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The effect of thinning on ground spider diversity and microenvironmental factors of a subtropical spruce plantation forest in East Asia

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Abstract Currently, information about the effect of forest management on biodiversity of subtropical plantation forests in Asia is quite limited. In this study, we compared the spider community structures and guild compositions of subtropical *Cryptomeria japonica* plantation forests receiving different degree of thinning (0, 25 and 50 %) in central Taiwan. The ground spider diversities and environmental variables were sampled/measured once every 3 months for 1 year before thinning and 2 years after thinning. Results showed that before thinning spider compositions did not differ significantly among three plantation forest types. Two years after thinning, spider species and family compositions of three plantation forest types differed significantly. In all three plantation forest types, the spider composition differed from year to year, indicating existence of temporal variations in spider diversity. Ground hunters (increased 200–600 % in thinned forests), sheet web weavers (increased 50–300 % in thinned forests) and space web weavers (decreased 30–50 % in thinned forests) were the major contributors of the observed spider composition differences among plantation forests receiving different treatments. The stands receiving thinning treatments also had higher illumination, litter decomposition rate, temperature and understory vegetation density. Thinning treatments might have changed the structures of understory vegetation and canopy cover and consequently resulted in abundance and diversity changes of these guilds. Moreover, the heterogeneity in understory vegetation recovery rate and temporal variation of spider composition might further generate spider diversity variations in subtropical forests receiving different degree of thinning.

Keywords *Cryptomeria japonica* · Forest management · Araneae · Taiwan · Thinning

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Introduction

There is a worldwide concern about involving biodiversity conservation while conducting plantation forest management, and studies regarding the responses of fauna or flora to plantation forest management have increased recently (Kerr 1999; 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 the ecosystems to the pre-disturbed state in aspects such as structure, function and biodiversity (Hobbs and Norton 1996). Several studies showed that thinning might potentially alter the developmental trajectory of young stands, generating a 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 increase light inputs to the ground and consequently result in a diverse mosaic of microhabitats (Son et al. 2004). Some studies have shown that stands receiving different degrees of thinning exhibit variations in relevant environmental parameters. Alterations in microhabitats in turn influence the animal communities in aspects such 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). However, keeping certain areas of unthinned patches is vital because they can provide refuges for particular species that are susceptible to thinning (Montaña et al. 2006). So, to determine appropriate management policies to enhance biodiversity of 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.

Cryptomeria japonica (Japanese cedar), a member of the conifer family Cupressaceae, is an endemic species of Japan. *C. japonica* is one of the most important plantation trees in Japan and is widely cultivated in other temperate areas such as China. In Taiwan, *C. japonica* was introduced from Japan in 1896 and was extensively cultivated for economic uses. At present, about 45,000 ha of plantations is established in mountainous regions (Taiwan Forestry Bureau 1995). A few decades ago in Taiwan, *C. japonica* was mainly used for construction and planking. However, timbers of this tree species are no longer popular in Taiwan. The relatively soft timber due to fast growing rate in a subtropical climate and a dark central area in the trunk cross section resulted in low economic values of this plantation tree. Due to these reasons, most stands of *C. japonica* in Taiwan are currently designated as forest reserve areas to facilitate ecosystem functioning, recreation, conservation and educational purposes.

Spiders are suitable ecological indicators used to assess the effects of silvicultural practices on biodiversity (Uetz 1975; Hatley and Macmahon 1980; Bultman and Uetz 1982; Oxbrough et al. 2005). Spiders are one of the dominant arthropod predators in many terrestrial ecosystems, and they play an important role in ecosystem functioning (Wise 1993; Nyffeler 2000). They occupy an influential niche in terrestrial food webs and regulate the insect populations in various communities (Wise et al. 1999). According to their particular ecological demands, 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 will generate significant changes in spider communities (Clough et al. 2005; Tsai et al. 2006; Ziesche and Roth 2008). The species richness and abundance of spiders were also reported to be closely associated with large-scale landscape complexities (Gurdebeke et al. 2003; Schmidt et al. 2005). Spider communities were found to be significantly different in plantation forest stands of various patch types, size scales and age classes (Whitehouse et al. 2002; Finch 2005; Ziesche and Roth 2008). Ground spiders are sensitive to both short-term and long-term local scale ecosystem disturbances in landscapes and therefore are a suitable ecological indictor to access how thinning affects various microenvironmental variables and consequently influences arthropod diversity (Pearce and Venier 2005).

In Asia, studies about the effects of plantation forest management on biodiversity are mostly conducted in temperate areas such as Japan. In general, thinning increased the richness and abundance of longhorn beetle (Ohsawa 2004), Coleoptera (Maleque et al. 2007a), Hymenoptera (Maleque et al. 2007b) and other insect taxa (Ohsawa 2005; Ohsawa and Nagaike 2006, Taki et al. 2010), although particular taxa with specific habitat requirements (such as those only inhabiting isolated old primary forest) were unaffected by such treatment (Ohsawa 2007). Results of studies also showed that among forests receiving different management practices, the compositions and community structures of beetles were different (Maeto et al. 2002). Thinning may influence understory vegetation composition in a profound way by creating new gaps (Igarashi and Kiyono 2008; Taki et al. 2010), although dominant tree species and topographic variation are also major determining factors (Ito et al. 2003). Various functional groups of insects in turn were positively correlated with the species richness of understory vegetation (Maleque et al. 2007a, b). However, all these conclusions were derived from studies conducted in temperate Northeastern Asian forests. Currently, information about the effects of thinning on biodiversity of subtropical plantation forests in Asia is very limited. Available empirical evidence from few studies showed the responses of warm and wet subtropical plantation forests which cover a vast area in Eastern/Southeastern Asia to thinning were different from those reported from temperate forests. Weng et al. (2007) showed that the microclimatic conditions, abundant understory vegetation and canopy recovery of the thinned stands in subtropical plantations returned to the pre-thinning status faster than temperate forest. Huang et al. (2011) showed that different degrees of thinning practices in subtropical plantations created habitats exhibiting different spider assemblages while similar studies conducted in temperate regions in Europe and Japan reported species richness/abundance-enhancing effects of thinning practices.

In this study, the effects of management on biodiversity of a subtropical plantation forest in East Asia were assessed by comparing the ground spider community structure and guild composition in *C. japonica* plantation forests in central Taiwan. Ground spider diversities of *C. japonica* plantation forests before and after different degrees of thinning were compared, and biotic and abiotic environmental factors were measured to identify key environmental variables contributing to the observed spider diversity variations. Results of this study can help realize the effects of thinning on arthropod diversity in East Asian subtropical plantation forests and the potential underlying mechanisms.

Materials and methods

Study site

The study sites were established in a subtropical montane spruce (*Cryptomeria japonica* D. Don) plantation forest in Ren-Lun, Nantou County, Taiwan (N 23°44′, E 120°53′). The *C. japonica* stands were established in 1971. The study area encompasses about 78 ha and extends from 1,200 to 1,500 m in elevation. The air temperature averaged 15 °C and annual precipitation was 2,400 mm. We set up 12 100 m × 100 m (1 ha) plots and performed three different degrees of thinning treatments on them. The thinning treatments included unthinned (control), moderate thinning and heavy thinning. Results of a survey conducted before thinning showed that the initial tree density of *C. japonica* stands in Ren-Lun was about 950–1,500 trees/ha. The silviculture practices in these stands were geometric thinning (Fujimori 2001). In this method, trees are removed or retained according to simple criteria such as a defined distance or a defined number of rows (Fujimori 2001). In this study, a specific way of geometric thinning called gap geometric thinning was used. In each one hectare sampling plot, 25 20 m × 20 m squares were set up and each square was further divided into four 10 m × 10 m subsquares. The plots receiving moderate thinning treatment ($n = 4$) were achieved by removing trees from one regularly chosen 10 m × 10 m subsquares from each of the 25 20 m × 20 m squares. Special attention was paid to prevent chosen subsquares from being adjacent to each other. The plots receiving heavy thinning treatment ($n = 4$) was achieved by removing trees from two regularly chosen 10 m × 10 m subsquares located on opposite side of each square from each of the 25 20 m × 20 m subsquares. The thinning practice was conducted between November 2006 and February 2007. In the stands receiving thinning operations, the logged trees were pruned. The branches and leaves were left on the stands, and therefore, the litter mass was increased. After that, the logged trunks were cut to equal length and stacked on the side of the trails adjacent the sampling sites. The process of shipping timbers would crush the shrub and seedlings in parts of the stands. In each one ha plot, we set up three 10 m × 10 m sampling plots and the distance between neighboring plots was about 20 m. The distribution of sampling plots among the logged and undisturbed subsquares might greatly determine local spider composition due to this organism's sensitivity to small-scale habitat differences (Muff et al. 2009). The sampling plots were all located on subsquares receiving thinning operations. A small number of the sampling plots were shifted 1–2 m due to the limit of topography. Overall, a total of 36 sampling plots were established in three forest types.

Specimen collection

Four field trips were conducted before thinning in November 2005 and February, May, and August of 2006. Eight field trips were conducted after thinning from November 2007 to September 2009. In each 1 ha sampling plot, three pitfall traps were established to collect ground spiders. Each pitfall trap consisted of four plastic cups, and three polystyrene plastic sheets arranged into a Y form. Four plastic cups were placed in the middle and at each end of the Y form polystyrene plastic sheets. The cup was 15 cm in height and 10 cm in diameter. The polystyrene plastic sheets were used to enhance the catching efficiency of traps, and each was 40 cm in height and 1 m in length. These cups were covered by a plastic plate secured with sticks to prevent fallen leaves or rainwater from entering the traps. In each field trip, the traps were filled with 500 ml 70 % alcohol and were opened consecutively for 7 days.

The invertebrate specimens collected were first classified into spiders, insects and other arthropods. Spiders were first separated into adults and juveniles, and adult spiders were sorted into morphospecies and if possible identified to species by palpal organ or epigynum. All spiders (including juveniles) were sorted into families. In addition, we used the classification system given in Cardoso et al. (2011) to categorize both adult and juvenile spiders into foraging guilds according to spiders' foraging strategy, prey range, vertical stratification and circadian activity ("Appendix"). Spiders were assigned to the following guilds: (1) orb web weaver: Araneidae and Tetragnathidae; (2) space web weaver: Leptonetidae, Mysmenidae, Pholcidae and Theridiidae; (3) sheet web weaver: Agelenidae, Hahniidae, Hexathelidae, Linyphiidae and Psechridae; (4) specialists: Dysderidae and Zodariidae; (5) ground hunters: Gnaphosidae, Liocranidae, Lycosidae and Oonopidae; (6) sensing web weaver: Atypidae, Ctenizidae and Segestriidae; (7) ambush hunters: Thomisidae; (8) other hunters: Clubionidae, Ctenidae, Philodromidae, Oxyopidae, Salticidae and Sparassidae.

Quantification of environmental factors

In order to identify the factors responsible for the observed spider diversity variations among plots receiving different thinning treatments, we measured twelve environmental variables in each sampling plot. First we used data loggers to monitor the temperature and relative humidity of sampling plots. In each sampling plot, one data logger (HOBO Pro series, thermograph/hygrometer, Onset, USA) was placed at 1 m high and in each field trip, the data were recorded for a week. Soil temperature (ST) and soil moist (SM) at 5 cm depth were measured with a TT4 multi-sensor thermocouple (T-type, ICT International Pty, Ltd., Australia), and the data were recorded every 60 min for a week. Decomposition rates (D) were also quantified within each study site. To quantity vegetation structures, we measured the illumination within the plantation (I), percent canopy openness (PCO) and understory vegetation density (UVD) of each sampling plot in each field trip. Illumination receptors (Li-Quantum LI190SB-L, 400–700 nm) were used to monitor the photosynthetic active radiation (PAR) of sampling plots. In the center of each sampling plot, one receptor was placed at 1.5 m high. In each field trip, the data was recorded every 150 s for a week and the recorded values were automatically averaged every 5 min. A fish-eye lens mounted on a Nikon 4,500 digital camera was used to measure PCO. The camera was mounted on a tripod placed in the center of the sampling plot with the lens facing upward to take hemispheric photographs. The photographs were analyzed by a Gap Light Analyzer, Version 2.0 (Frazer et al. 1999) after being transformed into black-and-white images. We used a red cloth (1 m × 1 m) as the background, and the density of vegetation in front of it was used to quantify UVD. The red cloth was held by one person standing at each of the four cardinal edges of the 10 m × 10 m sampling plot. Another person standing in the center of the plot took pictures of the red cloth and the vegetation in front with a Nikon 4500 digital camera. In each of the four cardinal directions, the cloth was placed at two different heights (low: ground to 100 cm; high 100–200 cm) to have a better representation of the vertical stratification of the understory vegetation. These photographs were transformed into black-and-white images using Photoshop, data from the four cardinal directions and two heights were averaged, and the mean was used as the UVD of the plot. Undecomposed leaf litters were collected from *C. japonica* plantations around the experimental stands. Decomposition rates were quantified as percent mass loss of the collected leaf litters in 12 months.

Statistical analyses

Bray-Curtis similarity (Krebs 1989) between sampling plots based upon species and guild compositions was calculated (data squared root transformed). Permutation MANOVA (PERMANOVA) tests which are based upon the values of Bray-Curtis similarity were performed to test for the statistical significance of the grouping pattern. Similarity percentage (SIMPER) analyses were used to examine the relative contribution of various spider guilds to the observed spider assemblage differences. In order to realize the relationship between environmental variables and spider composition, redundancy analysis (RDA) was used to determine the subset of variables that were most significantly correlated with spider guild compositions. Temperature, relative humidity, ST, SM, D, PCO, UVD and I were used as the potential environmental variables. PERMANOVA, SIMPER and RDA tests were performed using PRIMER 6 and PERMANOVA+ (Clarke and Warwick 2001; Anderson et al. 2008).

Results

Spider specimens collected

A total of 4,339 spider specimens were obtained; among them, 2,162 were adults. From the adult specimens, 139 morphospecies belonging to 29 families were identified. From the field trips conducted in the year before thinning, a total of 979 spider specimens were obtained. From the first and second year after thinning, 1,145 and 2,215 specimens were obtained, respectively. The most abundant spider family was Lycosidae (42.34 %, 1,837 specimens), followed by Linyphiidae (15.00 %, 651 specimens), Theridiidae (8.57 %, 372 specimens) and Agelenidae (6.52 %, 283 specimens). Linyphiidae had the highest number of species (26), followed by Agelenidae (18), Theridiidae (15) and Salticidae (10). The 25 % thinning plantation had the highest number of species (91), followed by 50 % thinning (90) and unthinned plantation forest (80). From the field trips conducted in the year before thinning, a total of 80 morphospecies were obtained. From the first year after thinning, 59 morphospecies were obtained and 26 (44.1 %) of them were not collected in the previous year (Table 1a). From the second year after thinning, 85 morphospecies were obtain and 34 (40 %) of them were not collected in the year before thinning (Table 1a). Most morphospecies not collected from the year before thinning were rare species (<10 individuals), and only one wolf spider morphospecies was relatively dominant (more than 30 individuals). The dominant spider families of the major guilds were shown in Table 1b. In addition to the dominant family of sensing web weavers (Ctenizidae), in all other families, the number of species collected from 3 years differed. After thinning, in Lycosidae, Linyphiidae and Theridiidae, the number of species not collected in the year before thinning ranged from 2 to 5 (Table 1b).

Comparison of spider community composition among treatments and years

Results of two-way permutation MANOVA tests showed that spider species and guild compositions of plots

Table 1 Species numbers of dominant families of the major spider guilds

	Number of species		
	B1	A1	A2
(a) All species	80	59 (26)	85 (34)
(b) Families			
Lycosidae (ground hunters)	7	6 (2)	9 (2)
Linyphiidae (sheet web weavers)	17	12 (3)	11 (5)
Theridiidae (space web weavers)	10	4 (2)	7 (3)
Ctenizidae (sensing web weavers)	1	1 (0)	1 (0)

Number in parenthesis represents number of species not collected in 1 year before thinning. B1, 1 year before thinning, A1, the first year after thinning, A2, the second year after thinning

Table 2 Results of two-way permutation MANOVA examining the effects of thinning treatments and year (and their interaction) on spider morphospecies and guild compositions

Comparisons	Morphospecies		Guild	
	Pseudo-F	*p*	*Pseudo-F*	*P*
Thinning	2.8493	0.0001	7.3137	0.0001
Year	8.2415	0.0001	13.856	0.0001
Thinning × year	1.3247	0.0326	1.9062	0.0274

receiving different thinning treatments differed significantly. Those of plots collected from different years also differed significantly, and there was a significant interaction between thinning treatment and year (Table 2).

Analysis of the pairwise permutation tests showed that in the year before thinning, spider species and guild composition of three types of plantation forests did not differ significantly (Table 3a, b). However, in the first year after thinning, spider species composition of unthinned plantation differ significantly from that of 50 % thinning plantation while those of two types of thinning plantation forests did not differ significantly (Table 3a). Spider guild composition of unthinned plantation plots differed significantly from those receiving thinning treatments while those of 25 and 50 % thinning plots did not differed significantly (Table 3b). In the second year after thinning, in most pairwise comparisons, spider species or guild compositions differed significantly (Table 3a, b), except that the species compositions of 25 and 50 % thinning plots did not differ significantly (Table 3a).

Results of permutation tests examining temporal variation of spider species and guild compositions in each treatment showed that most pairwise comparisons were statistically significant (Table 3c, d). Even in the unthinned plantation plots, spider compositions varied significantly from year to year. The only exceptions were that the spider species (Table 3c) and guild (Table 3d) compositions of unthinned plantation plots collected from first and second year after thinning did not differ significantly.

Result of SIMPER analyses showed that after thinning in both years in most pairwise comparisons, ground hunter, sheet and space web weavers were the major contributors of the observed variations in spider guild composition (Table 4). In particular, the ground hunters were the major contributors which contributed around 42–49 % to the observed spider diversity variation in the first year after thinning (Table 4a) and about 63–83 % in the second year after thinning (Table 4b).

Spider composition versus microhabitat variables among treatments and years

Result of RDA on data obtained from plots of three types of plantation forests sampled in 3 years (Fig. 1) showed that about 55.3 % of total variation in spider guild composition was explained by environmental variables. Spider guild composition of plots sampled from three different years clustered into three different groups in RDA diagram along the first RDA axis. Plots of unthinned plantation sampled from 3 years clustered together and were grouped with the 25 and 50 % thinning plots sampled 1 year before thinning. Although the pattern was not obvious, plots of two thinning plantations sampled 2 years after thinning seemed to separate from each other along the second RDA axis.

The major contributors of the observed spider guild composition differences among thinning treatments and years were ground hunters (GH), sheet web weaver (SH), sensing web weaver (SE), space web weaver (SP) and orb web weaver (OW). Plots receiving 50 % thinning treatment sampled 2 years after thinning had higher ground hunter (GH), space web weaver (SP), lower sensing web weaver (SE) and orb web weaver (OW) abundance than those receiving other thinning treatments sampled 2 years after thinning (Table 5a, RDA1). Plots receiving two thinning treatments sampled from first year after thinning had higher abundance of sheet web weavers (SH) and lower space web weavers (SP) and ambush hunters (AH) than those sampled from 1 year before thinning and second year after thinning (Table 5a, RDA2). The major contributors of the observed environmental factor differences among thinning treatments and years were mean of illumination within the stand (Im), decomposition (Dm), temperature (Tm), relative humidity (RHm), percent canopy openness (PCOm), understory vegetation density (UVDm), standard deviation of temperature (Tsd) and understory vegetation density (UVDsd) (Table 6). Results of Pearson's correlation showed that environmental variables having negative correlation with the first RDA axis were mean of illumination within the stand (Im), mean of temperature (Tm), mean of

Table 3 Results of pairwise permutation tests comparing spider composition of plots receiving different thinning treatments and from different years

	Morphospecies composition						Guild composition					
	Pseudo-t B1	*p*	*Pseudo-t* A1	*p*	*Pseudo-t* A2	*p*	*Pseudo-t* B1	*p*	*Pseudo-t* A1	*p*	*Pseudo-t* A2	*p*
	a						*b*					
UP versus 25 %	1.07	0.35	1.39	0.08	1.48	0.06	0.58	0.81	2.28	0.03	1.78	0.05
UP versus 50 %	0.92	0.69	1.64	0.02	2.09	0.03	1.22	0.22	2.75	0.02	3.38	0.02
25 % versus 50 %	0.96	0.52	0.76	0.80	1.25	0.12	0.78	0.72	0.52	0.66	1.77	0.05
	UP		25 %		50 %		UP		25 %		50 %	
	c						*d*					
B1 versus A1	1.91	0.03	1.62	0.02	2.00	0.03	1.78	0.03	2.13	0.03	2.19	0.02
B1 versus A2	1.94	0.02	1.94	0.03	2.50	0.03	2.36	0.02	2.63	0.03	4.07	0.03
A1 versus A2	1.29	0.11	1.69	0.02	2.63	0.03	1.58	0.09	1.92	0.06	2.94	0.03

(a) Morphospecies composition between three forest types in 3 years. (b) Guild composition between three forest types in 3 years. (c) Morphospecies composition between years in three forest types. (d) Guild composition between years in three forest types

UP: unthinned plantation forest; 25 %: 25 % thinning plantation; 50 %: 50 % thinning plantation; B1: 1 year before thinning; *A*1: the first year after thinning; *A*2: the second year after thinning

percent canopy openness (PCOm) and standard deviation of understory vegetation density (UVDsd), while those having positive correlation were mean of litter decomposition (Dm), mean of relative humidity (RHm) and standard deviation of temperature (Tsd) (Table 5b, RDA1). Environmental variables having negative correlation with the second RDA axis were mean of temperature (Tm) and mean of understory vegetation density (UVDm), while those showing positive correlation were mean of illumination within the stand (Im) and mean of litter decomposition (Dm) (Table 5b, RDA2).

Results of two-way MANOVA tests showed that abundance of ground hunters and sheet web weavers collected from plots receiving different thinning treatments differed significantly. Those of plots collected from different years also differed significantly (Table 7). However, abundance of space web weavers and sensing web weavers only differed significantly from plots collected from different years and did not differ significantly from plots receiving different thinning treatments (Table 7).

Results of pairwise permutation MANOVA tests showed that in the year before thinning abundance of ground hunters, sheet web weavers, space web weavers and sensing web weavers in three types of plantation forests did not differ significantly (Table 8). In the first year after thinning, plots receiving thinning treatments had significantly higher abundance of ground hunters and sheet web weavers than those did not (Table 8a, b), while abundance of space web weavers and sensing web weavers collected did not differ significantly (Table 8c, d). In the second year after thinning, plots receiving 50 % thinning had significantly higher abundance of ground hunters than those of the other two types of plantations (Table 8a), while abundance of sheet web, space web and sensing web weavers did not differ significantly (Table 8b, c, d).

Results of pairwise permutation MANOVA tests showed that the abundance patterns of dominant families of each spider guild collected from plots receiving various thinning treatments in different years were similar to those of spider guilds reported above (Table 9). The dominant families of ground hunters, sheet web weavers, space web weavers and sensing web weavers were Lycosidae (comprising 87 %), Linyphiidae (comprising 65 %), Theridiidae (comprising 62 %) and Ctenizidae (comprising 84 %), respectively.

Discussion

Based on the results of our analyses, three major conclusions can be made. First, in our study sites, there were temporal differences in species compositions generated by population dynamic and climatological processes. The temporal variation in the number of species collected from unthinned plantations in 3 years reflected a dynamic spider community compositions, rather than different sampling intensities. Therefore, spiders in plantation forests appear to have more or less different "active" years. Sensing web weavers with long life cycles were an obvious example. Those spiders were the most dominant guild in B1, and only few were collected in A1and A2, even in the unthinned plantations. Secondly, thinning operations generated significant

Table 4 Results of SIMPER analyses determining the relative contribution of various spider guilds to the observed diversity variation among plots receiving different treatments

	Contribution (%)	Cumulative contribution (%)
(a) First year after thinning		
UP versus 25 %		
Ground hunter	42.34	42.34
Sheet web weaver	38.86	81.20
Space web weaver	8.50	89.70
Other hunters	4.71	94.41
UP versus 50 %		
Ground hunter	48.59	48.59
Sheet web weaver	34.65	83.24
Space web weaver	7.48	90.73
(b) Second year after thinning		
UP versus 25 %		
Ground hunter	62.83	62.83
Space web weaver	11.38	74.20
Sheet web weaver	10.93	85.13
Other hunters	10.51	95.65
UP versus 50 %		
Ground hunter	82.84	82.84
Sheet web weaver	7.07	89.92
Space web weaver	6.06	95.98
25 versus 50 %		
Ground hunter	78.94	78.94
Space web weaver	7.37	86.31
Sheet web weaver	7.07	93.38

Data presented are from the first and second year after thinning. UP: unthinned plantation forest; 25 %: 25 % thinning plantation; 50 %: 50 % thinning plantation

differences in spider compositions at species, family, as well as guild level. Spider guilds exhibiting specific environmental requirement for open structure (i.e., OW) were negatively affected, while those with requirement for dense structure and deeper litter (i.e., SP and GH) might benefit from the disturbance and habitat alteration caused by thinning. Thirdly, our result showed that thinning operation increased the opportunity of alien spider species from the forests around the manipulate plantations to colonize, although our data showed that most of these species were rare species.

Our analyses revealed that spider communities of *C. japonica* plantations receiving different thinning treatments varied. Responses of spider species and guilds with different habitat requirements varied considerably to disturbances. Moreover, we also found that spider species and guild compositions of sampling plots changed remarkably through time. Even in the unthinned plantation plots, spider compositions varied significantly from year to year. The irradiation within the stand, decomposition of litter and soil characteristics in the unthinned plantation varied between different years. Although the habitat structures of unthinned plantation forests were usually assumed to be less heterogeneous, a diverse microhabitat mosaic existed and various relevant environmental parameters such as irradiation, humidity, ground vegetation, litter layer and other soil characteristics might vary (e.g., Niemelä et al. 1996; Holst et al. 2004; Oheimb et al. 2005). The existence of a complex system where many microenvironmental factors interact and the variable edge habitats may have generated the observed temporal variation of undisturbed habitats (Murcia 1995; Niemelä et al. 1996; Lövei et al. 2006).

After thinning, the spider compositions of plantation stands receiving different thinning treatments differed, and ground hunters (GH), sheet web weavers (SH) and space web weavers (SP) were the major contributors of the observed spider diversity differences among forest types. Congruent with such a pattern was a significant difference in understory vegetation density and litter decomposition rate among forest types. The thinning practices altered the vegetation structure and the decomposition of litter. The understory vegetation opened in different scales by thinning treatments had different levels of fluctuation through time. The fine woody debris left from the thinning operations increased the depth of litter layer and decreased the decomposition ratio of litter. A more open vegetation structure and deeper litter might have benefited ground hunters (especially Lycosidae) and sheet web weavers (especially Linyphiidae) spiders through the creation of new microhabitats after thinning. However, members of orb web weavers might find such habitats unsuitable. In the second year after thinning, the understory vegetation of 50 % thinning plantation forests became more stable and deeper litter layer consequently maintained a high abundance of ground hunters (GH). Also, a more stable, open and relatively simpler vegetation structure and deeper litter layer of 50 % thinning plantation forests might have limited space web weavers (SP) with specific spatial need for web building and prey catching. These results indicate that spider functional groups respond quite differently to forest management practices. While some will closely respond to certain vegetation and ground layer characteristics, others are also influenced but their variation pattern exhibits a more complicated relationship with environmental factors.

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

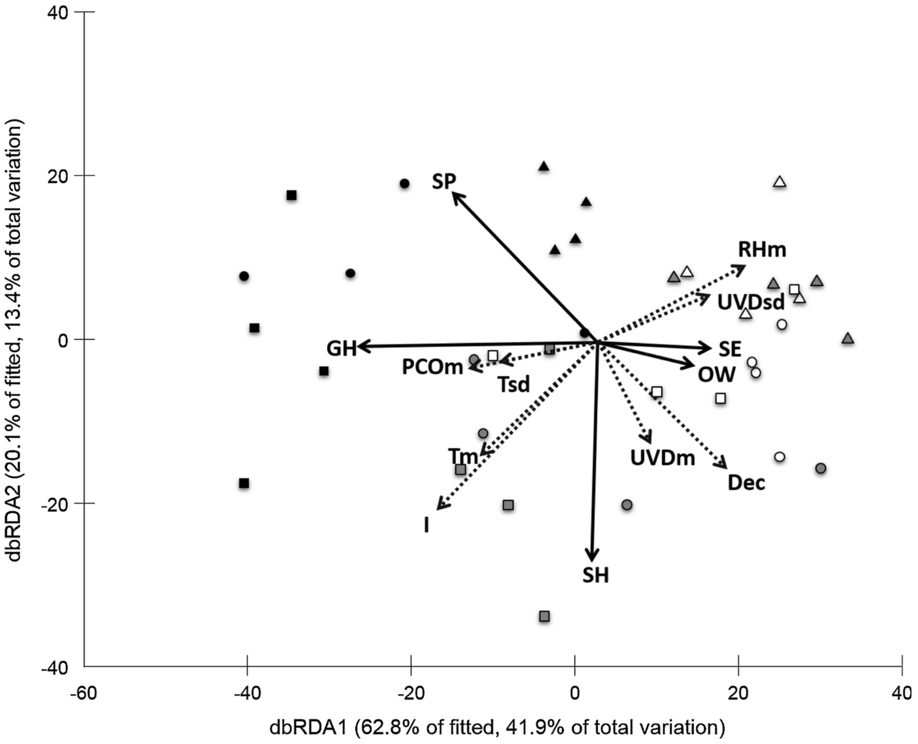

Fig. 1 RDA plots generated by spider guild composition of sampling plots receiving different thinning treatments in 3 years. Axis 1 explains 41.9 % of total variation and Axis 2 explained 13.4 % of total variation. (White symbols: 1 year before thinning; gray symbols: first year after thinning; black symbols: second year after thinning. Triangle: unthinned plantation forest; circle: 25 %-thinning plantation; square: 50 %-thinning plantation; AH: ambush hunters; GH: ground hunters; OW: orb web weavers; OH: other hunters; SE: sensing web weavers; SH: sheet web weaver; SP: space web weavers; m: mean; SD: standard deviation; I: illumination within the stand; D: decomposition of litter; T: temperature; RH: relative humidity; PCO: percent canopy openness; UVD: understory vegetation density)

Table 5 Pearson's correlation coefficients between various variables and RDA axis. (a) Spider guild composition. (b) Environmental factors

(a)	AH	GH	OW	OH	SE	SH	SP	S
RDA1	−0.263	-0.877^{***}	0.355^{*}	0.338^{*}	-0.416^{**}	−0.002	0.531^{***}	−0.175
RDA2	-0.496^{**}	0.001	−0.008	0.197	−0.002	-0.796^{***}	0.549^{***}	−0.302
(b)	Im	Dm	Tm	RHm	PCOm	UVDm	Tsd	UVDsd
RDA1	-0.588^{***}	0.468^{**}	-0.430^{**}	0.539^{**}	-0.474^{**}	0.193	0.362^{*}	-0.411^{*}
RDA2	0.617^{**}	0.462^{**}	-0.413^{*}	0.281	−0.010	-0.372^{*}	−0.007	0.172

AH: ambush hunters; GH: ground hunters; OW: orb web weavers; OH: other hunters; SE: sensing web weavers; SH: sheet web weaver; SP: space web weavers; S: specialist; m: mean; sd: standard deviation; I: illumination with in the stand; D: decomposition of litter; T: temperature; RH: relative humidity; PCO: percent canopy openness; UVD: understory vegetation density

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

composition of epigean spider communities, and dominant tree species, microclimatic conditions, UVD and canopy closure were the major determining factors (Pinkus-Rendón et al. 2006; Ziesche and Roth 2008). Pearce et al. (2004) and Magura et al. (2010) both showed that GH (mainly Gnaphosidae and Lycosidae) were positively correlated with disturbance intensity. Lycosidae, a ground-dwelling spider and a generalist predator, benefited from disturbance and became dominant. In our study, nine morphospecies were identified from Lycosidae (1,837 specimens) and two of them were especially dominant in 50 % thinning plots 2 years after thinning (412 specimens). Such results are congruent with those of studies conducted in Europe investigating effects of thinning on ground spiders.

Results of certain studies conducted in Japan showed that forests receiving different thinning intensities had

Table 6 Mean (+ SE) environmental variables of sampling plots measured from subtropical *Cryptomeria japonica* plantation forests receiving different thinning treatments in Ren-Lun, Taiwan, in 3 years

	Dec (g)	I (lx)	PCO (%)	RH (%)	SM	ST	T (°C)	UVD (%)
(a) Before thinning								
UP	60.6 ± 1.25	2,832 ± 1,236.3	11.2 ± 0.70	98.8 ± 1.06	10.3 ± 2.89	9.0 ± 5.12	15.5 ± 0.13	33.0 ± 6.44
25 %	60.6 ± 1.25	2,542 ± 1,092.5	12.0 ± 0.53	95.6 ± 2.49	17.6 ± 8.20	17.6 ± 8.70	15.8 ± 0.33	40.2 ± 6.94
50 %	58.1 ± 5.70	1,684 ± 525.8	11.5 ± 1.04	98.0 ± 0.70	12.6 ± 7.51	13.0 ± 7.86	16.1 ± 0.65	42.0 ± 11.67
(b) First year after thinning								
UP	79.2 ± 2.39	2,968 ± 1,721.7	16.6 ± 3.89	93.1 ± 2.91	19.8 ± 6.90	16.6 ± 0.84	16.0 ± 0.14	13.4 ± 6.80
25 %	75.1 ± 3.82	7,570 ± 2,772.0	21.8 ± 6.68	90.8 ± 4.54	21.9 ± 2.24	17.5 ± 0.87	16.3 ± 0.27	25.9 ± 14.02
50 %	73.6 ± 5.37	11,097 ± 4,251	17.1 ± 6.73	90.1 ± 2.97	22.8 ± 0.82	16.4 ± 0.81	16.3 ± 0.33	27.8 ± 12.20
(c) Second year after thinning								
UP	58.1 ± 5.70	2,273 ± 294.4	16.6 ± 3.87	93.1 ± 3.93	21.4 ± 0.26	17.7 ± 0.21	15.8 ± 0.14	16.1 ± 8.39
25 %	52.0 ± 5.84	5,514 ± 2,454.3	21.7 ± 6.44	89.4 ± 5.49	21.0 ± 1.73	18.3 ± 0.25	15.9 ± 0.55	26.0 ± 12.80
50 %	51.3 ± 11.99	10,120 ± 4,843	17.2 ± 6.25	90.4 ± 3.83	21.4 ± 0.01	18.2 ± 0.36	16.3 ± 0.78	27.8 ± 10.22

UP: unthinned plantation forest; 25 %: 25 % thinning plantation; 50 %: 50 % thinning plantation; Dec: decomposition rate of litter; I: illumination within the stand; PCO: percent canopy openness; RH: relative humidity; ST: soil temperature; SM: soil moisture; T: temperature; UVD: understory vegetation density

Table 7 Results of two-way permutation MANOVA examining effects of thinning treatments and years (and their interaction) on abundance of major spider guilds

	Ground hunters		Sheet web weavers		Space web weavers		Sensing web weavers	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Thinning	12.676	0.0001	8.479	0.001	0.127	0.881	0.457	0.838
Year	17.864	0.0001	7.026	0.003	28.102	0.0001	32.255	0.0001
Thinning × year	5.496	0.002	2.232	0.092	0.643	0.637	0.643	0.897

Table 8 Abundance of major spider guilds (mean ± SE) of sampling plots receiving various thinning treatments in different years in Ren-Luen, Central Taiwan

Comparisons		B1	A1	A2
(a) Ground hunter	UP	11.5 ± 4.78	13.8 ± 4.37^{b}	36.0 ± 18.26^{b}
	25 %	16.0 ± 5.35	42.8 ± 12.79^{a}	87.3 ± 27.10^{b}
	50 %	27.3 ± 9.10^{B}	63.0 ± 18.19^{a,B}	233.0 ± 50.16^{a,A}
(b) Sheet web weaver	UP	23.0 ± 3.65	16.8 ± 3.30^{b}	14.5 ± 2.40
	25 %	25.8 ± 4.96^{B}	45.5 ± 9.40^{a,A}	21.3 ± 4.64^{B}
	50 %	29.3 ± 4.92^{B}	48.8 ± 5.66^{a,A}	27.8 ± 5.68^{B}
(c) Space web weaver	UP	11.8 ± 1.43	12.0 ± 3.14	27.3 ± 4.01
	25 %	11.8 ± 2.36	6.3 ± 2.14	29.5 ± 5.49
	50 %	9.8 ± 1.65	8.5 ± 3.92	33.8 ± 6.71
(d) Sensing web weavers	UP	17.8 ± 1.05^{A}	1 ± 0.25^{B}	0.5 ± 0.18^{B}
	25 %	13.8 ± 0.93^{A}	1.3 ± 0.28^{B}	1 ± 0.25^{B}
	50 %	13.5 ± 0.92^{A}	1.3 ± 0.28^{B}	1.8 ± 0.33^{B}

Letters represent results of Tukey's post hoc tests. Lowercase letters represent comparisons between different treatments in the same year. Capital letters represent comparisons between different years for particular treatment

UP: unthinned plantation forest; 25 %: 25 % thinning plantation; 50 %: 50 % thinning plantation; B1: 1 year before thinning; A1: first year after thinning; A2: second year after thinning

different arthropod compositions and community structures (Maeto et al. 2002; Ohsawa 2007). Several studies conducted in Japan showed that thinning might increase the richness and abundance of many herbivorous beetle taxa (Ohsawa 2004, 2005; Ohsawa and Nagaike 2006). Other studies conducted in Asia had found a negative or little

Table 9 Abundance of dominant families (mean ± SE) of the major spider guilds of sampling plots receiving various thinning treatments in different years in Ren-Luen, Central Taiwan

Comparisons		B1	A1	A2
(a) Lycosidae	UP	8 ± 4.45	11.3 ± 4.17^{b}	27.5 ± 19.87^{b}
(86.6 % of ground hunters)	25 %	11 ± 4.49	40 ± 13.32^{a}	73.8 ± 22.10^{b}
	50 %	22 ± 7.60^{B}	$56 \pm 17.26^{a,B}$	$209.8 \pm 48.14^{a,A}$
(b) Linyphiidae	UP	7.8 ± 1.75	12.3 ± 3.04^{b}	7 ± 1.08
(64.8 % of sheet web weavers)	25 %	12.8 ± 1.11^{B}	$42 \pm 9.60^{a,\ A}$	14.5 ± 2.40^{B}
	50 %	11.3 ± 2.39^{B}	$41.8 \pm 5.57^{a,A}$	13.5 ± 1.44^{B}
(c) Theridiidae	UP	8 ± 1.08	3.5 ± 0.65	16.8 ± 1.75
(61.8 % of space web weavers)	25 %	7.3 ± 1.71	2 ± 0.71	23.5 ± 4.35
	50 %	7.8 ± 1.65	2 ± 0.71	22.3 ± 6.41
(d) Ctenizidae	UP	16 ± 3.53^{A}	0.5 ± 0.50^{B}	0.3 ± 0.25^{B}
(83.5 % of sensing web weavers)	25 %	10.5 ± 2.53^{A}	1.3 ± 0.95^{B}	0.8 ± 0.48^{B}
	50 %	12 ± 1.78^{A}	1 ± 0.41^{B}	0.8 ± 0.25^{B}

Letters represent results of Tukey's post hoc tests. Lowercase letters represent comparisons between different treatments in the same year. Capital letters represent comparisons between different years for particular treatment

UP: unthinned plantation forest; 25 %: 25 % thinning plantation; 50 %: 50 % thinning plantation; B1: 1 year before thinning; A1: first year after thinning; A2: second year after thinning

effect of thinning on the diversity and/or abundance of certain animal groups in plantation forests (Ohsawa 2005; Yuan et al. 2005; Ohsawa and Nagaike 2006). One reason for the lack of congruence in effects of thinning might be that different microhabitat requirements and community dynamic pattern of target indictors and temperate and subtropical plantation forests differ in dominant tree species and associated microhabitat/climates. Another major reason might be that the consequences of thinning in terms of temporal changes in environmental characteristics varied considerably between two regions. 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 as short as 2 years (Weng et al. 2007). The high growth rate of understory vegetation might have reduced the structural heterogeneity and niche diversity created by thinning. In our results, in the first year after thinning, 25 and 50 % thinning plantations had higher abundance of SH than unthinned plantation forest. In the second year after thinning, although the abundance of SH was still higher in plantations receiving thinning treatments, the abundance difference was no longer statistically significant. Therefore, in subtropical areas such as Taiwan, results of our study showed that thinning practices in plantation forest created habitats of different spider assemblages. If the overall plantation forest is regarded as a large regional biota in which all stands are embedded in it, different degrees of thinning generate forests of different spatial heterogeneity and microclimates, which in turn affects abundance patterns of spiders with specific environmental requirements.

Currently in Taiwan, *C. japonica* plantation is no longer managed for their economic values but to facilitate their functioning in ecosystem, recreation and biodiversity conservation. Our results show that thinning could be an appropriate conduct to enhance the biodiversity of *C. japonica* plantation forests by creating habitats of different microenvironmental features and niches for different organisms.

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Appendix

See Table 10.

Table 10 Main inhabiting zone, activity period and prey capture strategies of spider guilds (modified from Marc and Canard 1997)

Guild	Inhabiting zone	Capture behavior	Main prey
Ambush hunters	Shrubs, foliage and flowers	Sit and wait, ambush	Diurnal and nocturnal, creepy and flower-visitor insects
Ground hunters	Trunk, foliage, small space of litter and ground	Freely hunt, ambush	Diurnal and nocturnal, trunk, creepy, walking, jumping, running or flying, with frequent pauses insects
Orb web weavers	Open space between branches	Building orb web	Diurnal and nocturnal, jumping, long distance flying insects
Other hunters	Shrubs, foliage and ground	Freely hunt, ambush	Diurnal and nocturnal, foliage, creeping, walking, jumping, running or flying insects
Sensing web weavers	Under the bark of trees, Subsurface	Building trapdoor, ambush	Nocturnal, crawling, slow walking insects or arthropods
Sheet web weavers	Shrubs between lower foliage, grass	Building sheet web	Diurnal and nocturnal, jumping or short distance flying insects
Space web weavers	Shrubs, small space in ends of small branches	Building space web	Diurnal and nocturnal, creeping, walking, and bad-flying insects
Specialists	Decayed wood, litter and rocks on ground	Freely hunt, ambush	Diurnal and nocturnal, creeping, walking, running insects and woodlouse, ants

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