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Spider diversity in canopies of Xishuangbanna rainforest (China) indicates an alarming juggernaut effect of rubber plantations

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ABSTRACT

We were interested in how forest type and complexity of vegetation influence the diversity of canopy spiders in the rainforest of Xishuangbanna, southwestern China. We sampled spiders by fogging tree canopies in four replicate sites of five different forest types once in the middle of the rainy season, forest types were tropical seasonal rainforest; monsoon forest; mountain rainforest; *Aporusa yunnanensis* forest; and rubber plantation. From a total of 20 sites and 1000 m^2 projected area we collected 4999 adult spiders of 472 species. Vegetational structure (number of plant forms, such as herbs, shrubs, trees, epiphytes and lianas), tree coverage, shrub coverage, grass coverage, tree height and elevation characterize the environmental conditions in different types of forest. Species richness and mean abundance differed significantly between rubber plantations and natural habitats. Rubber plantations harbored only 42.6–50% of the spider species in the natural forests, and 63.8% of the species in the *A. yunnanensis* forests. Spider guild composition also differed among forest types. Sheet-line weavers dominated the spider assemblages in natural forests with complex vegetational structure, such as tropical seasonal rainforests and monsoon forests. In contrast, cursorial hunters dominated forests with a more simple structure, such as rubber plantations and *A. yunnanensis* forest. These results show that intensive management practices in rubber plantations decrease the complexity of the vegetation and, so, strongly influence the diversity and composition of canopy spider assemblages. A lower intensity of management and the restoration of native vegetation may help balance the opposing needs of economic development and biodiversity conservation in this region.

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1. Introduction

Globally, the loss and degradation of natural habitats results in the loss of biodiversity (Foley et al., 2005) and altered species distributions (Fischer and Lindenmayer, 2007). This may disrupt ecosystem functions and constitute a major threat to the long-term biodiversity conservation (Foley et al., 2005). The last few decades have witnessed an intensive destruction of tropical forests and replacement by plantations. In comparison to cropland, tree plantations and restored forests may conserve biodiversity and original ecosystem services. However, replacement forests will not match the composition and structure of the original forest cover (Chazdon, 2008). The rapid conversion of tropical forests has generated vast human-modified landscapes. Such developments potentially have dire consequences for tropical biodiversity (Foley et al., 2005; Laurance, 2007).

Xishuangbanna belongs to the Indo-Burma biodiversity hotspot (Myers et al., 2000). It has long been celebrated as being the most biodiverse area of China (Mann, 2009). In 1948, natural rainforest covered 67.7% of the area of Xishuangbanna. At that time, farmers widely practiced "slash and burn" agriculture. The quality and extent of natural forest declined continuously with the implementation of mechanized farming and an increasing population. These activities reduced the natural rainforest coverage of Xishuangbanna to 60% of the area by 1960 and to 51% by 1963. Five natural reserves were established in Xishuangbanna to protect the remaining natural forest, which covered approximately 240,000 ha, 12% of the total area (Li et al., 2007). Unfortunately, nature reserve policies have contributed to the continued loss of natural forests because land managers have considered the planting of rubber plantations to be a reforestation activity (Ziegler et al., 2009). A dramatic anthropogenic change from highly diverse tropical seasonal rainforest to monospecific rubber plantations has occurred in recent decades (Li et al., 2007; Li et al., 2008; Mann, 2009; Qiu, 2009; Ziegler et al., 2009). Currently, rubber plantations cover

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about 400,000 ha of Xishuangbanna Prefecture, representing 20% of the territory (Qiu, 2009).

Farmers usually plant rubber trees in sparse rows that form homogeneous and deciduous canopies. Frequently cultivation practices including the spraying of herbicides to kill weeds suppressed non-rubber vegetation. These activities result in a reduction of complexity of vegetation and a concomitant loss of biodiversity. For example, when compared with primary tropical forests, rubber plantations have greatly reduced diversity of plants (Zhu et al., 2004), birds (Aratrakorn et al., 2006), bats (Phommexay et al., 2011), and ground-dwelling arthropods (Zheng et al., 2009; Meng et al., 2012; Zhang et al., 2013). The removal of natural rainforest has catapulted the necessity of gathering biodiversity data that can be used to assess the consequences of land conversion to rubber plantations. Adept analyses of repeatable data can support conservation efforts, and a better insight can help managers to make decisions that maintain biodiversity and support the sustainable use of natural resources.

Spiders are key predators in forests, and they constitute relatively diverse and abundant components of the canopy fauna (Floren et al., 2011). Thus, spider assemblages can serve as indicators of biodiversity when comparing habitats because they are sensitive to a wide range of environmental factors, including habitat structure (Finch, 2005; Oxbrough et al., 2005). Unfortunately, no previous studies have focused on the effect of rubber plantations on canopy spider diversity in tropical regions of China.

Forest canopies represent the functional interface between 90% of Earth's terrestrial biomass and the atmosphere (Ozanne et al., 2003). They are among the most speciose yet most highly threatened terrestrial habitats. As concern for environment issues accelerates, studies of forest canopies are integral to understand biodiversity distribution, alterations of the global climate, and whole-forest interactions (Lowman and Wittman, 1996; Nadkarni et al., 2011). However, very few studies have addressed the changes in canopy spider assemblages in primary rainforests following anthropogenic disturbance in Southeast Asia (Floren and Deeleman-Reinhold, 2005; Floren et al., 2011).

Herein, we report on our investigation on the diversity, abundance, and distinctness of canopy spider assemblages across forest habitats that vary in vegetational structure. We focus on rubber plantations and contrast them with three natural forest habitats. We also sampled other tree monocultures of *Aporusa yunnanensis* (Euphorbiaceae) to generalize the effects of monoculture forests. Thereby, we (1) assess the magnitude of loss of diversity due to the conversion of natural forests to rubber plantations and (2) try to identify the causes of the decrease in diversity by correlating environmental variables with declines. Finally, from our results we (3) derive recommendations for forest (plantation) management for the conservation of biodiversity.

2. Materials and methods

2.1. Study area

The study was conducted in and nearby Menglun Nature Reserve, a subset of Xishuangbanna Nature Reserve, which was established in 1958. More specifically, collecting sites were near the town of Menglun (21°54′–21°58′ N, 101°11′–101°17′ E), Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan, China (Fig. 1). Lying in the East Asian monsoon region, the climate of Xishuangbanna is dominated by moist warm air masses from the Indian Ocean in summer and continental air masses from the sub-tropical regions in winter. The annual temperature averages 21.4 °C and annual rainfall averages about 1500 mm, of which 80% occurs in the rainy season (May–October; Li et al., 2012). The nature reserve partly consists of secondary forests regenerating from agricultural land prepared by slash-and-burn.

Twenty study sites (four repetitions for each forest type) were sampled in three natural forest types plus two types of monoculture (Fig. 1): tropical seasonal rainforest (TSRF), monsoon forest (MF), mountain rainforest (MRF), *A. yunnanensis* forest (AF; in fact, there are two sites of *A. yunnanensis* forest and two sites of *Paramichelia baillonii* (Magnoliaceae) forest, we just use the former as representative for ease of reading), and rubber plantation (RP). Forest types followed the classification of Wu et al. (1987). Details of the five habitats are given in Supplementary materials (Appendix 1, 2). To determine the vegetational complexity of each habitat where spiders were sampled, habitat structural diversity was defined by plant-form in five categories: (1) herbs, (2) shrubs, (3) trees, (4) lianas, and (5) epiphytes.

2.2. Spider sampling

Canopy fogging (pictures in Supplementary materials, Appendix 2) was used to sample spiders. All samples were collected between 19 July and 18 August 2007. Each sample site contained 50 m^2 of projected area from the canopy space. For each sample, ropes suspended at approximately 1.5 m above ground held 100 funnel-like 0.5 m^2 trays. A 50 mL tube with 25 mL 75% ethanol was placed at the bottom of each tray. On slopes, the traps were set in terraces. To avoid edge effects, fogging stations were established at least 50 m from the edges of forest. A portable thermal fogging machine (Swingfog SN-50, Germany, Model 2610E, Series 3) was used to disperse insecticide from the ground; fog drifted up through the canopy (Sørensen, 2004). For each sampling event, the fogger operated for 20 min and used 2 L of a 2.2% solution of pyrethroid dissolved in diesel oil as this dosage was proven to have low toxicity on vertebrates (Stork and Hammond, 1997). Fogging was conducted before sunrise to minimize fog-scatter because wind speeds were lowest at these times. Sampling never took place shortly after rain, or during windy or misty conditions. To prevent erroneous sampling of arthropods from the lower vegetational layer, small trees were bent and tied to the ground and low-lying branches were shaken to remove spiders prior to fogging.

The collecting trays were left for 2 h after fogging to maximize the number of arthropods sampled and to reduce the number of invertebrates escaping due to recovery from the toxic effects of the insecticide. All invertebrates were collected in the installed tubes and then preserved in 75% ethanol.

Adult spiders were sorted out and identified under a stereomicroscope. In case the adult spiders could not be determined as any known species, they were treated as morphospecies within the genus. Spiders were classified into four guilds according to their web-building and prey-catching behaviors following Sørensen (2004): (1) sheet-line weavers (SLW; Amaurobiidae, Dictynidae, Hahniidae, Linyphiidae, Pholcidae, Psechridae, Scytodidae, Sinopimoidae and Theridiidae); (2) orb weavers (OW; Anapidae, Araneidae, Mysmenidae, Nephilidae, Symphytognathidae, Tetragnathidae, Theridiosomatidae and Uloboridae); (3) ambush predators (AP; Ctenidae, Hersiliidae, Mimetidae, Oonopidae, Philodromidae, Sparassidae and Thomisidae); and (4) cursorial hunters (CH; Clubionidae, Corinnidae, Oecobiidae, Oxyopidae, Salticidae, Gnaphosidae, Lycosidae, Pisauridae and Zodariidae). All specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS).

2.3. Vegetational complexity

We recorded several environmental variables (Table 1) at each sampling site to explore factors that might be related to changes in the spider assemblages. These included forest age, estimated

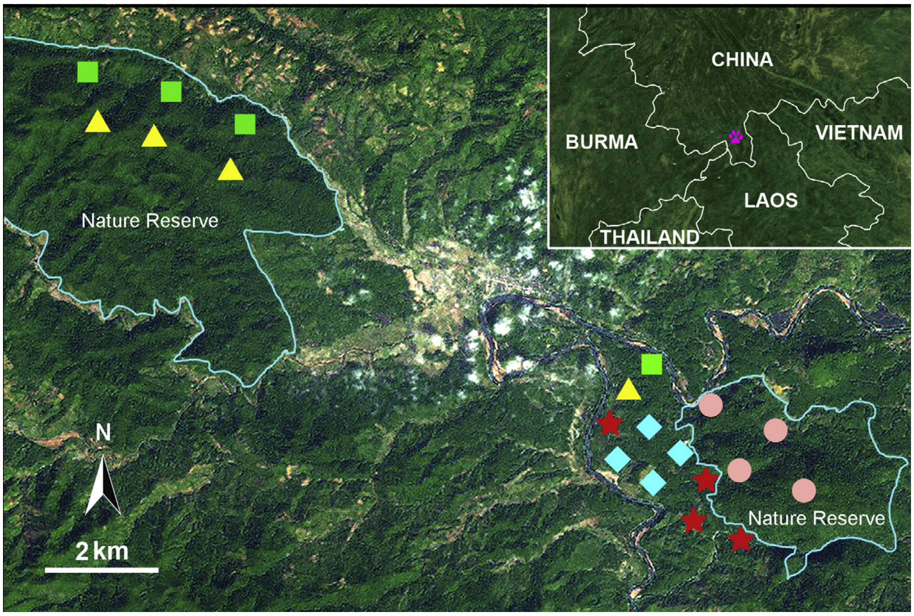

Fig. 1. Location of selected fogging stations in the present study in Menglun Town, Xishuangbanna, SW China. Note: Diamond, rubber plantation; Solid circle, monsoon forest; Square, mountain rainforest; Star, *Aporusa yunnanensis* forest; Triangle, tropical seasonal rainforest. Figure provided by Center for Earth Observation and Digital Earth, Chinese Academy of Sciences.

canopy height, as well as estimated percent cover of herbs, shrubs, and trees. Elevation was recorded using a Garmin eTrex Venture GPS. Vegetational complexity was ranked based on the presence or absence of five plant forms (herbs, shrubs, trees, lianas, epiphytes) and a degree of disturbance was assigned to each sampling plot.

2.4. Statistical analyses

We first conducted a Mantel test and Autocorrelogram in SAM (Rangel et al., 2010) to test for spatial autocorrelation. We used the Jaccard Index of pair-wise similarity among samples and geographic distance based on latitude–longitude coordinate pairs. We divided the data into 12 distance classes with an equal number of pairs per class. Tests of statistical significance were based on 1000 permutations.

For each sampling plot, we calculated mean abundance (all individuals including juveniles per m^2), Margalef Species Richness (D_{mg}), Evenness (J), Shannon–Wiener diversity index (H'), and Simpson's index (D) (Magurran, 1988; Krebs, 1989) for the spider assemblages. One-way analyses of variance (ANOVA) followed by Bonferroni correction were used to compare the values of all indices among the five types of forest. After testing the assumptions of variance analyses with Kolmogorov–Smirnov and Levene's tests, Tamhane's test was used to compare the mean abundance when the assumption of equal variance was not fulfilled. Species rarefaction curves, sample based but rescaled to individuals (Gotelli and Colwell, 2001), were employed to compare the total richness of species of our sampling for each forest type using EstimateS (Colwell, 2009). Mean abundance of each guild (individuals per m^2) from each sampling plot was calculated and then compared among the five types of forest using one-way ANOVA and Bonferroni correction comparisons, respectively. Tamhane's test was used to compare the densities of sheet-line weavers and ambush predators among habitats. All univariate statistical analyses were made with SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

Canonical correspondence analysis (CCA) and the Monte Carlo permutation test (4999 permutations) were performed using CANOCO (ter Braak and Šmilauer, 2002) to describe the influence of the environmental variables on assemblages of canopy spiders. The data were first log $(y + 1)$ transformed to prevent a few high values from unduly influencing the ordination. Detrended correspondence analysis (DCA) indicated that the length of the longest gradient was 3.2 for spider species. However, species data with many zeroes are often best analyzed with a unimodal method. Thus, CCA was considered suitable for these datasets. We ran a global CCA with the set of all explanatory variables to model the response-variable for each matrix. Forward selection was used to rank environmental variables according to their importance for determining the species-data because the global test was significant for a given set of variables (Blanchet et al., 2008). DCA indicated that the length of the longest gradient was less than 3 for spider guilds. Thus, a

Table 1
Environmental variables of the five habitats investigated in Xishuangbanna.

	Age (yr.)	Tree height[a] (m)	Tree coverage[a] (%)	Shrub coverage[a] (%)	Herb coverage[a] (%)	Elevation[a] (m)	Vegetational complexity rank	Disturbance degree
TSRF	>150	40.0 ± 3.5	89.8 ± 1.8	60.0 ± 3.5	55.0 ± 2.0	698 ± 47	V (herbs, shrubs, trees, lianas, and epiphytes)	I (Low)
MF	50	33.8 ± 2.4	84.3 ± 1.7	38.3 ± 3.8	28.8 ± 4.3	636 ± 9	IV (herbs, shrubs, trees and lianas)	I (Low)
MRF	40	24.0 ± 0.7	81.5 ± 2.0	45.8 ± 4.0	37.0 ± 4.3	827 ± 54	III (herbs, shrubs and trees)	I (Low)
AF	25	28.8 ± 1.1	67.8 ± 3.1	13.0 ± 1.2	94.5 ± 1.7	597 ± 14	III (herbs, shrubs and trees)	II (Intermediate)
RP	30	22.0 ± 1.2	70.0 ± 2.0	0	29.5 ± 2.1	585 ± 10	I (few herbs and trees)	IV (High)

[a] The corresponding data in the table were mean ± SE. Note: AF, *Aporusa yunnanensis* forest; MF, monsoon forest; MRF, mountain rainforest; RP, rubber plantation; TSRF, tropical seasonal rainforest.

redundancy analysis (RDA) (Rao, 1964; ter Braak and Prentice, 1988) was used to carry out direct gradient analysis of guilds as a function of the environmental variables.

3. Results

3.1. Sample similarity by distance

The Mantel autocorrelogram indicated significant autocorrelation ($P < 0.05$) for the closest sample pairs (ca. 0.4 km). For distances above the sites, no significant autocorrelation was detected and for the entire dataset, autocorrelation was not significant ($P = 0.141$). Consequently, sites were treated as being independent in all further analyses.

3.2. Spider assemblage composition and abundances

In total, 24,323 individual spiders were collected, including 4999 adults, representing 33 families and 472 species (see Supplementary materials, Appendix 3), including 95 species reported as new to science recently (see Supplementary materials, Appendix 4, 5). The three most abundant families, Clubionidae, Theridiidae, and Thomisidae (listed in order of abundance here and below) in the rubber plantation were similar to these present in the *A. yunnanensis* forest. In comparison, Theridiidae, Oonopidae, and Clubionidae were the three most abundant families in monsoon forest; Theridiidae, Oonopidae, and Thomisidae were most common in mountain rainforest; Pholcidae, Linyphiidae, and Theridiidae were dominant in tropical seasonal rainforest. The results showed that the two most abundant families, Pholcidae (23.5%) and Linyphiidae (16.7%) in tropical seasonal rainforest comprised no more than 4.4% of the spider populations in the *A. yunnanensis* forest and rubber plantation. Indeed, Linyphiidae were not found in rubber plantation. Furthermore, Clubionidae, the most abundant family in the *A. yunnanensis* forest (23.1%) and rubber plantation (31.6%), only accounted for 8.0% of the individuals in tropical seasonal rainforest.

Species composition of canopy spiders varied among the five forest types. The three most abundant species in rubber plantation differed completely from the species in the three types of natural forest, especially tropical seasonal rainforest. The three most abundant species found in the rubber plantation – *Clubiona* sp3 (Clubionidae), *Amyciaea forticeps* (Thomisidae), and *Clubiona* sp2 – represented only 0.2% or less of the total number of spiders collected in tropical seasonal rainforest. In contrast, the three most abundant species in tropical seasonal rainforest either were not found (*Belisana* sp.1 belongs to Pholcidae and *Vittata forfictus* belongs to Linyphiidae) or made up only 0.6% (*Orchestina* sp.1 belongs to Oonopidae) of the population in the rubber plantation, respectively. The three most abundant species in *A. yunnanensis* forest – *Clubiona* sp1, *Orchestina* sp.2, and *Orchestina* sp.1 – is also dominant species in monsoon forest, mountain rainforest, and three types of natural forest, respectively (Appendix 6).

The mean abundance of spiders (including juveniles) varied significantly among the five forest types ($F = 34.44$, $df = 19$, $P < 0.0001$). It was highest in monsoon forest, followed by mountain rainforest, tropical seasonal rainforest, *A. yunnanensis* forest, and lowest in rubber plantation (Fig. 2). The portion of adults was highest in tropical seasonal rainforest (26.7%), followed by *A. yunnanensis* forest (20.9%), monsoon forest (18.9%), mountain rainforest (18.5%), and lowest in rubber plantation (14.9%).

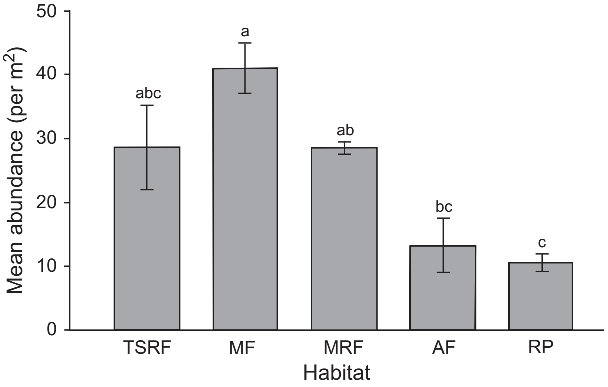

Fig. 2. Mean abundance (individuals including juveniles per m^2, showing 95% CI) of spiders in five types of forest. Lower case letters designate statistically different means ($P < 0.05$; ANOVAs with Tamhane's test). Note: AF, *Aporusa yunnanensis* forest; MF, monsoon forest; MRF, mountain rainforest; RP, rubber plantation; TSRF, tropical seasonal rainforest.

3.3. Spider diversity

The number of species was highest in monsoon forest, followed by tropical seasonal rainforest, mountain rainforest, *A. yunnanensis* forest, and lowest in rubber plantation (Table 2). The significantly lower number of species in rubber plantation is mainly owed to the sharp decline of the most speciose families, such as Linyphiidae, Oxyopidae, Theridiidae, Thomisidae and Salticidae (Appendix 3). As a result, both of Margalef Species Richness (D_{mg}) and Shannon–Wiener diversity index (H') were lowest in rubber plantation. Margalef Species Richness was significantly lower in rubber plantation than those of natural forests; Shannon–Wiener diversity index was significantly lower than those of monsoon forest and mountain rainforest. Although diversity indices showed no significant difference between rubber plantation and *A. yunnanensis* forest, the latter harbored seven more families and 54 more species than the former. Evenness (J) and Simpson's indices (D) were lowest in tropical seasonal rainforest, mainly due to the dominance of three species; together *Belisana* sp.1, *Orchestina* sp.1 (Oonopidae), and *Vittata forfictus* which together comprised 36.5% of all adult spiders in tropical seasonal rainforest.

Because each of the rarefaction curves was based on the same number of samples (four) and sampling areas (200 m^2), an examination of the rarefaction curve per type of forest served to visually compare the total species richness among habitats (Fig. 3). The steep curves suggested that the collections were incomplete. However, the graph revealed that monsoon forest had the highest number of species, followed by the other two natural habitats and *A. yunnanensis* forest; the lowest was in rubber plantation.

3.4. Spider guild structure

Spider guild composition (see Supplementary materials, Appendix 3) in the monoculture forests differed most conspicuously from those of the natural forests in having a higher proportion of cursorial hunters and a smaller proportion of sheet-line weavers. Cursorial hunters dominated spider assemblages in *A. yunnanensis* forest and rubber plantation by constituting 41.2% and 43.9% of all adults, respectively. Tropical seasonal rainforest had a high proportion of sheet-line weavers (56.2% of all adults). Monsoon forest assemblages had a somewhat smaller proportion of sheet-line weavers (33.5%) and a higher proportion of cursorial hunters (36.7%) than tropical seasonal rainforest. Sheet-line weavers (37.0%) and ambush predators (36.0%) dominated in mountain rainforest assemblages. Orb weavers made up the lowest proportion of spider guilds in each habitat.

Spider guild densities (individuals per m^2) differed among habitats. Sheet-line weaver populations were significantly more abundant in tropical seasonal rainforest than in other habitats, followed by monsoon forest, mountain rainforest, *A. yunnanensis* forest, and

Table 2
Number of spider species, Margalef Species Richness (D_{mg}), Evenness (J), Shannon–Weiner function (H') and Simpson index (D) of sampling plots in five habitats in Xishuangbanna, and the results of ANOVA test followed by Bonferroni correction. a – shows a statistically significant higher than those with b; ab – shows no significant difference with either a or b.

Habitat	Species	D_{mg}	J	H'	D
TSRF	207	13.72 ± 0.96^{a}	0.75 ± 0.01^{b}	3.32 ± 0.10^{ab}	0.90 ± 0.02^{b}
MF	223	15.71 ± 1.60^{a}	0.85 ± 0.02^{ab}	3.85 ± 0.20^{a}	0.96 ± 0.02^{a}
MRF	190	14.39 ± 0.44^{a}	0.85 ± 0.01^{ab}	3.76 ± 0.06^{a}	0.95 ± 0.01^{a}
AF	149	11.52 ± 1.42^{ab}	0.91 ± 0.01^{a}	3.66 ± 0.11^{ab}	0.96 ± 0.00^{a}
RP	95	7.82 ± 0.70^{b}	0.85 ± 0.05^{ab}	3.15 ± 0.10^{b}	0.94 ± 0.01^{ab}
F	–	7.70	4.04	5.96	5.44
$P <$	–	0.01	0.05	0.01	0.01

Note: AF, *Aporusa yunnanensis* forest; MF, monsoon forest; MRF, mountain rainforest; RP, rubber plantation; TSRF, tropical seasonal rainforest.

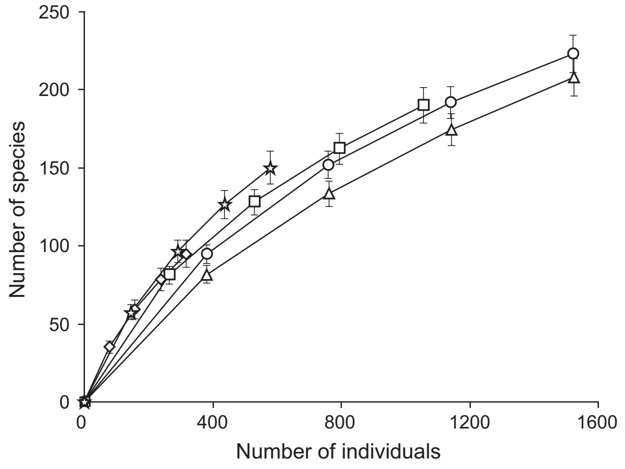

Fig. 3. Rarefaction curves (showing SD) of spider from tree canopy in five forest types. Note: Diamond, rubber plantation; Solid circle, monsoon forest; Square, mountain rainforest; Star, *Aporusa yunnanensis* forest; Triangle, tropical seasonal rainforest.

finally rubber plantation ($F = 57.33$, df = 3, $P < 0.0001$). Orb weavers did not differ significantly among habitats ($P = 0.42$). Cursorial hunters were significantly higher in monsoon forest than other habitats ($F = 9.23$, df = 3, $P < 0.001$). Ambush predators were significantly higher in mountain rainforest and monsoon forest than in the two types of monoculture forests ($F = 4.81$, df = 3, $P < 0.05$).

3.5. Relationships with environmental variables

The first axis of the global CCA accounted for 22.8% of the variance and separated sites along a disturbance to vegetational complexity/coverage gradient. The second axis accounted for 18.7% of the variance and separated sites mainly along an elevation gradient (Fig. 4). The results of forward selection analyses showed that disturbance ($F = 2.33$; $P < 0.001$), elevation ($F = 2.02$; $P < 0.001$), vegetational complexity ($F = 1.73$; $P < 0.001$), shrub coverage ($F = 1.30$; $P < 0.05$), and herb coverage ($F = 1.30$; $P < 0.05$) significantly influenced canopy spider assemblages. All other variables had no significant influence. Environmental variables explained 67.3% of the total variance. The species-environment correlations were 0.992 on the first axis and 0.996 on the second axis. A Monte-Carlo simulation with 4999 permutations indicated that species distribution along the axes was not random (first canonical axis, $F = 1.503$, $P < 0.001$; all canonical axes, $F = 1.528$, $P < 0.001$).

The first axis (CCA-I) mainly represented a gradient of disturbance and vegetational variables. The sites of rubber plantation, with the highest disturbance degree and the lowest vegetational complexity rank, were distributed on the lower right of the CCA biplot. In contrast, the sites of tropical seasonal rainforest, with

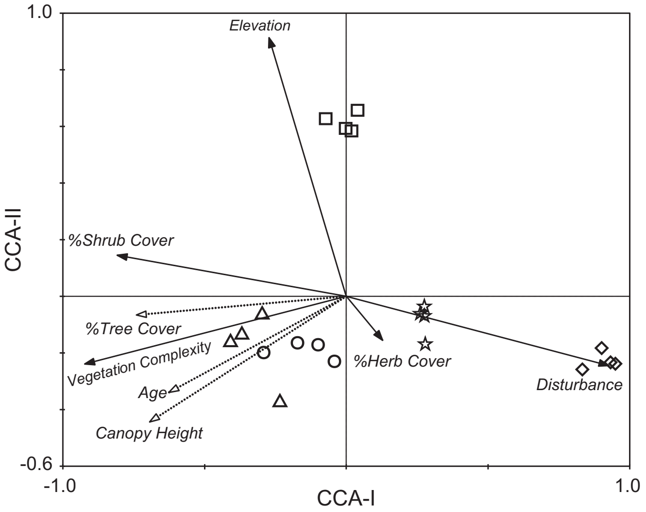

Fig. 4. CCA ordination biplot showing relationships between spider species assemblages and environmental variables in Xishuangbanna. All environmental variables (with both significant (solid arrows) and non-significant (dotted arrows) influence on canopy spider assemblages) are shown. Note: Diamond, rubber plantation; Solid circle, monsoon forest; Square, mountain rainforest; Star, *Aporusa yunnanensis* forest; Triangle, tropical seasonal rainforest.

low disturbance degree and the highest vegetational complexity rank were distributed on the lower left of the CCA biplot. The second axis (CCA-II) mainly reflected a gradient from high-elevation sites represented by mountain rainforest to low-elevation sites; as well as the gradient of herb coverage, which also influence on the spider assemblages in canopy (Fig. 4).

With regard to spider guilds, the first axis of the RDA accounted for 80.6% of the variance and separated sites mainly along vegetational complexity to disturbance gradient. The second axis accounted for 11.5% of the variance, and separated sites mainly along a canopy height gradient (Fig. 5). The results of forward selection analyses showed that disturbance ($F = 21.60$; $P < 0.001$), canopy height ($F = 5.39$; $P < 0.01$), vegetational complexity ($F = 3.48$; $P < 0.05$), and elevation ($F = 3.92$; $P < 0.05$) significantly influence canopy spider guilds. The other variables did not significantly influence assemblages of canopy spider guilds. Environmental variables explained 100% of the total variance. The species-environment correlations were 0.950 on the first axis and 0.910 on the second axis. A Monte-Carlo simulation with 4,999 permutations indicated that species distribution along the axes was not random (first canonical axis, $F = 23.11$, $P < 0.001$; all canonical axes, $F = 7.27$, $P < 0.001$).

The first axis (RDA-I) mainly represented a gradient of disturbance and environmental habitats variables. The sites of rubber plantation were distributed on the left of the RDA biplot;

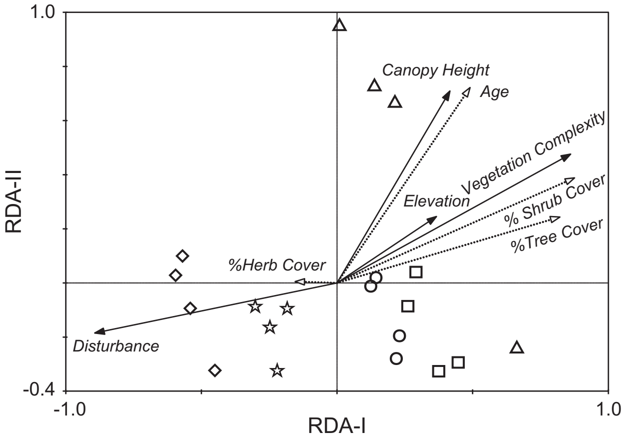

Fig. 5. RDA ordination biplot showing relationships between spider guild assemblages and environmental variables in Xishuangbanna. All environmental variables (with both significant (solid arrows) and non-significant (dotted arrows) influence on canopy spider assemblages) are shown. Note: Diamond, rubber plantation; Solid circle, monsoon forest; Square, mountain rainforest; Star, *Aporusa yunnanensis* forest; Triangle, tropical seasonal rainforest.

A. yunnanensis forests were also distributed on the left. While almost all the sites of natural forests were distributed on the right of the RDA biplot. The second axis (RDA-II) mainly reflected a gradient from high-canopy height sites represented by tropical seasonal rainforest to low-canopy height sites (Fig. 5).

4. Discussion

The recent decades in Xishuangbanna have witnessed a shift in the dominant type of land-use from natural forests to rubber plantations. This has led to an aggregate decline of ecosystem services. Significant changes have occurred in the ecological functions of these forests, such as nutrient cycling, erosion control, climate regulation, the provisioning of raw materials, and the availability of habitat or refuge for wildlife (Hu et al., 2008). Another aftermath of the rubber plantation juggernaut in Xishuangbanna relates to the biodiversity crisis via local extinction. High species diversity resides in tropical forest canopies (Ellwood and Foster, 2004), whereas large areas of tropical rainforest are being lost in this region nowadays. Our study provides the first analysis of spiders that dwell in the crowns of rubber trees. We compare them with those in natural forests and other man-made monoculture forests. Our study confirms that the species richness of canopy spiders have reduced greatly during this ecological transformation, accompanied by change in species composition and decrease in abundance.

4.1. Sample similarity by distance

Although overall spatial autocorrelation among samples is not statistically significant, our finding of significant autocorrelation among the closest sample pairs (ca. 0.4 km) suggests that similar future studies should space samples greater than this minimum distance. A minimum distance of 1 km would be more than adequate. Nevertheless, we contend that any distortion of our data due spatial autocorrelation is minimal and will not undermine the larger pattern this study obtains.

4.2. Spider assemblage composition and abundances

Our results show that the compositional assembly of canopy spiders differs among types of forest, although Floren and Linsenmair (2005) demonstrated that such differences usually cannot be related to dissimilarities between forest types because the regional species-pool is rarely sampled adequately. Notwithstanding, the species, families, and guilds in the crowns of rubber trees obviously deviate from those of natural forests, especially compared with tropical seasonal rainforest. Some species of *Clubiona* in rubber plantation have relatively high abundance but are rare or absent in natural forests. In contrast, numerous commonly found species in natural forests are rare or absent from the rubber plantations. The species of tree(s) was thought to not influence the composition of spider assemblages (Russell-Smith and Stork, 1995; Floren and Deeleman-Reinhold, 2005; Floren et al., 2011). Our results do not necessarily reject this conjecture. Intense anthropogenic disturbance was considered the key factor that drives a simplistic spider fauna of rubber plantation by changing niches, food resources, and potential refuges present within tree-crowns. Such changes greatly affected the nature of the canopy spider assemblages.

Low spider mean abundance in the canopy of rubber plantation is acutely obvious in our study. It comprises no more than 1/3 of the spider mean abundance of monsoon forest and only about 1/2 of that of other natural forests. Spider mean abundance in rubber plantation is much lower than that reported previously. For example, Russell-Smith and Stork (1995) found 4.7 adult spiders per m^2 in Southeast Asia and Sørensen (2004) found 5.8 adult spiders per m^2 in montane forest in Tanzania. Curiously, the highest percentage of singletons and doubletons (70.0%) was found in rubber plantation, and this is much higher than that of other habitats (e. g., TSRF, 59.6%; MF, 53.4%; MRF, 60.0%; AF, 61.6%) and previous studies conducted in natural forest, e.g., Sørensen (2004) 35.6% and Hsieh and Linsenmair (2011) 43.8%. These results indicate the incapacity of rubber plantation in protecting canopy spiders than other forests.

4.3. Spider diversity

It is not surprising that rubber plantations host the lowest spider species diversity. However, the extent of loss is shocking. Compared with natural forests, rubber plantation carries only from 42.6% to 50.6% of spider species. Oxbrough et al. (2012) and Barsoum et al. (2014), however, demonstrated that mixed woods may not always possess higher biodiversity than monoculture stands. Compared with rubber plantation, *A. yunnanensis* forest hosts more spider species and a higher mean abundance. Thus, shrubs and herbs provide an important habitat that affects canopy spider assemblages, which is also confirmed by the result of CCA. The open canopy cover and relatively less disturbance of *A. yunnanensis* forest permit the development of a dense layer of herbs and a few shrubs. This additional layer provides important refuge and a source of prey, which helps to promote the diversity of canopy spiders. Although rubber plantation has the same type of relatively open canopy cover as *A. yunnanensis* forest has, it does not have a dense herb layer and the shrubs because of cultivation practices. This finding correspond with those of Fischer and Lindenmayer (2007) who considered that the loss of some structural elements can have particularly severe negative effects on native species, and is especially likely to trigger extinction cascades. Further, rubber plantation defoliates during the dry season in Xishuangbanna, which decreases the suitability of rubber tree crowns for spiders. Thus, canopy spiders that favor natural habitats will become rare or even disappear from rubber plantations.

Low values of the Evenness and Simpson indices in tropical seasonal rainforest indicate a few highly abundant species dominate its spider assemblages. We speculate that previous slash-and-burn cultivation in Xishuangbanna may have reduced the abundance of the original dominant species and, consequently, increased the diversity of the spiders in secondary forests, such as in monsoon forest and mountain rainforest. Thus, higher spider diversity indices were found in these habitats.

4.4. Relationships with environmental variables

Our correspondence analysis resolves a pair of factors that have opposing effects. Anthropogenic disturbance and vegetational complexity strongly influence the assemblages of canopy spiders. Intense anthropogenic disturbances usually impose negative effects on the diversity of arthropods in forest canopies. Compared with tropical rainforests, the frequent disturbances that occur during rubber cultivation, including regular herbicide spraying, not only disrupt the complex vertical stratification and resource-use in the canopy, but also eliminate layers of shrubs and herbs. This high level of disturbance results not only in the lowest diversity of spiders, but also the changed species composition and decreased abundance. In accordance with our finding, Floren and Linsenmair (2001) reported that anthropogenic disturbances reduced the size of the species pool dramatically.

Our findings confirm the discoveries of other studies that vegetational complexity has a positive relationship with the diversity of canopy spiders (Halaj et al., 2000; Pinkus-Rendón et al., 2006). Gómez and Abril (2011) showed that a reduction in vegetational structure could drive changes in assemblages of forest ants. Vegetational complexity closely relates to the presence or absence of shrubs and herbs and this significantly affects assemblages of canopy spiders in important ways. The relatively higher diversity of canopy spiders in *A. yunnanensis* forest when compared with rubber plantation supports the observation. Our findings correspond with those of Ziesche and Roth (2008) in that herb coverage is one of the key factors affecting spider assemblages. Similarly, Purchart et al. (2013) suggested that herbs explained a significant level of species diversity in assemblages of ground-dwelling spiders. In addition, similar to Sørensen (2004) and Russell-Smith and Stork (1994), our result showed that elevation also affects the abundance and composition of canopy spider fauna.

Our results show that canopy height, a factor that is related to the age of forest, was important for the spider guild assemblages. The age of forests was proved to be an important factor affecting spider assemblages (Purchart et al., 2013). Floren et al. (2011) also suggested that canopy spider assemblages were clearly determined by forest age. Hsieh and Linsenmair (2011) revealed that old-growth trees possessed the greatest diversity and evenness when compared with younger forests. Similar positive correlation between Carabidae forest species richness and increasing stand age has also been observed in Britain (Jukes et al., 2001; Mullen et al., 2008). Ellwood and Foster (2004) and Sørensen (2004) revealed that in tropical seasonal rainforests, the familiar occurrence of epiphytes, mosses, and lichens that are positively related to forest age may affect assemblages of canopy spiders.

5. Conclusion and recommendations

Our study on the diversity of spiders in the canopy of Xishuangbanna represents the first assessment of canopy-dwelling arthropods among different types of forest in tropical China. Although this study is a snapshot of canopy spiders, and hence does not reflect seasonal variation, our analyses present a clear picture showing that spider diversity strongly decreases in the canopy of rubber plantations in Xishuangbanna. Nowadays, tropical seasonal rainforests are highly fragmented by rubber plantations (Li et al., 2007). Wittemyer et al. (2008) argued that the long-term viability of existing reserves is often strongly affected by patterns of human activity in adjacent areas. Therefore, the future of canopy spiders in Xishuangbanna depends more than ever on the effective management of human-modified landscapes by conservation practitioners and land-use managers.

The increasing demand for high-priced natural rubber will most likely lead to the continued expansion of rubber plantations in Southeast Asia. To reduce the negative effects of rubber plantations on canopy spiders, we suggest increasing vegetational complexity by establishing multiple layers. The planting of cash-crop tea, coffee, or cocoa within rubber monocultures may accomplish this goal. Rubber plantations should retain herbs in the understory. Shade tea could promote the development of a diverse fauna of ground-dwelling spiders (Zheng et al., 2009). Rubber plantations with a tea understory have been shown to be very productive (Xie, 1989). Thus, this alternative approach to rubber plantations can help balance the conflicting needs of economic development and conservation, including that of spider diversity. A second and equally important approach, however, is the adoption of more effective measures by the forestry administrative department. Effective administrative guidance could preclude further destruction of tropical forests in Xishuangbanna, especially below 800 m. Scientific analyses on the dynamics of biodiversity and their implications for conservation can guide the formation of management plans by decision makers and conservationists alike. Thus, we appeal to scientists to pay close attention to the environment and dynamics of biodiversity in rubber plantation. We encourage the production of more reliable and comprehensive information that can support sustainable development in this region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.11.031.

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