S_{est}). Using EstimateS, we also calculated 95% confidence intervals of the observed species richness (using MaoTau function).

We used permutational multivariate analysis of variance (PERMANOVA: Anderson et al. 2008) to assess the effects of forest stand (*C. japonica* and *L. kaempferi*), layer (upper and lower canopy), sampling month and their interactions on canopy spider assemblages. Likewise, we investigated the effects of stand and month on the forest floor spider assemblages. The design of the analysis is analogous to a repeated measures ANOVA, where we treated the effect of monthly variation as a random effect factor and the differences in stand and layer as fixed factors. Although PERMANOVA was developed primarily for multivariate analysis, univariate analysis is possible using Euclidean distances, which yield Fisher's traditional univariate *F* statistic (Anderson et al. 2008). Type III sums of squares were used to calculate *F* statistics (pseudo-*F* statistics: Anderson et al. 2008). *P* values were calculated using 4999 permutations of residuals under a reduced model. Post-hoc pair-wise analyses were conducted for some of the variables by calculating *t* statistics and *P* values using 4999 permutations of the data (available within PERMANOVA routine: Anderson et al. 2008). We also used non-metric multidimensional scaling (NMDS) ordinations, available in PRIMER6 (Clarke & Gorley 2006), to visually represent the species compositions

Table 1.—Species richness of spiders in the upper (UC) and lower canopies (LC) and on the forest floors (FF) of the *Cryptomeria japonica* (CJ) and *Larix kaempferi* (LK) stands.

		CJ			LK		
		UC	LC	FF	UC	LC	FF
Number of individuals[1]	*n*	832	889	39	662	888	299
Number of observed species	S_{obs}	43	40	16	11	34	27
Number of estimated species	S_{est}	49	45.1	19.5	11.3	36.9	31.5

[1] Excluding juvenile and unidentified individuals.

of canopy spiders in the upper and lower layers of the *C. japonica* and *L. kaempferi* stands. We did not use NMDS ordinations for the forest floor spiders because we collected very few individuals in the *C. japonica* stand (Table 1). Ordinations were conducted based on the abundance-based (Bray-Curtis index) and incidence-based (Sørensen index) similarity measures, with 25 restarts.

RESULTS

Spider assemblages in the canopy.—In total, we collected 3,609 individuals (excluding 51 juveniles and unidentified individuals), representing 100 species and morphospecies from both the canopy and forest floor during the study period (Appendix 1). We collected 43 (with 95% confidence interval of ± 8.7) and 40 ± 8.8 spider species in the upper and lower canopy layers of the *C. japonica* stand and 11 ± 0 and 34 ± 3.9 species in the *L. kaempferi* stand, respectively (Table 1). The estimated number of arboreal species was similar between in the upper (49.0 species) and lower canopy layers (45.1 species) in *C. japonica*, but was noticeably smaller in the upper canopy layer (11.3 species) than in the lower layer (36.9 species) in *L. kaempferi* (Table 1). With the exception of the upper layer of *L. kaempferi*, the estimated species richness fell within 95% confidence intervals of the observed number of species.

Species richness of arboreal spiders was significantly influenced by stand and layer, although their interaction effect was also significant (Table 2). Post-hoc pair-wise comparisons showed that species richness was significantly greater in the lower than in the upper layer in *L. kaempferi* ($t = 0.24$, $P < 0.05$), but not *C. japonica* ($t = 0.24$, $P = 0.81$). Unlike species richness, monthly variation was the only (but highly significant) factor influencing spider abundance (Table 2). The densities of spiders in both canopy layers peaked from August to October in both stands and then tended to decrease toward December (Fig. 1a, b).

Among the functional groups, wandering spiders were a significantly more abundant and species-rich group than orb-web weavers and space-web builders in the canopies of both the *C. japonica* and *L. kaempferi* stands (PERMANOVA, pseudo-$F = 12.8$, $P < 0.001$ for abundance; pseudo-$F = 12.6$, $P < 0.001$ for species richness: see Fig. 2a, b). Orb-web weavers were the second most abundant group in the *C. japonica* canopy, whereas space-web builders were much more abundant than orb-web weavers in the *L. kaempferi* canopy. The proportions of orb-web weavers were lower in abundance but higher in species richness in the lower canopy of the *L. kaempferi* stand (Fig. 2a, b). Statistical tests showed that the stand had a significant influence on proportional abundances of space-web builders and orb-web weavers, whereas the layer was only

Table 2.—Summary results of PERMANOVA, showing pseudo-*F* values and degrees of freedom (*df*) of stand, layer, month and their interaction effects on spiders collected from the canopy. Spiders were analyzed using species composition (assemblage), total abundance, species richness and three major functional groups, based on the abundance-based (upper half of the table) and incidence-based (lower) data. Functional groups were analyzed using proportional abundance (upper) or species richness (lower) per site.

	df	Assemblage (abundance-based)		Abundance		Prop. abund. SW		Prop. abund. OW		Prop. abund. WS	
Stand	1	7.33	**	0.87	n.s.	13.01	*	15.73	*	3.27	n.s.
Layer	1	8.09	**	6.25	n.s.	1.82	n.s.	35.89	**	0.58	n.s.
Month	5	8	***	35.96	***	32.08	**	7.48	*	17.22	**
Stand × Layer	1	5.86	*	1.71	n.s.	1.24	n.s.	9.28	*	0.08	n.s.
Stand × Month	5	5.68	***	0.25	n.s.	16.43	**	14.09	**	11.91	**
Layer × Month	5	1.06	n.s.	0.77	n.s.	2.1	n.s.	1.22	n.s.	1.73	n.s.
Residual	5										

	df	Assemblage (incident-based)		Species richness		Prop. species SW		Prop. species OW		Prop. species WS	
Stand	1	7.86	**	99.46	**	0.79	n.s.	2.76	n.s.	0.06	n.s.
Layer	1	6.3	**	14.43	*	0.002	n.s.	18.1	*	19.16	*
Month	5	6.08	**	8.39	*	22.18	**	1.74	n.s.	15.67	**
Stand × Layer	1	9.35	*	7.35	*	1.93	n.s.	7.38	*	17.54	**
Stand × Month	5	5.45	**	0.23	n.s.	14.42	**	2.22	n.s.	14.76	**
Layer × Month	5	1.51	n.s.	0.63	n.s.	2.43	n.s.	0.92	n.s.	0.87	n.s.
Residual	5										

*: $P < 0.05$.
**: $P < 0.01$.
***: $P < 0.001$.
n.s.: $P > 0.05$.
SW: Space-web builders, OW: Orb-web weavers, WS: Wandering spiders.

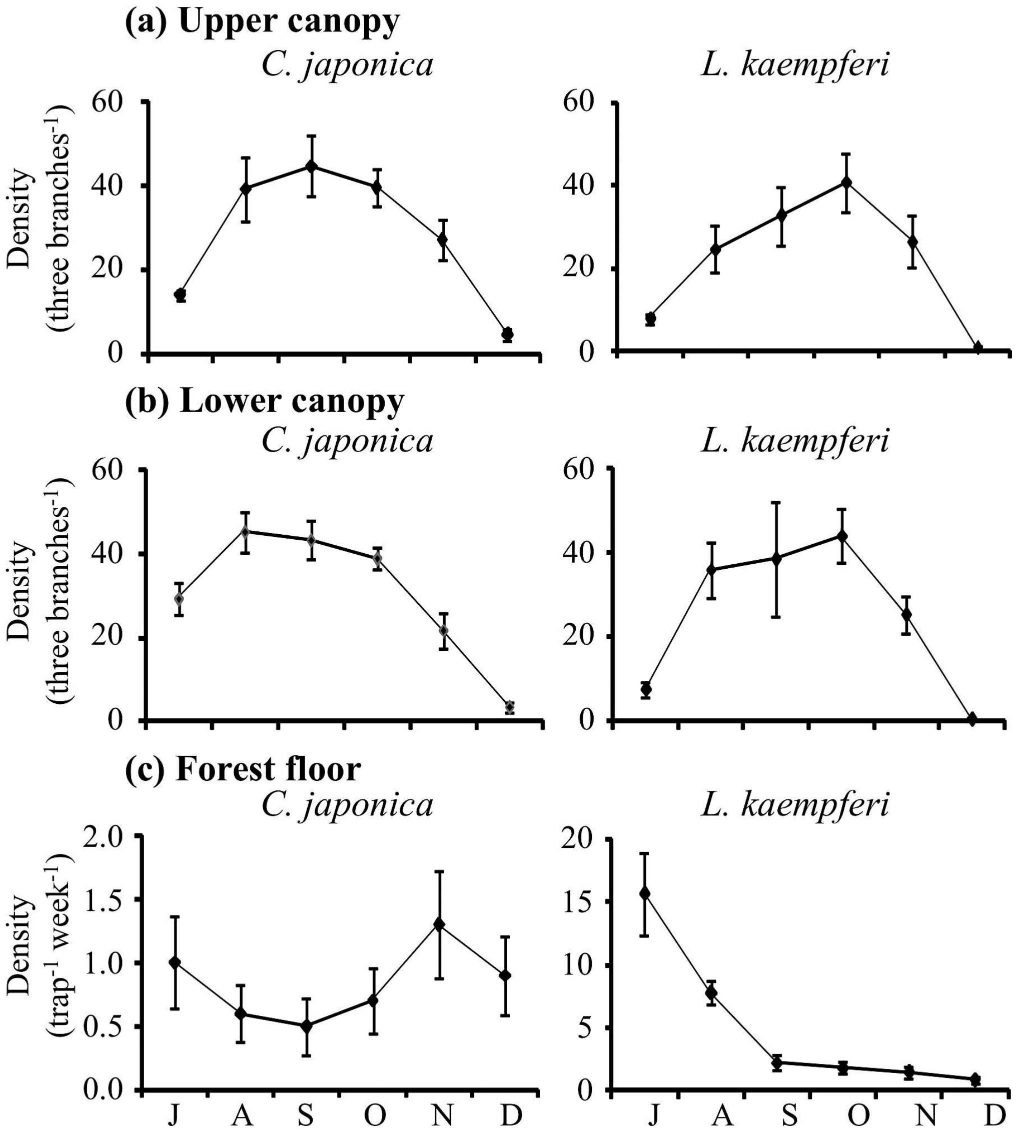


Figure 1.—Seasonal changes in the densities of spiders in the a) upper and b) lower layers of the canopy and c) on the forest floors in the *Cryptomeria japonica* and *Larix kaempferi* stands. Values represent mean ± standard error.

significant with respect to orb-web weavers (Table 2). However, as suggested by the significant interaction effect of stand and month, proportional abundances of space-web builders were higher in *L. kaempferi* than in *C. japonica*, but marked differences were observed in winter only (viz. November and December: Table 2, Fig. 2a). Likewise, proportional abundances of orb-web weavers were generally greater in *C. japonica*, but the differences were much greater in lower layers in early summer (July). Monthly variation was significant in abundances of all three functional groups; however, the differences were more pronounced within the *L. kaempferi* canopy than within *C. japonica* (Table 2, Fig. 2a). A significantly greater proportional species richness of wandering spiders was observed within the upper than the lower canopy layers in *L. kaempferi*, but similar trends were not observed in *C. japonica*, presumably due to the interaction effect between stand and layer (Table 2, Fig. 2b). Likewise, a greater proportional species richness of orb-web spiders was observed in the lower than in the upper canopy layers of *L. kaempferi*, but not in *C. japonica* (Table 2, Fig. 2b). Significant monthly variations were suggested for wandering spiders; however, due to the presence of interaction effects, such a variation was observed only in *L. kaempferi*, where the species richness declined to zero in winter. As opposed to wandering spiders, proportional species richness of space-web spiders increased in winter in the *L. kaempferi* stand (Table 2, Fig. 2b).

The community compositions of arboreal spider species according to both the abundance-based and incidence-based measures differed significantly between stands and between layers; however, there was also an interaction effect between these two factors (Table 2). NMDS ordinations and post-hoc pair-wise comparisons showed that all four treatments significantly separated species assemblages when using abundance-based Bray-Curtis measures (Fig. 3). When we used incidence-based Sørensen measures, however, spider assemblages did not differ significantly between the upper and lower canopies of the *C. japonica*.

Spider assemblages on the forest floor.—We sampled 39 individuals of 16 (with 95% confidence interval of ± 6.6)

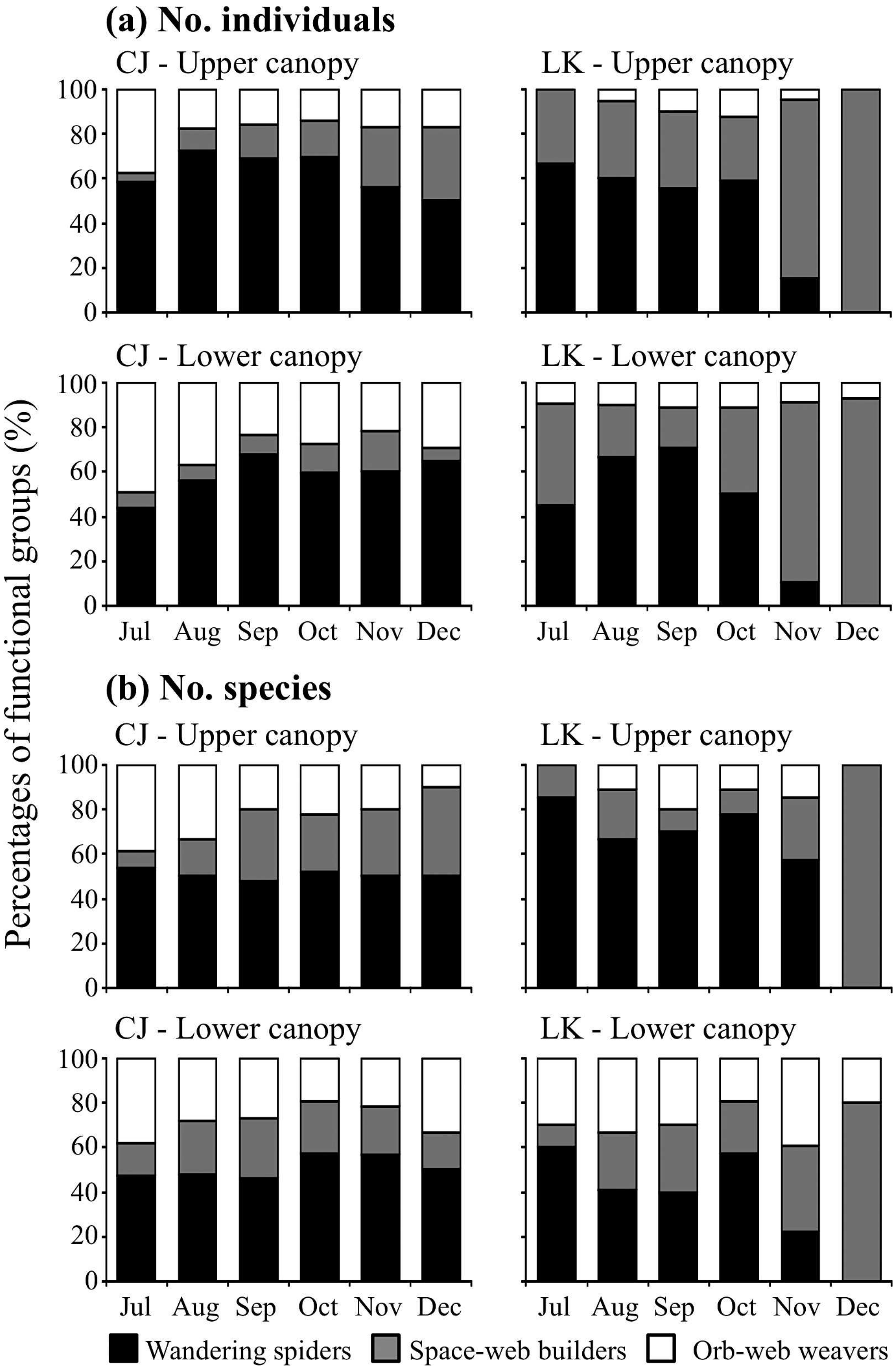
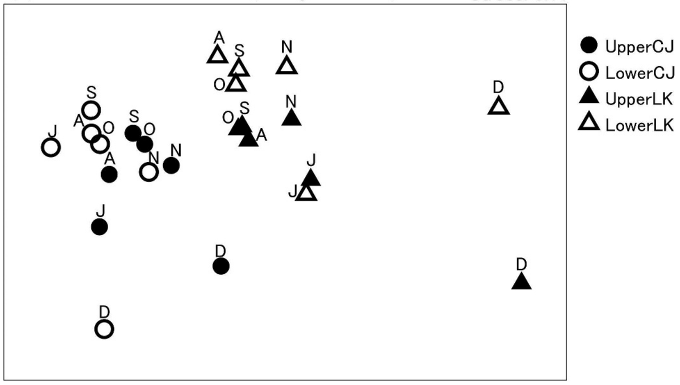


Figure 2.—Seasonal changes in the percentages (%) of a) individuals and b) species richness of functional groups in the upper and lower layers of the canopy in the *Cryptomeria japonica* (CJ) and *Larix kaempferi* (LK) stands.

species (excluding juveniles and unidentified individuals) and 299 individuals of 27 ± 5.3 species on the forest floors of the *C. japonica* and *L. kaempferi* stands, respectively (Table 1). Only three spider species were found both in the canopy and on the forest floor: *Octonoba sybotides* (Bösenberg & Strand 1906), *Tetragnatha yesoensis* S. Saito 1934 and *Pseudomicrargus latitegulatus* (Oi 1960) (Appendix 1). The estimated number of forest-floor species (19.5 species) was smaller than those in the

(a) Abundance-based (Bray-Curtis)



(b) Incidence-based (Sørensen)

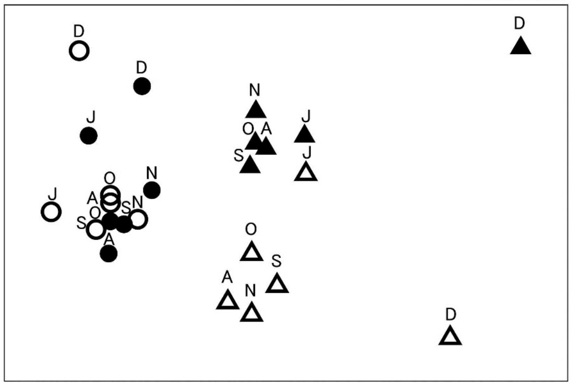


Figure 3.—Nonmetric multidimensional scaling ordination plots for spider assemblages in the upper and lower layers of the canopy in the *Cryptomeria japonica* (CJ) and *Larix kaempferi* (LK) stands according to a) abundance-based (Bray-Curtis index) and b) incidence-based (Sørensen index) similarity measures. J: July, A: August, S: September, O: October, N: November, D: December.

upper (49.0 species) and lower canopy layers (45.1 species) of *C. japonica*, whereas the value for the forest floor in *L. kaempferi* (31.5 species) was larger than that in the upper canopy layer (11.3 species). The active density of ground-dwelling spiders on the forest floor of the *C. japonica* stand was relatively constant across the study period, whereas the density showed a peak in July and tended to decrease toward December on the forest floor of the *L. kaempferi* stand (Fig. 1c).

The abundance of space-web builders accounted for a greater proportion than that of wandering spiders in the *C. japonica* stand, whereas the opposite was found within the *L. kaempferi* stand (Fig. 4). Few orb-web weavers and edaphic spiders were collected throughout the study period.

DISCUSSION

Our results showed that arboreal spider assemblages assessed by the abundance-based measure differed significantly between the upper and lower layers of the *C. japonica* and *L. kaempferi* stands, but those assessed by the incidence-based measure differed significantly between layers of the *L. kaempferi* stand only. This result may partly support the first hypothesis that different spider assemblages would be established between the upper and lower layers of *C. japonica* trees because of differences in potential resources for spider habitats between the layers (i.e., living foliage versus dead foliage). Two possible factors may be responsible for the existence of different spider assemblages within the canopy of *C. japonica* and *L. kaempferi* stands. First, arboreal spiders might prey on phytophagous arthropods in the upper canopy layer and on detritivorous microarthropods in the lower layer of *C. japonica* trees. The different composition of spider assemblages within the canopy might not depend on the physical structure of the habitats because the structural complexity was not so different between the upper layer (mainly living foliage) and lower layer (dead foliage) of the canopy in *C. japonica*. Shimazaki & Miyashita (2005) suggested that on the forest floor in *C. japonica* stands, smaller web-building spiders depend more on the prey derived from the detrital food web than do larger spiders. Although we did not perform a quantitative comparison, the evidence that detrital microarthropods (e.g., Collembola) were abundant specifically on the dead foliage of *C. japonica* (Yoshida & Hijii 2005) supports the dominance of smaller spiders in the lower layer of the canopy.

Second, the difference in spider assemblages between the canopy layers in the *L. kaempferi* stand was attributed to a large number of less abundant species (mainly orb-web weavers) in the lower layer (these species were largely absent in the upper layer). The less abundant species might colonize from understory vegetation that is next to the lower canopy layer. Although we did not collect spiders from this layer, some studies have shown that understory vegetation shared some spider species with those found on the canopy (Sørensen 2003; Larrivée & Buddle 2009; Aikens & Buddle 2012; Pinzon et al. 2013). Turnbull (1960) reported that in general spider species were stratified across the vertical structure of forests, but that they also frequently extended their distributions beyond each of their preferred strata. Pinzon et al. (2013) showed a species turnover along the vertical gradient (forest floor, understory and lower canopy) of white spruce stands. Pinzon et al. (2013) predicted that the community composition in the upper canopy was also different from other strata, and Aikens & Buddle (2012) and our result support their prediction.

Several studies have shown that the community composition of spiders differed between the canopy and forest floor, but that some spider species shared strata in coniferous (Pinzon et al. 2013), deciduous (Turnbull 1960), and montane (Sørensen 2003) forests. Pinzon et al. (2011) showed that spiders on the forest floor are more similar to those in the canopy than to those on the understory vegetation, suggesting that the two habitats could be linked by spiders moving along tree trunks. Our findings, however, indicated that the canopy habitats shared few spider species with the forest floor in the *C. japonica* and *L. kaempferi* stands. The reason is unknown, but may be attributed to the microenvironment of tree trunks (e.g., bark structure) and understory vegetation (e.g., biomass and/or architecture), which can serve as a 'habitat filter' between the canopy and forest floor.

The proportions of functional groups also differed between the canopy and forest floor. Wandering spiders were dominant in both layers in the *L. kaempferi* stand, whereas wandering spiders and orb-web builders were dominant in the canopy and space-web builders on the forest floor in the *C. japonica* stand. Although we need to be cautious about differences in sampling methods, this difference between the layers could be

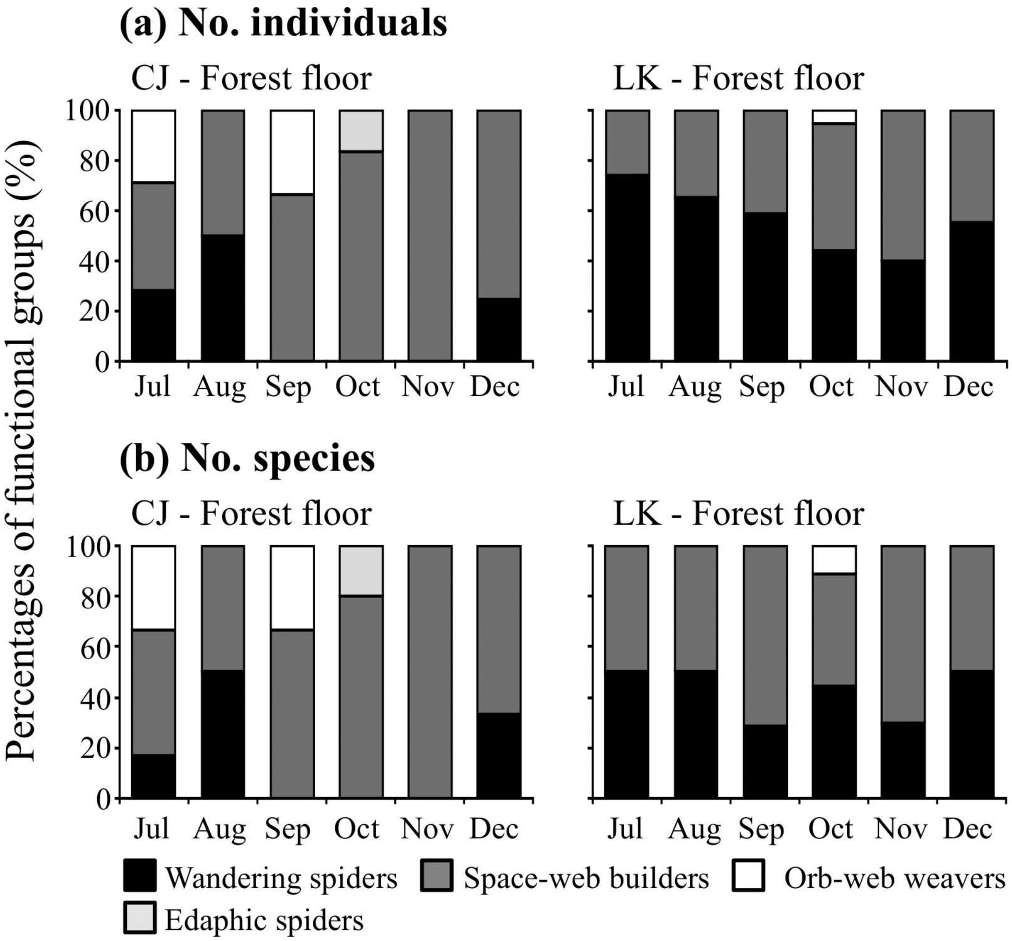


Figure 4.—Seasonal changes in the percentages (%) of a) individuals and b) species richness of functional groups on the forest floors in the *Cryptomeria japonica* (CJ) and *Larix kaempferi* (LK) stands.

related to the differences in structural complexity of the habitat substrates. Field manipulations of foliage density by Hatley & MacMahon (1980) and Halaj et al. (2000) showed that wandering spiders decreased with the removal of foliage, but increased when branches were tied up, as opposed to web-building spiders, which showed weaker responses to foliage manipulations. In our study, the relative abundances of wandering spiders in the *L. kaempferi* canopy substantially decreased in November and were almost absent in December. This would be due to the decrease in structural complexity of foliage associated with the seasonal leaf fall of *L. kaempferi* in late autumn (Miyaura & Hozumi 1988). Thus, both the canopies of *C. japonica* and *L. kaempferi* trees would provide dense foliage structures more favorable for wandering spiders than for web builders. On the forest floor of the *C. japonica* stand, branches with dead foliage made a structurally heterogeneous litter layer with much interstitial space. The structural complexity of the accumulated litter layer allowed a greater abundance of web-building spiders (Bultman & Uetz 1982), and space-web builders are known to build webs in narrow spaces, such as those formed between the needles of conifer trees (Stratton et al. 1979). Accordingly, the space-web builders might have dominated the forest floor of the *C. japonica* stand.

In conclusion, our analyses in the *C. japonica* and *L. kaempferi* stands suggest that distinctive spider assemblages were established between vertical strata, reflecting the differences in factors, such as resource quality (i.e., living- or dead foliage, accumulated litter) and association with adjacent layers, along the vertical gradient of the forests. Basset et al. (2003) noted that arthropod stratification in forests could be determined by four types of factors: abiotic factors, forest physiognomy and tree architecture, resource availability and arthropod behavior. Further quantitative approaches related to these factors are required for a comprehensive understanding of the vertical stratification and horizontal spacing of spider assemblages in forest ecosystems.

ACKNOWLEDGMENTS

We thank Mr. Y. Imaizumi, Mr. N. Yamaguchi, Mr. N. Takabe and all the members of the Laboratory of Forest Protection, Nagoya University, for their assistance with fieldwork. This study was funded by the Japan Society for the Promotion of Science KAKENHI program (grant numbers 17380091, 21380093 and 24780144).

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Manuscript received 10 May 2013, revised 16 December 2013.

Appendix 1.—Numbers of individuals of spiders collected from upper (UC) and lower layers (LC) of the canopy and forest floor (FF) in the *Cryptomeria japonica* (CJ) and *Larix kaempferi* (LK) stands. Juveniles and unidentified spiders (denoted by asterisks) were not included in the analyses.

Functional group		CJ			LK		
family	species	UC	LC	FF	UC	LC	FF
Edaphic spiders		**0**	**0**	**1**	**0**	**0**	**0**
Antrodiaetidae	*Antrodiaetus roretzi* (L. Koch 1878)	-	-	1	-	-	-
Space-web builders		**131**	**89**	**30**	**279**	**336**	**99**
Agelenidae	*Alloclubionoides* sp.	-	-	-	-	-	1
	Coelotes personatus Nishikawa 1973	-	-	4	-	-	2
	Coelotes decolor Nishikawa 1973	-	-	1	-	-	2
	Coelotes gifuensis Nishikawa 2009	-	-	-	-	-	3
	Coelotes spp.	-	-	-	-	-	25
	Orumcekia satoi (Nishikawa 2003), n. comb.	-	-	3	-	-	12
	Tegecoelotes corasides (Bösenberg & Strand 1906)	-	-	1	-	-	-
	Agelenidae juvenile *	2	8	8	-	-	-
Cybaeidae	*Cybaeus nipponicus* (Uyemura 1938)	-	-	2	-	-	-
	Cybaeus kirigaminensis Komatsu 1963	-	-	4	-	-	-
	Cybaeus tottoriensis Ihara 1994	-	-	1	-	-	-
	Cybaeus sp.1	-	-	8	-	-	-
	Cybaeus spp.	-	-	-	-	-	3
Dictynidae	*Lathys maculosa* (Karsch 1879)	62	38	-	-	-	-
	Lathys sexoculata Seo & Sohn 1984	1	15	-	-	-	-
Hahniidae	*Hahnia corticicola* Bösenberg & Strand 1906	-	-	-	-	-	1
	Aprifrontalia mascula (Karsch 1879)	-	-	-	-	-	1
	Ceratinopsis setoensis (Oi 1960)	-	-	-	-	-	4
Linyphiidae	*Floronia exornata* (L. Koch 1878)	-	-	-	-	9	-
	Gonatium japonicum Simon 1984	-	-	-	-	-	1
	Neolinyphia fusca Oi 1960	-	-	-	-	4	-
	Neriene brongersmai (van Helsdingen 1969)	-	-	5	-	-	-
	Neriene spp.	-	-	-	-	-	3
	Nippononeta obliqua (Oi 1960)	-	-	1	-	-	35
	Porrhomma spp.	-	-	-	-	-	2
	Prolinyphia limbatinella (Bösenberg & Strand 1906)	4	11	-	-	-	-
	Pseudomicrargus latitegulatus (Oi 1960)	-	1	-	-	-	4
	Strandella yaginumai H. Saito 1982	-	1	-	-	-	-
	Turinyphia yunohamensis (Bösenberg & Strand 1906)	8	6	-	-	11	-
Theridiidae	*Anelosimus crassipes* (Bösenberg et Strand 1906)	1	-	-	-	-	-
	Chikunia albipes (S. Saito 1935)	-	-	-	-	3	-
	Chrysso foliata (L. Koch 1878)	-	-	-	-	3	-
	Coleosoma octomaculatum (Bösenberg & Strand 1906)	1	-	-	-	-	-
	Enoplognatha abrupta (Karsch 1879)	1	-	-	-	-	-
	Enoplognatha caricis (Fickert 1876)	-	-	-	-	1	-
	Episinus affinis Bösenberg et Strand 1906	2	3	-	2	4	-
	Euryopis flavomaculata (C. L. Koch 1836)	7	-	-	-	-	-
	Parasteatoda japonica (Bösenberg & Strand 1906)	1	1	-	-	-	-
	Phoroncidia altiventris Yoshida 1985	-	1	-	-	-	-
	Takayus chikunii (Yaginuma 1960)	5	1	-	-	-	-
	Takayus takayensis (S. Saito 1939)	37	11	-	277	273	-
	Yunohamella lyrica (Walckenaer 1842)	1	-	-	-	28	-
Orb-web weavers		**147**	**281**	**3**	**53**	**92**	**1**
Araneidae	*Alenatea fuscocoloratus* (Bösenberg & Strand 1906)	1	1	-	-	1	-
	Araneus acusisetus Zhu & Song 1994	21	23	-	2	13	-
	Araneus macacus Uyemura 1961	-	1	-	-	-	-
	Araneus rotundicornis Yaginuma 1972	-	-	-	-	1	-
	Araneus stella (Karsch 1879)	1	-	-	-	-	-
	Araneus uyemurai Yaginuma 1960	1	-	-	-	-	-
	Araneus viridiventris Yaginuma 1969	-	1	-	-	-	-
	Araneus spp.	6	12	-	-	-	-
	Araniella displicata (Hentz 1847)	6	-	-	-	-	-
	Araniella yaginumai Tanikawa 1995	-	-	-	-	6	-
	Cyclosa ginnaga Yaginuma 1959	-	-	-	-	2	-
	Eriophora sachalinensis (S. Saito 1934)	3	4	1	-	9	-

Appendix 1.—Continued.

Functional group		CJ			LK		
family	species	UC	LC	FF	UC	LC	FF
	Neoscona punctigera (Doleschall 1857)	1	-	-	-	-	-
	Neoscona scylla (Karsch 1879)	1	-	-	-	2	-
	Neoscona subpullata (Bösenberg & Strand 1906)	-	1	-	-	1	-
	Parazygiella disper (Kulczyñski 1885)	-	2	-	-	9	-
	Yaginumia sia (Strand 1906)	3	2	-	-	-	-
	Araneidae juvenile *	1	-	-	-	-	-
Tetragnathidae	*Leucauge subblanda* Bösenberg & Strand 1906	-	-	1	-	-	-
	Leucauge sp.	-	-	-	-	1	-
	Tetragnatha shinanoensis Okuma & Chikuni 1978	11	21	-	-	2	-
	Tetragnatha yesoensis S. Saito 1934	79	99	-	51	45	1
Uloboridae	*Octonoba sybotides* (Bösenberg & Strand 1906)	13	114	1	-	-	-
Wandering spiders		**554**	**519**	**5**	**330**	**460**	**199**
Anyphaenidae	*Anyphaena pugil* Karsch 1879	51	46	-	8	3	-
Araneidae	*Chorizopes nipponicus* Yaginuma 1963	1	1	-	-	-	-
Clubionidae	*Clubiona jucunda* (Karsch 1879)	69	22	-	-	-	-
	Clubiona kurosawai Ono 1986	2	5	-	-	5	-
	Clubiona lena Bösenberg & Strand 1906	-	-	-	-	-	1
	Clubiona spp.	46	30	1	11	29	1
Corinnidae	*Otacilia komurai* (Yaginuma 1952)	-	-	-	-	-	1
Gnaphosidae	*Drassyllus shaanxiensis* Platnick & Song 1986	-	-	-	-	-	9
	Drassyllus sasakawai Kamura 1987	-	-	-	-	-	2
	Drassyllus spp.	-	-	-	-	-	3
	Gnaphosa akagiensis Hayashi 1994	-	-	-	-	-	1
Lycosidae	*Pardosa laura* Karsch 1879	-	-	-	-	-	170
	Pirata clercki (Bösenberg et Strand 1906)	-	-	-	-	-	8
	Pirata yaginumai Tanaka 1974	-	-	4	-	-	-
Philodromidae	*Philodromus subaureolus* Bösenberg & Strand 1906	60	8	-	25	3	-
Salticidae	*Evarcha albaria* (L. Koch 1878)	-	-	-	-	3	-
	Evarcha sp.	-	-	-	-	1	-
	Plexippoides annulipedis (S. Saito 1939)	3	1	-	-	-	-
	Plexippoides doenitzi (Karsch 1879)	-	-	-	13	21	-
	Rhene atrata (Karsch 1881)	1	-	-	-	-	-
	Sibianor kochiensis (Bohdanowicz & Prószyñski 1987)	-	-	-	-	-	1
	Sibianor spp.	-	-	-	-	-	2
	Sitticus spp.	-	-	-	-	5	-
	Stertinius kumadai Logunov, Ikeda & Ono 1997	6	34	-	-	-	-
	Yaginumaella striatipes (Grube 1861)	15	20	-	-	-	-
	Salticidae juvenile *	-	1	-	-	-	-
Theridiidae	*Argyrodes cylindratus* Thorell 1898	-	5	-	-	-	-
	Ariamnes cylindrogaster Simon 1888	-	1	-	-	-	-
	Keijia sterninotata (Bösenberg et Strand 1906)	81	212	-	-	-	-
	Phycosoma amamiense (Yoshida 1985)	1	-	-	-	8	-
	Phycosoma mustelinum (Simon 1888)	45	11	-	-	-	-
	Rhomphaea sagana (Dönitz et Strand 1906)	-	1	-	-	-	-
Thomisidae	*Diaea subdola* O. Pickard-Cambridge 1885	128	13	-	74	71	-
	Lysiteles coronatus (Grube 1861)	32	15	-	160	241	-
	Synaema chikunii Ono 1983	12	94	-	39	61	-
	Tmarus rimosus Paik 1973	1	-	-	-	-	-
	Xysticus spp.	-	-	-	-	9	-
	Unidentified *	13	9	3	4	2	-
	Total	**848**	**907**	**50**	**666**	**890**	**299**