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Effects of Thinning on Spider Diversity of an East Asian Subtropical Plantation Forest

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Pao-Shen Huang, Hui-Chen Lin, I-Min Tso, and Chung-Ping Lin (2011) Effects of thinning on spider diversity in an East Asian subtropical plantation forest. *Zoological Studies* **50**(6): 705-717. Studies examining the effects of forest management on biodiversity in Asia are scarce and conducted mostly in temperate areas. In this study, the effects of the management on the biodiversity of a subtropical plantation forest were assessed by comparing the composition of spiders in *Chamaecyparis formosensis* plantations located in central Taiwan that received different degrees of thinning. Sampling plots were established in *C. formosensis* plantation stands receiving no, moderate, and heavy thinning treatments and a nearby natural broadleaf forest. The responses of spider communities in different strata of the plantation forests to thinning treatments varied. Heavy thinning treatment generated lower diversity indices in ground spiders and higher abundances in canopy spiders. Sampling plots in plantation stands receiving various thinning treatments differed in the compositions of ground, understory, and canopy spiders. Such composition variations resulted from abundance changes of ground weavers on the ground and orb weavers in the understory layer, which in turn seemed to be generated by reduced understory vegetation complexity due to the thinning treatments. Results of this study show that although thinning practices do not increase species richness in a subtropical *C. formosensis* plantation, they can generate alterations in understory vegetation structures which can lead to increased habitat heterogeneity and spider diversity in plantation forests. http://zoolstud.sinica.edu.tw/Journals/50.6/705.pdf

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There is growing concern about considering biodiversity conservation when conducting forest management, and studies investigating the responses of fauna and flora to forest management practices have recently increased (Fermon et al. 2000, Ohsawa 2004; Waltz and Covington 2004, Marra and Edmonds 2005, Ohsawa 2005, Yuan et al. 2005, Zausen et al. 2005, Ohsawa and Nagaike 2006, Ohsawa 2007). Currently, thinning is a commonly used practice, and such conduct can theoretically restore an ecosystem to a pre-disturbed state in such aspects as structure, function, and biodiversity (Hobbs and Norton 1996). Several studies showed that thinning might potentially alter the developmental trajectory of young stands, resulting in higher structural diversity and increased understory plant diversity (DeBell et al. 1997, Marañón et al. 1999, Thomas et al. 1999, Son et al. 2004). Thinning may also increase light inputs to the ground and consequently result in a diverse mosaic of microhabitats (Son et al. 2004). Some studies showed that stands receiving different degrees of thinning exhibit variations in several environmental parameters. Alterations in microhabitats in turn influence such aspects of animal communities as the number and diversity of niches, local abundance, and guild compositions (Waltz and Covington 2004, Homyack et al. 2005, Montaña et al. 2006, Maleque et al. 2007a b).

In Asia, studies examining the effects of forest

management on biodiversity are scarce, and most of them were conducted in temperate areas such as Japan. Studies conducted in Japan showed that among forests receiving different management practices, the compositions and community structures of beetles differed (Maeto et al. 2002), and thinning may increase the richness and abundance of many beetle taxa (Ohsawa 2004 2005 2007, Ohsawa and Nagaike 2006). Thinning may also influence the understory vegetation composition by creating new gaps (Igarashi and Kiyono 2008), or causing changes in dominant tree species and topographic variations (Ito et al. 2003). Such influences will significantly affect the fauna because various functional groups of insects were found to be positively correlated with the species richness of the understory vegetation (Maleque et al. 2007a b). However, all these conclusions were derived from studies conducted in Northeast Asian temperate forests with cool climates. Characteristics of temperate plantation forests considerably differ from those of warm and wet subtropical plantation forests, which constitute a vast area in East and Southeast Asia. Currently, information about the effects of thinning on the biodiversity of subtropical plantation forests in Asia is still limited.

Taiwan is an East Asian continental island, and nearly 60% of its area is covered by forests. Forests in Taiwan contain both subtropical and tropical elements, but the former is more dominant. In Taiwan, over the past few decades, studies examining the effects of thinning focused on the growth, productivity, and quality of commercial trees (Wang and Ko 1998, Wang et al. 2003). Only a few studies examined the impacts of thinning practices on microclimatic changes and biodiversity. Weng et al. (2007) showed that structural heterogeneity created by thinning significantly affected microclimates and generated higher-variation ranges in thinned stands. Yuan et al. (2005) suggested that thinning of plantation forests changed the vegetation structure by allowing more plant species to colonize the stand, which in turn had short-term impacts on various animal communities. However, Yuan et al. (2005) did not provide microhabitat data, and hence the proposed mechanisms generating the observed wildlife variations could not be confirmed. Concluding from the aforementioned studies, knowledge regarding how various levels of thinning generate microenvironmental variations and changes in wildlife communities in subtropical forests in Taiwan is still limited. To

determine appropriate management policies to enhance the biodiversity of subtropical plantation forests, it is essential to understand how thinning practices affect various environmental factors and consequently influence the composition and distribution of plant and animal communities.

In this study, the effects of thinning management on the biodiversity of a subtropical Asian plantation forest were assessed by comparing the community structure and guild composition of spiders in plantation forests of central Taiwan. Spiders are suitable ecological indicators to assess the effects of silvicultural practices on biodiversity. Many spiders rely on a distinct complex of microhabitats, and their diversity is sensitive to changes in environmental conditions (Cardoso et al. 2004a b, Ziesche and Roth 2008). There is evidence that habitat alterations and landscape heterogeneity due to forest succession, natural disturbances, or forestry practices generate significant changes in spider communities (Whitehouse et al. 2002, Gurdebeke et al. 2003, Clough et al. 2005, Finch 2005, Schmidt et al. 2005, Tsai et al. 2006, Schuldt et al. 2008, Ziesche and Roth 2008). Recent studies showed that structures of ground and understory vegetation and the associated microclimatic conditions are important factors determining the composition and distribution of spiders (Uetz 1991, Schuldt et al. 2008, Ziesche and Roth 2008). We first compared spider diversities between primary and plantation forests in central Taiwan. We then compared spider communities in plantation forests which had received different degrees of thinning. In addition, biotic and abiotic environmental factors were measured to identify key environmental variables contributing to the observed variations in spider diversity. Results of this study represent the first demonstration of the effects of thinning on arthropod diversity in East Asian subtropical plantation forests and their potential underlying mechanisms.

MATERIALS AND METHODS

Study sites

Study sites were established in a cypress (*Chamaecyparis formosensis*) plantation forest at Mt. Da-Shiue in a mid-elevation area of central Taiwan (24°15'40N, 120°59'18E). The elevation of the study sites ranged 1800-2000 m, and the gradient ranged 20°-25°. The *C. formosensis*

stands at Mt. Da-Shiue were established about 30 yr ago. We set up sampling plots in 3 stands of *C. formosensis* plantations: without thinning (the control stand, 8 ha in area), with moderate thinning (12 ha), and with heavy thinning (10 ha). Results of a preliminary survey conducted before thinning showed that the overall density of *C. formosensis* stands at Mt. Da-Shiue was about 900-1800 trees/ ha. Thinning was conducted in 2004 in 2 stands. In the stand receiving moderate thinning, 35% of the trees were removed, and the post-thinning density was around 1000 trees/ha. In the stand receiving heavy thinning, 45% of the trees were removed, and the post-thinning density was about 825 trees/ha. In the unthinned stand, the density was around 1200 trees/ha. In each plantation type, we set up 9 sampling plots, and the distance between the nearest neighbors was about 50 m. Sampling plots were located in the center of each plantation stand, and the distance of any plot to the edge of the stand was more than 100 m to avoid edge effects. In addition, sampling plots were also established in a broadleaf forest (dominated by Lauraceae and Fagaceae) near the heavily thinned stand to serve as a control. Overall, 36 sampling plots were established in 4 forest types.

Although the plots in each forest type were located in a single stand and thus might incur pseudoreplication problems, we regarded these sampling plots as independent of each other. Because of spiders' unique foraging requirements, these small-bodied organisms are very sensitive to fine-scale microhabitat characteristics (Ziesche and Roth 2008). The dispersal abilities of spiders range from small-scale cursorial dispersal to large-scale ballooning, which result in variable responses depending on the groups associated with different microhabitats (Bonte et al. 2004, Herrmann et al. 2010). Most of the spiders in our study area were rather small (with body lengths less than 5 mm), and many of them (such as all types of web builders) are sit-and-wait predators that exhibit very limited movement ranges (Foelix 1996). Considering the limited mobility, small size, and sensitivity to local microhabitats of spiders in our study site, sampling plots separated by a distance of 50 m can reasonably be treated as independent samples.

Specimen collection

Four field trips were conducted in Nov. of 2005, Feb., May, and Aug. of 2006. In each sampling plot, a set of pitfall traps was established

to collect ground spiders. Each set of pitfall traps consisted of 4 plastic cups and 3 polystyrene plastic sheets arranged in a Y form (1 trap at each end of the Y and 1 in the middle). The polystyrene plastic sheets (40 cm high and 100 cm long) were placed between the pitfall traps to enhance the efficiency of catching ground spiders. The cup was 15 cm in height and 10 cm in diameter and was covered by a plastic plate secured with sticks to prevent fallen leaves or rainwater from entering. On each field trip, each trap was filled with 500 ml of 70% alcohol (evenly distributed among the 4 cups) and was left open for 7 d. Sweep nets were used to collect spiders in the understory vegetation. The collector swept back and forth from ground-layer herbs to shrubs up to 2 m in height until all vegetation in the sampling plot had been thoroughly swept. To standardize the collection effort, the operation time of sweep-netting was designated as 5 min. Spiders in the canopy were collected by sweeping tree branches in the sampling plot (up to 10 m high) with insects nets (80 cm in diameter and 120 cm long) mounted on 8-m-long fishing poles. One collector stood in the center of the plot, put the branches in the net, and then shook them vigorously until all branches within the sampling plot had been thoroughly sampled. We standardized the effort by sampling each plot for 10 min.

Invertebrate specimens were classified into spiders, insects, and other arthropods. Spiders were separated into adults and juveniles, and adult spiders were sorted into morphospecies and if possible identified to species by the palpal organ or epigynum. Juvenile spiders were sorted into families. In addition, we used classification systems given in Uetz et al. (1999), Höfer and Brescovits (2001), and Tsai et al. (2006) to categorize adult and juvenile spiders into foraging guilds according to the spider's web-building and prey-catching behaviors. Spiders were assigned to the following guilds: (1) orb weaver (Araneidae and Tetragnathidae); (2) space weaver (Dictynidae, Pholcidae, and Theridiidae); (3) ground weaver (Hahniidae, Liocranidae, and Linyphiidae); (4) foliage runner (Clubionidae, Mimetidae, Oxyopidae, Philodromidae, Pisauridae, Salticidae, Scytodidae, and Thomisidae); (5) ground runner (Gnaphosidae, Lycosidae, Oonopidae, and Zodariidae); and (6) ground sedentary weaver (Agelenidae and Amaurobiidae). Insects obtained from each sampling plot were weighed after being oven-dried at 60°C for 2 d. Their dry biomass was used as an indication of environmental productivity

and was incorporated in subsequent multivariate analyses assessing relationships between spider diversity and environmental factors.

Quantification of environmental factors

We measured environmental variables to identify the factors responsible for differences in spider composition among forest types. We used data loggers to monitor the temperature and relative humidity (RH) of sampling plots. In each sampling plot, 1 data logger (HOBO Pro series, thermograph/hygrometer, Onset, Bourne, MA, USA) was placed at a height of 1 m, and during each field trip, data were recorded for 1 wk. Leaf litter was collected from 4 randomly selected 30 × 30-cm quadrants (with an overall collecting area of 0.36 m^2 per plot) within sampling sites. The leaf litter was carried back to the laboratory and weighed before and after being oven-dried at 40°C for 1 wk. To quantify the vegetation structure, we measured the percent canopy cover (PCC) and understory vegetation structural complexity (as the understory vegetation density; UVD) of each sampling plot. A fish-eye lens mounted on a Nikon 4500 digital camera (Tokyo, Japan) was used to measure the PCC. The camera was mounted on a tripod placed in the center of the sampling plot with the lens facing upward to take hemispheric photographs. Photographs were analyzed by a Gap Light Analyzer, vers. 2.0 (Frazer et al. 1999) after being transformed into black-and-white images. To quantify the UVD, we used a red cloth (1 × 1 m) as the background and estimated the density of vegetation in front of it. The red cloth was held by 1 person standing at each of the 4 cardinal edges of the sampling plot. Another person standing in the center of the plot took pictures of the red cloth and the vegetation in front of it with a Nikon 4500 digital camera. To represent the vertical stratification of the understory vegetation, the cloth was placed at 2 different heights (from ground to 100 cm and from 100 to 200 cm). These photographs were transformed into black-and-white images using Photoshop (Adobe Systems; Mountain View, CA, USA), and data from the 4 cardinal directions and 2 heights were averaged as the UVD of the plot.

Statistical analysis

Previous studies demonstrated that spiders inhabiting different strata of habitats may respond differently to changes in environmental factors (Hermann et al. 2010). In the present study, spider specimens collected from ground level, understory vegetation, and the canopy layer were separately analyzed to see if the effects of thinning differed across various strata of the forests.

We used the Margalef species richness (D_{mg}), Shannon-Wiener index (H'), Simpson index (D), and evenness (J) (Krebs 1989) to quantify the community structures of spiders among different forest types. These calculations were based upon spider species compositions of the sampling plots. To compare all these indices, one-way analysis of variance (ANOVA) tests and Tukey's mean comparisons were used. Both tests were performed with SYSTAT 9.0 (SPSS, Chicago, IL, USA).

Bray-Curtis similarity (Krebs 1989) between sampling plots based upon species (only adult specimens were used), family, and guild compositions (both adult and juvenile specimens were used) was calculated between each pair of sampling plots. An analysis of similarities (ANOSIM) was then performed to test for the statistical significance of the grouping pattern. Similarity percentage (SIMPER) analyses based on the Bray-Curtis similarity were used to examine the relative contributions of spider guilds to the observed differences in spider assemblages. ANOSIM and SIMPER tests were performed using PRIMER 5 (Clarke and Warwick 2001). Furthermore, we also used a one-way ANOVA and Tukey's tests to compare the relative abundances of spider guilds among the 4 forest types.

The BIO-ENV function of PRIMER 5 was used to determine the variables that were most correlated with spider guild compositions. Temperature, RH, leaf litter, PCC, UVD, and the dry biomass of insects were used as potential environmental variables. The RELATE function of PRIMER 5 was used to determine whether each correlation was statistically significant. Prior to the analysis, these different environmental factors were tested for inter-correlations using Pearson correlations. An environmental factor matrix was constructed using Euclidean distances. We also used one-way ANOVA and Tukey's post-hoc comparisons to test whether each of the environmental variables differed among the 4 forest types.

RESULTS

Spider composition among forest types

From 4 field trips, 3484 (1163 from pitfall traps, 1459 from sweep netting, and 862 from canopy sweep netting) spider specimens were obtained; among them, 1160 (814 from pitfall traps, 214 from sweep netting, 137 from canopy sweep netting) were adults. From the adult specimens, 141 morphospecies belonging to 22 families were identified. The most abundant spider family was the Linyphiidae (28.7%), followed by the Tetragnathidae (15.6%) and Araneidae (13.7%). The Linyphiidae had the greatest number of species (40), followed by the Agelenidae (21) and Theridiidae (17).

Environmental variables among forest types

Results of ANOVA tests showed that plots in the broadleaf forest had the highest UVD, followed by the control and 2 thinned plantation stands (Fig. 1A, Table 1). Plots in the broadleaf forest also had the highest leaf litter weight (Fig. 1B, Table 1), but the lowest RH and PCC (Fig. 1C, D, Table 1). Sampling plots in the control plantation stand had the highest mean temperature (Fig. 1E, Table 1). The dry biomass of insects of plots in the 4 forest types did not significantly differ (Fig. 1F, Table 1). Results of the Pearson correlations showed that there were significant inter-correlations among the environmental variables examined (Table 2). The PCC showed a significant positive correlation with RH but negative correlations with UVD and leaf litter. Temperature showed a significant negative correlation with RH, which in turn also exhibited negative correlations with UVD and leaf litter. A significant positive correlation was found between the UVD and leaf litter. Finally, the dry biomass of insects did not show a significant correlation with any of the environmental factors examined in this study.

Specimens collected from pitfall traps

For specimens collected from pitfall traps, the broadleaf forest and heavily thinned plantation had a slightly higher number of species (Table 3A). Plots in the 4 forest types did not significantly differ in overall spider abundances, but those in the heavily thinned plantation forests had significantly higher adult abundances (Table 3A). Most of the diversity indices of the sampling plots in the 4

forest types did not differ, but those in the heavily thinned plantation stand had a significantly lower evenness and Simpson index than the other 2 plantation stands (Table 3A). Results of the ANOSIM tests showed significant differences in spider species, family, and guild compositions among the 4 forest types (Table 4A). Most pairwise comparisons were statistically significant; the only exception was that the guild composition of sampling plots in the broadleaf forest and control stand did not significantly differ (Table 4A). Sampling plots in the heavily thinned plantation stand had significantly more ground weavers, while the abundances of other spider guilds were similar among the 4 forest types (Table 5A). Results of the SIMPER analyses showed that in all pairwise comparisons, ground weavers were the major contributors to the observed variations in the spider guild composition among the forest types (Table 6). For spider specimens collected from pitfall traps, according to the BIO-ENV function of PRIMER 5, the combination of temperature, UVD, and litter weight was best correlated with patterns of variation in spider guild compositions among the forest types (RELATE test, Spearman rank coefficient ρ = 0.152, p = 0.03).

Specimens collected by sweep netting

For spider specimens collected by sweep netting, plots in the moderately thinned plantation stand had a slightly lower number of species (Table 3B). Plots in the 4 forest types did not significantly differ in overall spider abundances or the diversity indices examined, but those in the control stand had significantly higher adult abundances (Table 3B). Due to the low abundance of adult specimens in sweep-net samples, we only compared spider family and guild compositions between the different forest types. Results of the ANOSIM tests showed that family and guild compositions of sampling plots in the broadleaf forest and control stand did not significantly differ. Similar results were also found between plots in the moderately and heavily thinned stands. All other pairwise comparisons were statistically significant (Table 4B). Sampling plots in the broadleaf forest had significantly more space weavers (Table 5B). However, sampling plots in the heavily and moderately thinned plantation stands had more orb weavers, while those in the control stand had more ground weavers (Table 5B). Results of the SIMPER analyses showed that in most pairwise comparisons, orb weavers were

the major contributors to the observed variations in spider guild compositions among forest types (Table 7). For spider specimens collected by sweep netting, according to the BIO-ENV function of PRIMER 5, the UVD was best correlated with patterns of variation of the spider guild composition among forest types (RELATE test, Spearman rank coefficient $\rho = 0.130$, $p = 0.06$).

Specimens collected by canopy sweep netting

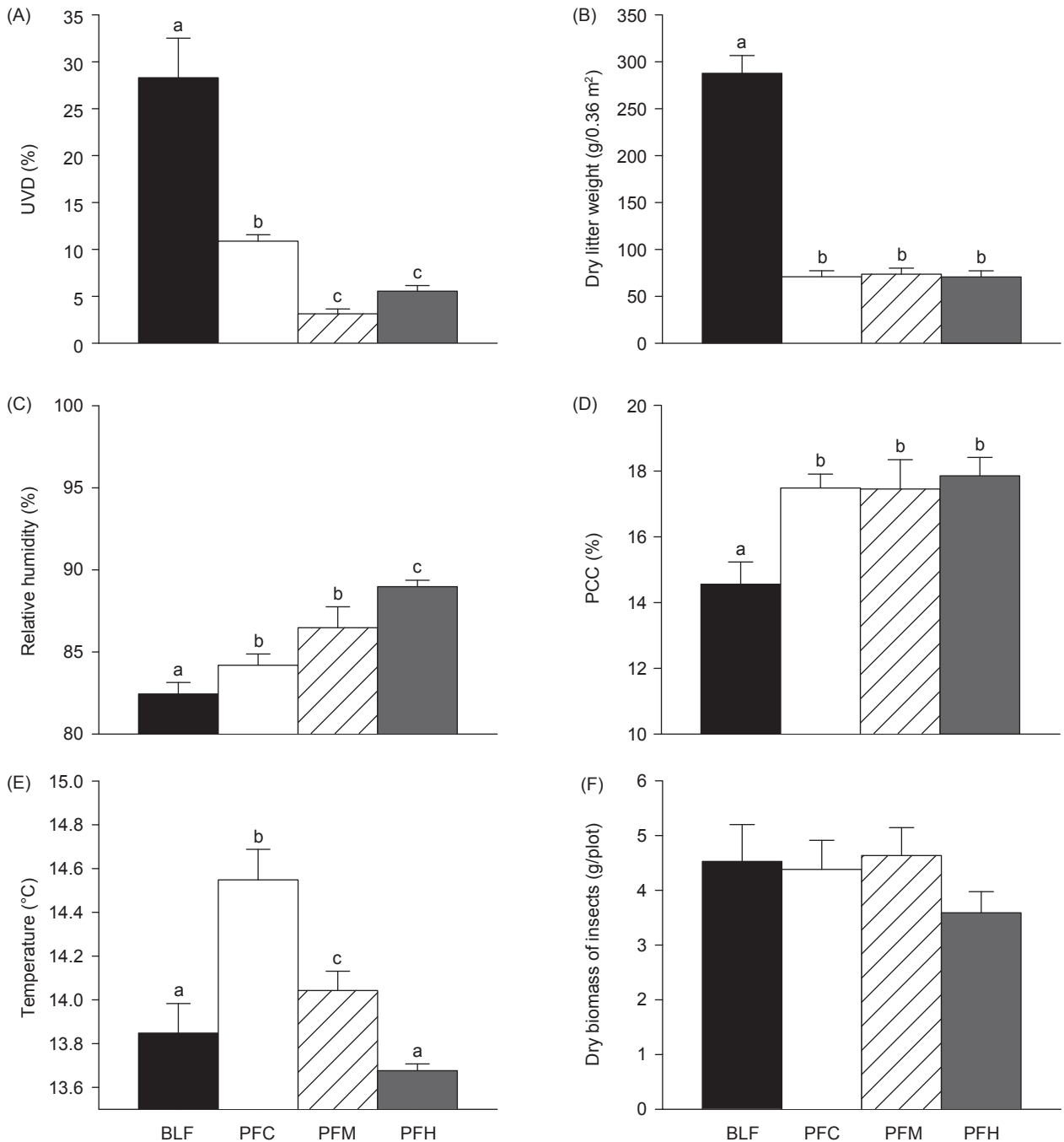For spider specimens collected by canopy

Fig. 1. Mean (± standard error) understory vegetation density (UVD) (A), dry leaf litter weight (B), relative humidity (C), percent canopy cover (D), temperature (E), and dry biomass of insects (F). ■, broadleaf forest; ▢, control plantation stand; ▨, moderately thinned plantation stand; ▨ (grey), heavily thinned plantation stand.

sweep netting, sampling plots in the broadleaf forest and control plantation stand had slightly higher numbers of species (Table 3C). Adult spider abundances and diversity indices of plots in the 4 forest types did not significantly differ, but those in the heavily thinned plantation stand had a significantly higher overall abundance (Table 3C). Due to the low abundances of adult specimens in sweep-netting samples, we only compared spider family and guild compositions among the different forest types. Results of the ANOSIM tests showed that family and guild compositions did not significantly differ between sampling plots in the control stand and moderately thinned plantation stand. All other pairwise comparisons were statistically significant (Table 4C). Sampling plots in the heavily thinned plantation stand had significantly more orb weavers and foliage runners (Table 5C). However, sampling plots in the broadleaf forest had the highest abundance of ground weavers (Table 5C). Results of the SIMPER analyses showed that in most pairwise comparisons, ground weavers, orb weavers, and foliage runners were the major contributors to the observed spider guild variations among forest types (Table 8). For spider specimens collected by canopy sweep netting, the BIOENV function of PRIMER 5 could not identify any environmental factor that exhibited a significant correlation pattern with observed spider guild variations among forest types.

DISCUSSION

This is one of the 1st studies to systematically examine impacts of forest management practices on the spider composition and community structure in subtropical plantation forests of East Asia. Results of our study showed that when broadleaf primary forests are transformed to *C. formosensis* plantations, the canopy openness will decrease and lead to changes in environmental factors such as temperature, RH, and UVD. Thinning treatments did not cause significant changes in most of the diversity indices among the different forest types, but they did generate considerable changes in spider compositions. The significantly different spider species and family compositions but similar guild compositions between broadleaf and plantation forests indicate that different spider taxa occupied similar ecological niches. Results of our study also showed that the responses of spider communities in different strata of plantation forests to thinning treatments varied. Heavy thinning resulted in a lower evenness and Simpson index in ground spiders, but did not affect the relevant community attributes of spiders in other strata of the plantation forests. On the other hand, although both heavy and moderate thinning caused significant changes in family and ground compositions of ground spiders, moderate thinning did not generate significant changes in canopy spider compositions. Therefore, the influence of thinning appeared to be more pronounced on ground-layer spider communities. The effects of thinning treatment on spider compositions might be generated by a reduced understory vegetation structural complexity. Among subtropical forests of Taiwan, broadleaf forests and untreated plantation stands usually exhibit a very dense and complex understory vegetation layer. Such habitat is suitable for space web builders, which require multiple attach points to build webs. After

Table 1. Results of ANOVA tests and Tukey's mean comparisons comparing various environmental variables among different forest types. UVD, understory vegetation structural complexity; PCC, percent canopy cover

Environmental variable	$F_{3,35}$	p
UVD	20.332	0.0001
Litter weight	20.385	0.0001
Relative humidity	12.574	0.0001
PCC	5.911	0.0020
Temperature	10.358	0.0001
Dry biomass of insects	0.5036	0.6823

Table 2. Results of Pearson correlations examining relationships between various environmental variables in 4 forest types. T, temperature; RH, relative humidity; UVD, understory vegetation structural complexity; L, dry litter weight; B, dry biomass of insects; PCC, percent canopy cover

	T	RH	UVD	L	B
PCC	-0.0446	0.451**	-0.465**	-0.505*	-0.159
T	-	-0.476**	-0.0943	-0.0573	-0.150
RH	-	-	-0.481**	-0.549***	-0.289
UVD	-	-	-	0.749***	0.0772
L	-	-	-	-	0.284

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 3. Number of spider families, species and mean (± standard error) abundance (adult and overall), richness (Dmg), evenness (J), Shannon-Wiener index (H'), and Simpson index (D) of spider specimens collected from different strata of sampling plots in 4 forest types of Da-Shiue Mt., Taiwan and results of ANOVA tests and Tukey's mean comparisons. (A) Spiders collected by pitfall traps. (B) Spiders collected by sweep netting. (C) Spiders collected by canopy sweep netting. BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation stand; PFH, heavily thinned plantation stand

Habitat	Families	Species	Adults[a]	Overall[a]	D_{mg}[a]	J[a]	H'[a]	D[a]
(A) Pitfall								
BLF	14	45	21.4 ± 3.43[b]	27.9 ± 4.02	3.1 ± 0.28	0.90 ± 0.016[ab]	2.0 ± 0.12	0.88 ± 0.016
PFC	13	38	17.2 ± 2.30[b]	30.8 ± 3.58	3.2 ± 0.31	0.93 ± 0.004[a]	2.1 ± 0.14	0.91 ± 0.012
PFM	11	37	15.6 ± 1.89[b]	24.0 ± 2.25	3.1 ± 0.29	0.93 ± 0.009[a]	2.0 ± 0.13	0.91 ± 0.011
PFH	14	44	29.1 ± 4.17[a]	37.7 ± 5.22	2.9 ± 0.27	0.87 ± 0.024[b]	2.0 ± 0.11	0.86 ± 0.018
$F_{3,35}$	-	-	3.35	1.973	0.266	3.525	0.200	2.981
p	-	-	0.029	0.136	0.850	0.025	0.896	0.044
(B) Sweep netting								
BLF	10	27	4.8 ± 0.74[ab]	35.9 ± 4.01	2.0 ± 0.32	0.82 ± 0.111	1.3 ± 0.20	0.81 ± 0.110
PFC	9	25	8.7 ± 2.65[a]	35.8 ± 3.96	2.2 ± 0.23	0.92 ± 0.044	1.4 ± 0.15	0.88 ± 0.051
PFM	9	19	3.0 ± 1.07[b]	34.6 ± 7.95	1.1 ± 0.53	0.53 ± 0.177	0.7 ± 0.32	0.48 ± 0.173
PFH	7	26	5.7 ± 0.75[ab]	34.4 ± 5.22	2.3 ± 0.16	1.08 ± 0.006	1.6 ± 0.10	1.01 ± 0.023
$F_{3,35}$	-	-	2.53	0.2143	0.405	1.584	1.466	1.433
p	-	-	0.073	0.886	0.751	0.215	0.242	0.253
(C) Canopy sweep netting								
BLF	8	19	5.3 ± 0.80	24.3 ± 1.84[ab]	1.8 ± 0.30	0.81 ± 0.109	1.2 ± 0.19	0.77 ± 0.108
PFC	9	19	2.7 ± 1.08	15.2 ± 3.20[b]	1.1 ± 0.44	0.44 ± 0.173	0.7 ± 0.29	0.43 ± 0.171
PFM	7	12	2.4 ± 0.65	18.0 ± 2.79[b]	1.1 ± 0.29	0.65 ± 0.162	0.7 ± 0.19	0.60 ± 0.155
PFH	7	13	3.0 ± 0.69	30.3 ± 3.59[a]	1.2 ± 0.33	0.65 ± 0.163	0.8 ± 0.22	0.63 ± 0.160
$F_{3,35}$	-	-	2.95	5.418	0.974	1.091	1.283	0.935
p	-	-	0.046	0.003	0.416	0.366	0.295	0.434

[a]Per sampling plot (10 × 10 m), $d.f.$ = 35.

Table 4. Results of pairwise ANOSIM tests comparing species, family, and guild compositions of 3 stratum's spiders collected from 4 forest types. (A) Spiders collected by pitfall traps. (B) Spiders collected by sweep netting. (C) Spiders collected by canopy sweep netting. BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation stand; PFH, heavily thinned plantation stand

Comparison	Species composition		Family composition		Guild composition	
	R	p	R	p	R	p
(A) Pitfall						
Global R	0.449	0.001	0.444	0.001	0.225	0.001
PFC vs. PFM	0.469	0.001	0.463	0.001	0.237	0.005
PFC vs. PFH	0.836	0.001	0.615	0.001	0.344	0.001
PFC vs. BLF	0.505	0.001	0.217	0.002	0.014	0.379
PFM vs. PFH	0.255	0.001	0.247	0.006	0.186	0.041
PFM vs. BLF	0.344	0.001	0.522	0.001	0.324	0.004
PFH vs. BLF	0.363	0.001	0.589	0.001	0.258	0.010
(B) Sweep netting						
Global R	-	-	0.325	0.001	0.325	0.003
PFC vs. PFM	-	-	0.333	0.002	0.333	0.008
PFC vs. PFH	-	-	0.415	0.001	0.415	0.029
PFC vs. BLF	-	-	0.086	0.123	0.086	0.389
PFM vs. PFH	-	-	0.046	0.223	0.046	0.732
PFM vs. BLF	-	-	0.454	0.001	0.454	0.001
PFH vs. BLF	-	-	0.557	0.001	0.557	0.010
(C) Canopy sweep netting						
Global R	-	-	0.301	0.001	0.301	0.001
PFC vs. PFM	-	-	0.028	0.298	0.028	0.308
PFC vs. PFH	-	-	0.260	0.008	0.260	0.009
PFC vs. BLF	-	-	0.340	0.001	0.340	0.010
PFM vs. PFH	-	-	0.146	0.045	0.146	0.029
PFM vs. BLF	-	-	0.399	0.001	0.399	0.010
PFH vs. BLF	-	-	0.535	0.001	0.535	0.004

Table 5. Results of the ANOVA tests and Tukey's mean comparisons comparing abundances of various spider guilds among different forest types. Spiders collected by different methods were analyzed separately. (A) Spiders collected by pitfall traps. (B) Spiders collected by sweep netting. (C) Spiders collected by canopy sweep netting. BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation; PFH, heavily thinned plantation

Habitat	Space weaver	Orb weaver	Foliage runner	Ground runner	Ground weaver	Ground sedentary weaver
(A) Pitfall						
BLF	0.6 ± 0.28	0.3 ± 0.13	1.8 ± 0.59	3.5 ± 1.10	12.9 ± 2.08^{ab}	8.7 ± 1.39
PFC	2.2 ± 0.79	0.0	1.9 ± 0.35	2.9 ± 0.89	17.6 ± 2.56^{ab}	6.2 ± 1.30
PFM	0.1 ± 0.1	0.0	1.3 ± 0.33	2.9 ± 0.65	12.7 ± 2.42^{b}	6.0 ± 1.22
PFH	0.0	0.1 ± 0.1	1.1 ± 0.42	1.6 ± 0.47	24.0 ± 4.36^{a}	8.9 ± 1.41
$F_{3,35}$	-	-	0.641	0.787	3.296	2.27
p	-	-	0.594	0.509	0.032	0.0975
(B) Sweep netting						
BLF	5.3 ± 1.21^{a}	12.3 ± 1.49^{b}	10.3 ± 1.26	0	8.3 ± 1.35	0
PFC	1.4 ± 0.38^{b}	12.1 ± 1.52^{ab}	10.1 ± 1.47	0	12.1 ± 3.43	0
PFM	0.7 ± 0.36^{b}	22.9 ± 5.26^{ab}	8.3 ± 1.65	0.1 ± 0.11	5.2 ± 1.23	0
PFH	1.1 ± 0.45^{b}	25.0 ± 4.43^{a}	9.3 ± 0.85	0	5.5 ± 0.84	0
$F_{3,35}$	7.42	4.335	0.722	-	2.69	-
p	0.0005	0.01	0.546	-	0.06	-
(C) Canopy sweep netting						
BLF	2.3 ± 0.73	6.9 ± 0.97^{b}	6.7 ± 0.99^{b}	0	6.9 ± 1.19^{a}	0
PFC	1.6 ± 0.94	5.6 ± 1.18^{b}	5.1 ± 1.32^{b}	0.1 ± 0.11	2.8 ± 0.43^{b}	0
PFM	1.3 ± 0.37	8.9 ± 1.46^{ab}	5.2 ± 0.88^{b}	0	2.6 ± 1.13^{b}	0
PFH	1.6 ± 0.47	13.2 ± 2.04^{a}	12.1 ± 1.49^{a}	0	2.2 ± 0.80^{b}	0
$F_{3,35}5$	0.438	5.242	7.352	-	9.274	-
p	0.728	0.004	0.0006	-	0.0001	-

Table 6. Results of SIMPER analyses determining the relative contributions of spider guilds to the observed composition variation of spiders collected by pitfall traps among the 4 forest types. BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation stand; PFH, heavily thinned plantation stand

	Dissimilarity/average	Dissimilarity/SD	Contribution (%)	Cumulative contribution (%)
PFC vs. PFM				
Ground weaver	16.39	1.50	48.23%	48.23%
Ground sedentary weaver	6.51	1.02	19.16%	67.38%
Ground runner	4.57	1.29	13.43%	80.82%
Space weaver	4.29	1.89	12.62%	93.43%
PFC vs. PFH				
Ground weaver	18.97	1.52	50.65%	50.65%
Ground sedentary weaver	9.16	1.28	24.46%	75.11%
Space weaver	3.65	0.88	9.75%	84.85%
Ground runner	3.31	1.02	8.85%	93.70%
PFM vs. PFH				
Ground weaver	23.48	1.66	60.28%	60.28%
Ground sedentary weaver	9.17	1.20	23.55%	83.83%
Ground runner	3.89	1.09	9.98%	93.81%
PFM vs. BLF				
Ground weaver	15.89	1.44	43.85%	43.85%
Ground sedentary weaver	9.17	1.41	25.30%	69.15%
Ground runner	6.45	1.50	17.79%	86.94%
Foliage runner	3.09	1.12	8.54%	95.48%
PFH vs. BLF				
Ground weaver	22.52	1.55	56.04%	56.04%
Ground sedentary weaver	8.83	1.09	21.96%	78.00%
Ground runner	4.77	1.08	11.88%	89.88%
Foliage runner	2.68	1.10	6.66%	96.55%

thinning, subsequent operations in the understory render the herb layer vegetation more open and less complex. A more-open understory layer may provide suitable habitat for spiders that make webs on the ground layer, and provide larger space for orb weavers to construct 2-dimensional webs. However, the canopy orb weaver and foliage runner abundance patterns of the 3 plantation forest types were not congruent with patterns of variation of environmental factors. These results suggest that spider guilds respond differently to forest management practices. While some are sensitive to certain vegetation characteristics (such as orb weavers in understory vegetation), others (such as orb weavers in the canopy) are also influenced, but their patterns of variation exhibit more complicated relationships with environmental factors. On the other hand, although thinning treatments also resulted in changes in temperature and RH, these abiotic factors might have played a relatively minor role because despite the statistical significance, the differences between sampling plots in various forest types were rather small (< 1°C and 5% RH). Considering the relatively high ambient temperature and humidity in subtropical regions such as Taiwan, small-scale differences in these environmental variables should not affect spider compositions too much.

The effects of thinning on forest spider diversities were examined in several European and Asian countries in temperate regions. Most of the European studies focused on ground spiders collected by pitfall traps (Bonte et al. 2003, Gurdebeke et al. 2003, Clough et al. 2005, Finch 2005, Schmidt et al. 2005, Pinkus-Rendón et al. 2006, Ziesche and Roth 2008). Results of those studies showed that thinning treatments significantly influenced the composition of epigean spider communities, and dominant tree species, microclimatic conditions, UVD, and canopy closure were the major determinants (Pinkus-Rendón et al. 2006, Ziesche and Roth 2008). Results of the present study differ from those conducted in Europe in that we provided a more comprehensive assessment of components of the spider communities that might have been impacted by thinning practices. While results of European studies focused on ground-dwelling spiders, we found that arboreal spiders inhabiting the understory vegetation and canopy such as orb weavers also respond to forest management practices. In Asia, studies on the effects of thinning on forest arthropod diversity are few, and most were conducted in Japan (Maeto et al. 2002,

Ohsawa 2004 2005 2007, Ohsawa and Nagaike 2006). Recently, the effects of thinning temperate conifer plantations on herbivorous beetle diversity were investigated. Certain aspects of the results of those studies, which showed that forests receiving different thinning intensities had different arthropod compositions and community structures (Maeto et al. 2002, Ohsawa 2004 2005 2007, Ohsawa and Nagaike 2006), are similar to those of the present study. However, while several studies conducted in Japan showed that thinning may increase the richness and abundance of many herbivorous beetle taxa (Ohsawa 2004 2005, Ohsawa and Nagaike 2006), such a pattern was not found in our study. One reason for such an incongruence might be that the consequences of thinning in terms of changes in environmental characteristics considerably differ between temperate and subtropical plantation forests. Studies conducted in Japan showed that new gaps created by thinning may influence the understory vegetation structure and composition, and such influences lasted from the re-initiation stage through succession pathways to the mixed-forest stage (Igarashi and Kiyono 2008). Consequently, thinning in temperate forests creates long-lasting topographic variations which provide new ecological niches for species inhabiting understory vegetation (Ito et al. 2003). In subtropical regions, higher temperatures might enhance the rapid growth of understory vegetation after thinning, and the plant community might have reached a certain stabilized stage in time periods of as short as 2 yr (Weng et al. 2007). The high growth rate of understory vegetation might have reduced the structural heterogeneity and niche diversity created by thinning. Consequently, several years after thinning, the plots exhibited different rather than more-diversified ecological niches. This may explain why thinning practices in the subtropical plantation forests of Taiwan resulted in forests with different but more or less equally diverse spider communities.

This study showed that thinning practices in an East Asian subtropical plantation forest created habitats of different spider assemblages. Different degrees of thinning generated forests of different understory vegetation structural complexities and microclimates, which in turn affected abundance patterns of spiders with specific environmental requirements. While similar studies conducted in temperate regions in Europe and Japan reported species richness/abundance-enhancing effects of thinning practices, such a pattern was not detected in the present study. Nevertheless, we regard

Table 7. Results of SIMPER analyses determining the relative contributions of spider guilds to the observed composition variation of spiders collected by sweep netting among the 4 forest types (BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation stand; PFH, heavily thinned plantation stand)

	Dissimilarity/average	Dissimilarity/SD	Contribution (%)	Cumulative contribution (%)
PFC vs. PFM				
Orb weaver	15.59	1.37	42.14%	42.14%
Ground weaver	11.65	0.97	31.47%	73.60%
Foliage runner	7.87	1.27	21.27%	94.87%
PFC vs. PFH				
Orb weaver	17.13	1.42	50.42%	50.42%
Ground weaver	9.91	0.94	29.18%	79.59%
Foliage runner	5.15	1.22	15.17%	94.76%
PFM vs. BLF				
Orb weaver	15.83	1.38	41.52%	41.52%
Foliage runner	8.11	1.22	21.27%	62.79%
Ground weaver	7.60	1.17	19.92%	82.71%
Space weaver	6.59	1.23	17.29%	100.00%
PFH vs. BLF				
Orb weaver	17.60	1.51	50.86%	50.86%
Ground weaver	6.03	1.18	17.42%	68.28%
Space weaver	5.75	1.21	16.63%	84.91%
Foliage runner	5.22	1.17	15.09%	100.00%

Table 8. Results of SIMPER analyses determining the relative contributions of spider guilds to the observed composition variation of spiders collected by canopy sweep netting among the 4 forest types. BLF, broadleaf forest; PFC, control plantation stand; PFM, moderately thinned plantation stand; PFH, heavily thinned plantation stand

	Dissimilarity/average	Dissimilarity/SD	Contribution (%)	Cumulative contribution (%)
PFC vs. BLF				
Ground weaver	15.64	1.41	35.08%	35.08%
Foliage runner	12.01	1.25	26.94%	62.02%
Orb weaver	10.84	1.31	24.32%	86.34%
Space weaver	6.09	1.04	13.66%	100.00%
PFC vs. PFM				
Orb weaver	16.20	1.32	38.24%	38.24%
Foliage runner	12.47	1.39	29.42%	67.66%
Ground weaver	9.01	1.63	21.25%	88.91%
Space weaver	4.70	0.93	11.09%	100.00%
PFC vs. PFH				
Orb weaver	18.13	1.47	39.92%	39.92%
Foliage runner	17.95	1.59	39.53%	79.45%
Ground weaver	5.10	1.13	11.23%	90.68%
PFM vs. PFH				
Foliage runner	15.28	1.84	39.95%	39.95%
Orb weaver	13.21	1.33	34.55%	74.50%
Ground weaver	6.81	1.43	17.80%	92.30%
PFM vs. BLF				
Ground weaver	16.02	1.57	39.74%	39.74%
Orb weaver	10.91	1.23	27.08%	66.83%
Foliage runner	8.74	1.26	21.69%	88.52%
Space weaver	4.63	0.99	11.48%	100.00%
PFH vs. BLF				
Orb weaver	12.58	1.30	32.71%	32.71%
Foliage runner	11.47	1.61	29.83%	62.54%
Ground weaver	10.65	1.38	27.69%	90.22%

thinning management as an effective way of enhancing spider diversity in subtropical plantation forests. This is because different degrees of thinning generate habitat heterogeneity and novel ecological niches, and result in spider communities different from those of plantation forests receiving no thinning treatment. Currently, producing high-quality timber and enhancing biodiversity have become 2 equally important goals of plantation forest management. Since knowledge regarding the effects of thinning practices on Asian subtropical and tropical plantation forests is currently quite limited, we suggest that more manipulative studies should be conducted to determine whether the effects identified in the present study are also present for other organisms. Information regarding the responses of various organisms to thinning treatments will be valuable in designing appropriate management and conservation policies for plantation forests.

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