

# Diversity and assemblage structure of bark-dwelling spiders in tropical rainforest and plantations under different management intensities in Xishuangbanna, China

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**Abstract.** 1. In tropical Southeast Asia, large-scale establishment of forest plantations has reduced forest diversity and altered arthropod assemblages by changing plant communities and ecological properties. Few studies address the impacts of forest change on important predatory groups on tree trunks.

2. We compared spider assemblages on tree trunks in natural forests and three forest plantation types in the Xishuangbanna area of southwestern China, to determine how tropical forest management influences bark-dwelling spider composition. Spiders were sampled using trunk traps in tropical seasonal rain forests (TSRF), rubber plantations (RP), rubber-tea mixtures (RTM) and *Aporosa yunnanensis* plantations (AYP).

3. Spider species composition differed between TSRF and forest plantations. Canopy cover in both seasons and grass cover and shrub cover in the dry season well explained species assemblages. Spider diversity between TSRF and forest plantations differed more distinctly in the rainy season. AYP had an intermediate level of disturbance, which was associated with highest species richness, whereas TSRF had the highest beta diversity. The mean number of individuals was the highest in RP, but species richness and beta diversity were the lowest.

4. An intermediate level of disturbance increased alpha diversity of bark-dwelling spiders, whereas intensive management that altered vegetation structure had adverse effects on these spiders. Preservation or enhancement of surface vegetation in RP may maintain or increase species richness of bark-dwelling spiders. The highest beta diversity of the TSRF indicated that undisturbed natural forests better conserved regional spider diversity than plantations.

**Key words.** Araneae, human management, rain forest, rubber plantation, trunk traps, Xishuangbanna.

## Introduction

The forest cover of tropical Asia has declined dramatically in recent decades, as various kinds of agricultural areas and forest plantations have replaced natural forests. Such

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large-scale change in land use has had important effects on arthropod diversity and abundance (Lawton *et al.*, 1998), not only by reducing the size of the species pool but also by changing abundance dynamics in these ecosystems (Floren & Linsenmair, 2001). The tropical rainforests of Xishuangbanna, southwestern China, are considered 'hotspots' for biodiversity and have higher species richness than other tropical rainforests of Southeast Asia (Zhu *et al.*, 2006). Forest management, mainly clear-felling followed by the establishment of rubber plantations, however, has simplified natural forests and reduced the area of tropical rainforest (Li *et al.*, 2007; Mann, 2009; Qiu, 2009; Ziegler *et al.*, 2009). Rainforest covered 10.9% of the region in 1976, but only 3.6% in 2003 (Li *et al.*, 2007). Previous studies showed that the species richness of vertebrates (Aratrakorn *et al.*, 2006; Phommexay *et al.*, 2011) and arthropods (Zheng *et al.*, 2009, 2015; Meng *et al.*, 2012) has significantly decreased in rubber plantations compared to natural forests in Xishuangbanna. The drastic reduction in the extent of natural ecosystems in Xishuangbanna has motivated the need for greater knowledge of biodiversity to support future conservation and management decisions. Comprehensive information on how rubber plantations affect biodiversity of species living on tree trunks will inform future conservation decisions here and elsewhere in the tropics, and may have implications for other managed low-diversity vegetation types, such as tea, pine and *Eucalyptus* plantations.

Tree trunks are characterised by numerous unique biotic and abiotic environmental factors (Menzel *et al.*, 2004; Szinetár & Horváth, 2005), such as bark structure, wind and humidity that differ from that of both ground level and tree canopies. Tree trunks are important links between the canopy and forest floor, especially for flightless vertebrates and invertebrates that move from the forest floor to feed or breed on tree trunks or higher in the canopy (Moeed & Meads, 1983). Thus, tree trunks represent the essential physical and biological connection between ground and canopy, as well as being a habitat for arthropods in their own right (Proctor *et al.*, 2002). Tree trunks are also a key component for maintaining biodiversity and associated ecosystem function in both managed and unmanaged forests (Franklin *et al.*, 2002). Bark habitats provide food resources, shelter and sites for oviposition, as well as other resources for organisms.

Spiders are a dominant group of bark-dwelling predatory arthropods (Moeed & Meads, 1983; Majer *et al.*, 2003; Horváth *et al.*, 2005). They are high-ranked predators within food chains and their phenology and assemblage structure are sensitive to changes in vegetation structure and other disturbances (Hsieh *et al.*, 2003). Therefore, they are useful indicators for comparing biodiversity across environments (Cardoso *et al.*, 2008). Most previous studies on spider diversity have focused at the ground level (e.g. Uetz & Unzicker, 1976; Topping & Sunderland, 1992; Oliver & Beattie, 1996; Pinkus-Rendón *et al.*, 2006; Zheng *et al.*, 2009; Buchholz, 2010; Gaigher

& Samways, 2014), on bushes (e.g. Johnson, 1996; Kampichler *et al.*, 2000) and in foliage or canopy (e.g. Erwin, 1982; Mason, 1992; Kitching *et al.*, 1993, 1997, 2001; Russel-Smith & Stork, 1994; Stork *et al.*, 1997; Halaj *et al.*, 2000; Sørensen, 2004; Zheng *et al.*, 2015). Only limited information is available for spiders on tree trunks, although high species numbers have been collected from bark habitat (Szinetár & Horváth, 2005; Larrivé & Buddle, 2010; Blick, 2011). To the best of our knowledge, this is the first study in China to address the diversity and assemblage structure of bark-dwelling spiders.

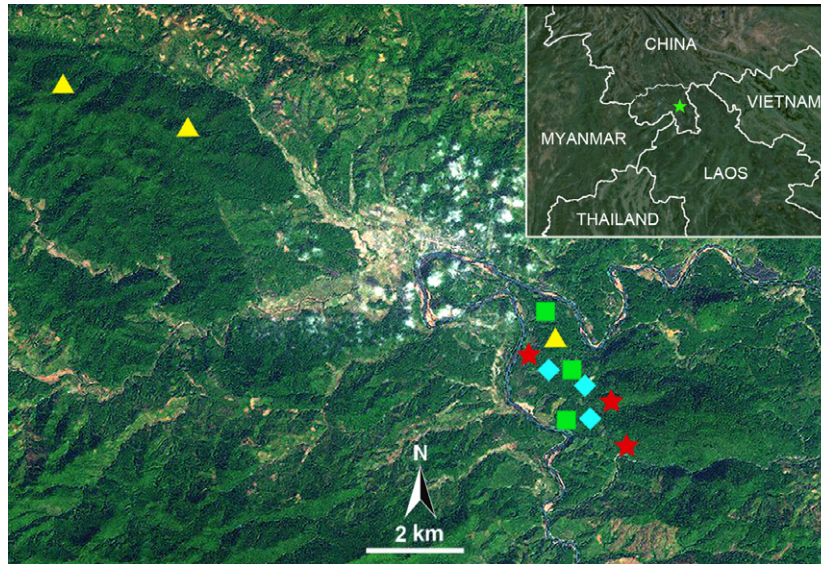
Spider species composition on bark has been shown to be strongly influenced by the dominance ranking of the tree species (Pinzón & Spence, 2010), tree bark characteristics (Horváth *et al.*, 2005) and changes in vegetation due to anthropogenic causes (Duelli *et al.*, 1990; Epstein & Kulman, 1990). Hence, shifts in plant composition caused by land-use changes may directly and/or indirectly affect spider assemblages. Changes in spiders associated with tree trunks following land-use changes have not yet been examined in tropical regions.

Herein, we compared bark-dwelling spider assemblages among four different land-use types in the Xishuangbanna region, which included (i) tropical seasonal rainforests (TSRF), (ii) *Aporosa yunnanensis* (Pax & Hoffm.) Metc. (Euphorbiaceae) plantations (AYP), (iii) rubber and tea mixtures (RTM), and (iv) rubber plantations (RP). RP are the most common plantation type and they cover 20% of the land in Xishuangbanna (Qiu, 2009). AYP are similar to RP in that they both have one primary tree species; however, a lack of management in AYP results in a dense low-level vegetation layer consisting primarily of weed populations and some shrubs, and thus differs from RP. RTM mixture receives fine-scale management similar to RP, but they have a regular shrub layer of tea [*Camellia sinensis* var. *assamica* (Mast.) Chang (Theaceae)]. As plant diversity increases from RP, RTM, AYP, to TSRF (Xiao *et al.*, 2014), the intensity of disturbance and the complexity of vegetation structure differs. We addressed two questions: (i) how do spatial-seasonal distributions of bark-dwelling spider assemblages differ among the four land-use types, and (ii), does vegetation complexity and diversity of herbs and shrubs (tea bushes) in plantations increase spider diversity?

## Methods

### Study area

The study area was located in and near the Menglun Nature Reserve (21°54'–21°58'N, 101°11'–101°17'E), in Yunnan, China (Fig. 1). Lying in the East Asian Monsoon Region, Xishuangbanna is dominated by warm and wet air masses from the Indian Ocean in the rainy season and cooler, drier continental air masses in the dry season. Average annual rainfall was 1539 mm, of which 82% occurred in the rainy season (May–October) and 18%



**Fig. 1.** Location of selected trapping stations in this study in Menglun Town, Xishuangbanna, SW China. Note: Diamond, rubber plantation; Square, rubber and tea mixture; Star, *Aporosa yunnanensis* plantation; Triangle, tropical seasonal rainforest. Figure provided by Center for Earth Observation and Digital Earth, Chinese Academy of Sciences. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

occurred in the dry season (November–April). Average annual temperature was 21.4 °C (Cao & Zhang, 1997).

Plant composition and current management practices in each land-use type were as follows: TSRF (>150 years old) occur in wet ravine habitat. The canopy of TSRF has three indistinct tree layers, and is dominated by *Pometia tomentosa* (Blume) Teijsm. & Binn. (Sapindaceae), *Couratari* spp. (Lecythidaceae) and *Terminalia myriocarpa* Heurck & Muell (Combretaceae) with an average canopy height of 30 m, with emergents reaching 45 m (Table 1). Trees with buttress roots and cauliflory (trees with flowers/fruits emerging from main stems) are common, and both large woody lianas and vascular epiphytes are abundant in this type of habitat. *Bolbitis heteroclita* (C. Presl) Ching (Bolbitidaceae) and other ferns comprise most of the herbaceous plants in the ground layer. TSRF have a low level of disturbance limited to traditional collection of mushrooms and nuts. Two sites of TSRF were in natural reserve and another one was in Xishuangbanna Tropical Botanical Garden (XTBG). There is a deficiency in sampling sites selection in that two of the sites are far away from others. However, these are the nearest sites to these plantations in the area, and vice versa. AYP (*c.* 25 years old) include two sites of *A. yunnanensis* plantations and one site of *Paramichelia baillonii* (Pierre) Hu (Magnoliaceae) plantation; we used the former as representative for better flow and clarity. AYP have an average canopy height of approximately 25–30 m (Table 1). Herbaceous plants are very abundant in AYP, and common species are *Digitaria sanguinalis* (L.) Scop. (Gramineae) and *Selaginella tamariscina* (P. Beauv.) Spring (Selaginellaceae). AYP are disturbed slightly by light grazing and seedlings removal. RTM (*c.* 30 years old) have one regular tree layer of *Hevea brasiliensis* Mull. Arg. (Euphorbiaceae) of

20–25 m in height and a regular shrub layer of tea (Table 1). RP (*c.* 30 years old) have one regular canopy layer of *H. brasiliensis*, with an average canopy height of 20–25 m (Table 1). Rubber trees were usually planted in rows both in RTM and RP, with homogeneous deciduous canopies in Xishuangbanna. Herbaceous plants are rare because of herbicide spraying and frequent disturbance from collecting rubber latex. All three sites of RTM and three sites of RP were in XTBG.

#### Environmental variables

Three 200 m-long transects were selected in each land-use type. Five sampling points were equally spaced along each transect at 0 m, 50 m, 100 m, 150 m and 200 m. Sampling points were at least 50 m from forest edges to minimise edge effects. Each transect was in a separate plantation block and transects were separated by more than 1 km from each other. The minimum distance between transects from different land-use types was 600 m. We recorded environmental variables (Table 1) in each transect to explore factors that might relate to spider assemblages in early March and July 2007, including forest age. In each transect, canopy height, and percent cover of trees, shrubs and herbs were estimated by experienced ecological station staff members of the Xishuangbanna Tropical Botanical Garden. Litter depth was recorded by direct measurement using a ruler. Elevation was recorded using a Garmin eTrex Venture GPS. The degree of disturbance was ranked by the number of human visitation and cultivation activity. Environmental variables were collected at the centre of each transect; however, litter depth was measured at each sampling point.



**Table 1.** Environmental variables of the four habitats investigated in Xishuangbanna, China (all values are means + SE, except age).

	TSRF	AYP	RTM	RP
Age (years)	>150	25	30	30
Elevation (m)	698 ± 47	597 ± 14	566 ± 10	585 ± 10
Bark roughness	Moderate	Moderate	Moderate	Moderate
Degree of disturbance <sup>†</sup>	I	II	IV	IV
Tree height (m)	40.0 ± 3.5	28.8 ± 1.1	20.0 ± 1.2	22.0 ± 1.2
Dry season				
Tree cover (%)	73.3 ± 3.3	50.0 ± 2.9	16.0 ± 1.0	15.0 ± 0
Shrub cover (%)	58.3 ± 3.3	18.3 ± 1.7	35.0 ± 2.9	0
Herb cover (%)	43.3 ± 1.7	94.3 ± 2.3	23.3 ± 1.7	19.3 ± 2.3
Leaf-litter depth (cm)	2.43 ± 0.38	1.17 ± 0.17	9.83 ± 0.15**	9.80 ± 0.20**
Rainy season				
Tree cover (%)	79.0 ± 2.1	65.3 ± 2.7**	65.0 ± 2.9**	63.3 ± 1.7**
Shrub cover (%)	60.0 ± 5.0	25.0 ± 2.9	49.3 ± 3.0*	0
Herb cover (%)	55.0 ± 2.9	97.7 ± 1.3	37.3 ± 5.0	30.0 ± 2.9
Leaf-litter depth (cm)	1.67 ± 0.33	1.27 ± 0.37	1.50 ± 0.17	1.33 ± 0.16

AYP, *Aporosa yunnanensis* plantation; RP, rubber plantation; RTM, rubber and tea mixture; TSRF, tropical seasonal rain forest.

\* $p < 0.05$ ; \*\* $p < 0.01$  (p-Values showing paired sample *t*-tests between the dry season and rainy season).

<sup>†</sup>Measured by the number of visiting people and the strength of their activity.

### Spider sampling

Spiders were collected using trunk traps (Fig. 2), which intercepted spiders that moved down along the trunk. At each sampling point, two trunk traps were deployed each on individual trees. Trunk traps were approximately 72 cm in height, and were installed 1.5 m above the ground on *P. tomentosa* and *T. myriocarpa* in TSRF, on *A. yunnanensis* or *Paramichelia baillonii* (Pierre) Hu (Magnoliaceae) in AYP and on *H. brasiliensis* in RTM and RP. All selected trees had diameter at breast height between 22 and 26 cm, and had similar bark structure with moderate roughness and cracking. The edges of the netting girdle of traps were covered with adhesive to prevent spiders from escaping. Each trap had a 600 mL plastic collecting bottle containing *c.* 200 mL of preservative (formaldehyde:detergent:water = 4:1:95). A small hole was drilled in the centre of each trap such that rainwater could flow out. Trunk traps were operational continuously during the field work, and specimens were removed from traps every 15 days and subsequently preserved in 75% ethanol for later identification. Field work was conducted in the dry season (from January to April) and the rainy season (from May to July) in 2007.

All adult spiders were identified to species and nomenclature followed the World Spider Catalog (2016). Because of difficulties in identifying juveniles, only adult spiders were used in the analyses. All specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS).

### Data analyses

Captures of spiders from the two traps at each sampling point were not independent and therefore samples



**Fig. 2.** Trunk trap employed in study. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

were pooled for analyses. This resulted in three transects and 15 sampling points per land-use type and 60 samples and 13 temporal samples across the study.

Paired sample *t*-tests were employed to compare environmental variables between dry and rainy seasons in each land-use type (Table 1). We used different parameters, including mean catch (individuals per trap per month), Shannon–Wiener index ( $H'$ ), Simpson's index ( $D$ ), Margalef species richness ( $D_{mg}$ ), Evenness ( $J$ ) (Magurran, 1988; Krebs, 1989) and Sorensen index ( $\beta_{sor}$ ) to compare spider diversity among land uses. Sorensen index was used as an indication of species turnover among samples within each land use, with higher values indicating greater differences among assemblages. It was calculated using the Betapart package (Baselga & Orme, 2012) in R (R Development Core Team, 2011). Next, we used a generalised linear mixed model (LMM) to assess responses of the six diversity parameters listed above to environmental variables (including land-use types, seasons and their interaction). Transect was treated as a random effect with temporal autocorrelation (first-order autoregressive process) among samples due to repeated sampling. Given that two TSRF sites are far away from all the other study sites, a pre-analysis (also using LMM) that included distance as a covariate was preformed, which found that distance did not significantly influence the Sorensen's results. Thus, we excluded distance from the final model. In addition, a stepwise linear regression was used to assess the influence of environmental variables (including tree cover, shrub cover, grass cover, litter and elevation) on the six diversity parameters. Data were checked for normality using the Kolmogorov–Smirnov test. Simpson and Evenness values were log-transformed to attain normal distributions. Tukey post hoc tests were used to test differences among habitats. This analysis was performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA). Sample-based rarefaction (Gotelli & Colwell, 2001) was employed to compare total species richness in each land-use type using EstimateS version 8.2 (Colwell, 2009).

Redundancy analysis (RDA; performed separately for the dry and rainy seasons) on Hellinger transformed data (Rao, 1964; ter Braak & Prentice, 1988; Legendre & Gallagher, 2001) was performed using CANOCO version 4.5 (ter Braak & Šmilauer, 2002) to describe influences of the chosen environmental variables on spider species composition. A significance test was used to identify the significant explanatory variables from the full set of variables, including tree cover, shrub cover, herb cover, leaf-litter depth, elevation and degree of disturbance. Singletons and doubletons were removed from the analysis to attain good support, as they did not contribute much to the variance in composition and patterns are revealed by abundant species.

## Results

### *Spider assemblages*

A total of 4639 spiders were trapped from the 60 trap stations, 1764 (40.4%) of which were adults. Thirty-one families and 226 species of adult spiders were identified. A

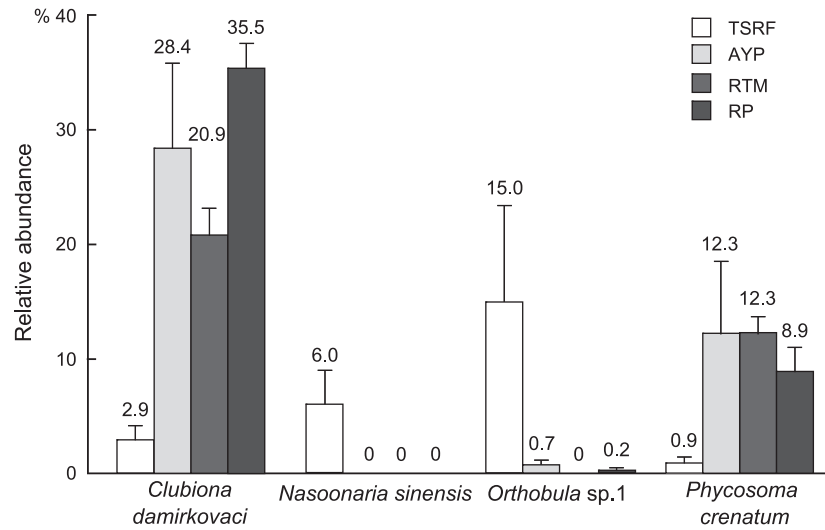
total of 246 individuals and 86 species in TSRF, 420 individuals and 120 species in AYP, 470 individuals and 87 species in RTM and 628 individuals and 72 species in RP were collected.

Spider assemblages in TSRF differed from those in the three forest plantations. The most abundant families (>10% of all adult specimens in each land-use type) were Corinnidae, Theridiidae, Linyphiidae and Salticidae in TSRF, contributing up to 61.8% of the adult specimens. In contrast, Theridiidae and Clubionidae dominated with 67.6%, 53.6% and 65.9% of all adult specimens in AYP, RTM and RP respectively. Moreover, the families Liocranidae, Selenopidae, Symphytognathidae and Atypidae were only found in TSRF, Lycosidae and Nesticidae only in AYP, Pisauridae only in RTM and Scytodidae, Nephilidae and Anyphaenidae only in RP.

Differences were also present at the species-level. Of the 226 species, 38 were restricted to the samples from TSRF, 54 to AYP, 28 to RTM and 18 to RP. Species shared between TSRF and AYP, TSRF and RTM, TSRF and RP were 35 (40.7% of species in TSRF), 29 (33.7%) and 23 (26.7%) respectively. The two most abundant species, belonging to the genera *Orthobula* (Phrurolithidae) and *Nasoonaria* (Linyphiidae), respectively, dominated TSRF, whereas *Clubiona damirkovaci* Deeleman-Reinhold (Clubionidae) and *Phycosoma crenatum* Gao & Li (Theridiidae) dominated the forest plantations. *Orthobula* sp.1 was underrepresented in forest plantations, and *Nasoonaria sinensis* Wunderlich & Song was only found in TSRF (Fig. 3).

### *Spider diversity*

Significant differences were detected for mean catch, Shannon–Wiener index, Simpson's index, Margalef species richness and Evenness models. Land-use type ( $F_{3,110} = 18.052$ ,  $P < 0.001$ ) and season ( $F_{3,110} = 31.734$ ,  $P < 0.001$ ; Table 2) significantly influenced mean catch. Mean catch was highest in RP, followed by RTM and AYP, and lowest in TSRF, which was significantly lower than RP and RTM in both seasons (Table 2). Land-use type ( $F_{3,110} = 3.118$ ,  $P < 0.05$ ), season ( $F_{3,110} = 6.380$ ,  $P < 0.05$ ) and their interaction ( $F_{3,110} = 4.607$ ,  $P < 0.01$ ) significantly influenced diversity as measured by Shannon–Wiener index; however, significant relationships were only detected in the rainy season, with highest values in AYP, followed by RTM and RP, and lowest in TSRF (Table 2). Land-use type ( $F_{3,110} = 3.107$ ,  $P < 0.05$ ), season ( $F_{3,110} = 4.773$ ,  $P < 0.05$ ) and their interaction ( $F_{3,110} = 7.025$ ,  $P < 0.001$ ) significantly influenced Simpson's index; however, significant relationships were only detected in the rainy season, with highest values in AYP, followed by RTM and RP, and lowest in TSRF (Table 2). Land-use type ( $F_{3,110} = 5.248$ ,  $P < 0.01$ ) and the land-use type and season interaction ( $F_{3,110} = 3.322$ ,  $P < 0.05$ ) significantly influenced Margalef species richness; however, significant relationships were only detected in the rainy



**Fig. 3.** The percentages (showing SE) of the most abundant species on tree trunk in the four land-use types. Note: AYP, *Aporusa yunnanensis* plantation; RP, rubber plantation; RTM, rubber and tea mixture; TSRF, tropical seasonal rainforest.

**Table 2.** Results of generalised linear mixed model (GLMM) analysis with Tukey post hoc test comparing mean ( $\pm$ SE) individuals, Shannon–Wiener index ( $H'$ ), Simpson's index ( $D$ ), Richness ( $D_{mg}$ ), Evenness ( $J$ ) and Sorensen's index among land uses and between seasons.

Species	Individuals <sup>†</sup>	$H'$	$D$	$D_{mg}$	$J$	$\beta_{sor}$
Dry season						
TSRF 58	2.90 $\pm$ 0.35 <sup>*,c</sup>	1.86 $\pm$ 0.10 <sup>*</sup>	0.82 $\pm$ 0.02	2.80 $\pm$ 0.21	0.93 $\pm$ 0.02 <sup>a</sup>	0.90 $\pm$ 0.02 <sup>a</sup>
AYP 70	4.99 $\pm$ 0.71 <sup>*,b,c</sup>	1.80 $\pm$ 0.11	0.76 $\pm$ 0.03	2.83 $\pm$ 0.23	0.73 $\pm$ 0.03 <sup>b</sup>	0.73 $\pm$ 0.02 <sup>b</sup>
RTM 51	5.24 $\pm$ 0.48 <sup>*,b</sup>	1.78 $\pm$ 0.09	0.80 $\pm$ 0.02	2.20 $\pm$ 0.17	0.86 $\pm$ 0.02 <sup>a</sup>	0.76 $\pm$ 0.03 <sup>b</sup>
RP 48	7.64 $\pm$ 0.74 <sup>***,a</sup>	1.80 $\pm$ 0.09	0.77 $\pm$ 0.03	2.38 $\pm$ 0.18	0.73 $\pm$ 0.04 <sup>b</sup>	0.68 $\pm$ 0.02 <sup>b</sup>
Rainy season						
TSRF 48	2.11 $\pm$ 0.41 <sup>b</sup>	1.16 $\pm$ 0.20 <sup>b</sup>	0.57 $\pm$ 0.08 <sup>b</sup>	1.84 $\pm$ 0.30 <sup>b</sup>	0.93 $\pm$ 0.04	0.95 <sup>*</sup> $\pm$ 0.03 <sup>a</sup>
AYP 72	3.51 $\pm$ 0.40 <sup>a,b</sup>	1.88 $\pm$ 0.12 <sup>a</sup>	0.81 $\pm$ 0.02 <sup>a</sup>	3.03 $\pm$ 0.23 <sup>a</sup>	0.90 $\pm$ 0.03 <sup>***</sup>	0.88 $\pm$ 0.03 <sup>a</sup>
RTM 61	4.31 $\pm$ 0.37 <sup>a</sup>	1.76 $\pm$ 0.12 <sup>a</sup>	0.79 $\pm$ 0.03 <sup>a</sup>	2.33 $\pm$ 0.18 <sup>a,b</sup>	0.90 $\pm$ 0.01 <sup>*</sup>	0.88 $\pm$ 0.02 <sup>a</sup>
RP 43	5.04 $\pm$ 0.46 <sup>a</sup>	1.63 $\pm$ 0.10 <sup>a</sup>	0.75 $\pm$ 0.03 <sup>a</sup>	2.03 $\pm$ 0.18 <sup>b</sup>	0.85 $\pm$ 0.03 <sup>*</sup>	0.74 $\pm$ 0.03 <sup>b</sup>

AYP, *Aporusa yunnanensis* plantation; RP, rubber plantation; RTM, rubber and tea mixture; TSRF, tropical seasonal rain forest. Note, means with letters in common are not significantly different.

\* $p < 0.05$ ; \*\*\* $p < 0.001$  (showing differences between the dry season and rainy season).

<sup>†</sup>Spider individuals per trap sampling in 1 month.

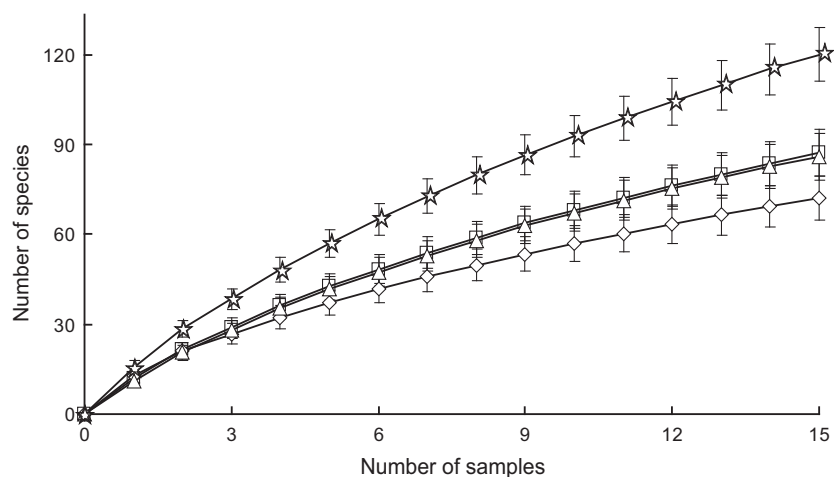
season, with highest values in AYP, followed by RTM and RP, and lowest in TSRF (Table 2). Land-use type ( $F_{3,110} = 10.463$ ,  $P < 0.001$ ), season ( $F_{3,110} = 18.210$ ,  $P < 0.001$ ) and their interaction ( $F_{3,110} = 3.975$ ,  $P < 0.01$ ) significantly influenced Evenness; however, significant relationships were only detected in the dry season, with higher values in TSRF and RTM than in AYP and RP (Table 2). Land-use type ( $F_{3,110} = 22.797$ ,  $P < 0.001$ ) and season ( $F_{3,110} = 23.773$ ,  $P < 0.001$ ) significantly influenced Sorensen index in both seasons. Sorensen index was significantly higher in TSRF than in the three forest plantations in the dry season, and it was significantly lower in RP than the other land-use types in the rainy season (Table 2).

Estimated species richness by rarefaction suggested that a higher number of species occurred in AYP compared to

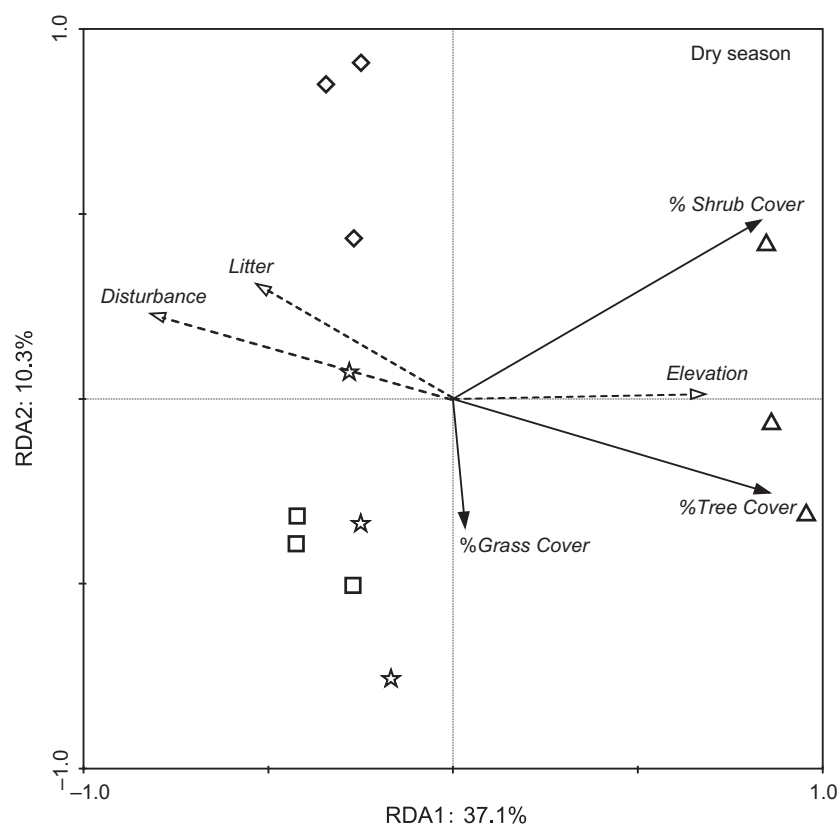
the remaining land-use types (Fig. 4). These steep curves suggested that collections were incomplete, and that more extensive sampling would have discovered additional species.

#### Relationships with environmental variables

During the dry season, RDA showed that environmental variables explained 53.7% (adjusted  $R^2$ ) of the total variance in the species assemblages. The first and second axes accounted for 37.1% and 10.3% of the constrained variance respectively (Fig. 5). The results of significance test showed that canopy cover ( $F = 4.20$ ;  $P = 0.0010$ ), grass cover ( $F = 2.31$ ;  $P = 0.0074$ ) and shrub cover ( $F = 1.69$ ;  $P = 0.0316$ ) significantly explained the variation in species



**Fig. 4.** Rarefaction curves (showing SD) of spiders collected from tree trunks in the four land-use types. Note: Diamond, rubber plantation; Square, rubber and tea mixture; Star, *Aporosa yunnanensis* plantation; Triangle, tropical seasonal rainforest.



**Fig. 5.** RDA ordination biplots showing relationships between spider species assemblages and environmental variables in Xishuangbanna in dry season. All environmental variables (with both significant (solid arrows) and non-significant (dotted arrows) influence on tree trunk spider assemblages) are shown. Note: Diamonds, rubber plantation; Squares, rubber and tea mixture; Stars, *Aporosa yunnanensis* plantation; Triangles, tropical seasonal rainforest.

composition. Disturbance degree, litter depth and elevation did not exhibit significant influences ( $P > 0.05$ ). The species-environment correlations were 0.986 on the first axis

and 0.944 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,

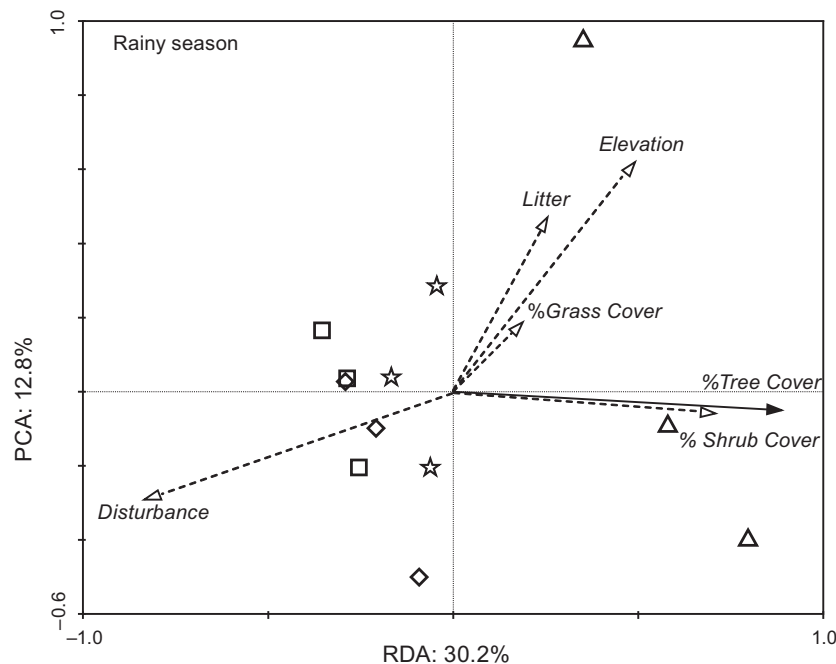
$F = 4.722$ ,  $P = 0.0030$ ; all canonical axes,  $F = 3.098$ ,  $P = 0.0002$ ). The first axis (RDA1) mainly represented impacts of canopy cover and shrub cover. While sites in TSRF were positively correlated with canopy cover and shrub cover (region on the right of the RDA tri-plot), sites in the tree forest plantations showed negative correlations (region on the left). The second axis (RDA2) mainly reflected a grass cover gradient increasing from top to bottom of the RDA (Fig. 5).

During the rainy season, RDA showed that environmental variables explained 68.5% (adjusted  $R^2$ ) of the total variance in the species assemblages. The first and second axes accounted for 30.2% and 12.8% of the constrained variance respectively (Fig. 6). The results of significance test showed that canopy cover ( $F = 3.42$ ;  $P = 0.0014$ ) was the only variable that significantly influenced species assemblages. Disturbance degree, litter depth, elevation, grass cover and shrub cover lacked significant influences ( $P > 0.05$ ). The species-environment correlations were 0.964 on the first axis and 0.939 on the second axis. A Monte-Carlo simulation with 4999 permutations indicated that species distribution along the axes was not random (first canonical axis,  $F = 2.166$ ,  $P = 0.0438$ ; all canonical axes,  $F = 1.814$ ,  $P = 0.0040$ ). The first axis (RDA1) mainly represented impacts of tree cover. TSRF, with the highest canopy cover and shrub cover, were distributed on the right part of the RDA tri-plot. The three forest plantations were all distributed on the left (Fig. 6).

The stepwise linear regression results indicated that shrub cover had a significant negative influence on mean catch of bark-dwelling spiders ( $F_{11} = 28.165$ ,  $P < 0.001$ ). Litter depth had a significant negative influence on Margalef species richness ( $F_{11} = 7.774$ ,  $P < 0.05$ ), and shrub cover had a significant positive influence on Evenness ( $F_{11} = 28.868$ ,  $P < 0.001$ ) and Sorensen index ( $F_{11} = 26.898$ ,  $P < 0.001$ ) in the dry season. In the rainy season, elevation had a significant negative influence on mean catch ( $F_{11} = 20.324$ ,  $P < 0.001$ ), Shannon–Wiener index ( $F_{11} = 26.476$ ,  $P < 0.001$ ) and Simpson's index ( $F_{11} = 21.688$ ,  $P < 0.001$ ). Elevation (negative) and grass cover (positive) significantly influenced Margalef species richness ( $F_{11} = 13.425$ ,  $P < 0.01$ ), and shrub cover had a significant positive influence on Sorensen index ( $F_{11} = 7.133$ ,  $P < 0.05$ ).

## Discussion

Spiders represent a dominant taxon of bark-dwelling predatory arthropods (Szinétár & Horváth, 2005). Without more focused studies, the factors that determine bark-dwelling spiders are little known, and consequently the implications for their management and conservation remain unknown. Our results suggest that forest management impacts bark-dwelling spider assemblages by altering vegetation structure of forest plantations in Xishuangbanna, southwestern China. Retaining understory



**Fig. 6.** RDA ordination biplots showing relationships between spider species assemblages and environmental variables in Xishuangbanna in rainy season. All environmental variables (with both significant (solid arrows) and non-significant (dotted arrows) influence on tree trunk spider assemblages) are shown. Note: Diamonds, rubber plantation; Squares, rubber and tea mixture; Stars, *Aporosa yunnanensis* plantation; Triangles, tropical seasonal rainforest.



vegetation such as shrubs and herbs in forest plantations may aid in conserving bark-dwelling spiders in this region. Species composition and diversity of the spider fauna in TSRF, however, differed from forest plantations. Considering the trends in forest conversion in the area and the possible homogenising effects of such activities, undisturbed natural forests are valuable for regional spider diversity conservation.

### *Spider assemblages*

Spiders have been seen as bottom-up regulated by prey availability (Carter & Rypstra, 1995) because certain species of spiders have feeding preferences for particular prey items (Harwood *et al.*, 2001). Therefore, variation in the presence or absence of spiders and the structure of their assemblages can reveal underlying trends of the ecosystem (Raymond *et al.*, 2013). In our study, highly abundant families and species differ substantially between TSRF and the three forest plantations. In addition, only 26.7% of bark-dwelling spider species from TSRF occur in RP; prey items appear to have changed. Predators, however, can also have strong indirect effects on plants by altering the way herbivores impact plants (Schmitz, 2003). For example, Louda (1982) demonstrated that lynx spiders prey upon seed consumers and thereby benefit the shrubs on which they lived. Carter and Rypstra (1995) also demonstrated top-down effects of spiders affecting herbivore damage in soybean agroecosystems.

Shochat *et al.* (2004) found that land-use alteration by humans increases the abundance of one or a few adaptable spider species. In our study, the increase in overall spider abundance in forest plantations is mostly caused by a sharp increase in a few open-habitat species, such as *C. damirkovaci* and *P. crenatum*. The former accounts for 20.9% to 35.0% of total individuals in the three forest plantations; but it accounts for only 2.4% in TSRF. The latter is approximately 11.5–15.8 times more common in forest plantations compared with TSRF (Fig. 3). The dramatic increase in the percentages of dominant species in forest plantations may cause a general loss of diversity, even local extinction of endemic species that dwell in natural rainforests, hence radically changes spider composition and local diversity. For example, *Orthobula* sp.1 and *Nasoonaria sinensis* are the two most common species in TSRF, however, the former is underrepresented in forest plantations, and the latter occurs in TSRF only; *Sinopimoa bicolor* Li & Wunderlich, a unique species that belongs to Sinopimoidae, occurs only in canopies of TSRF in Xishuangbanna (Li & Wunderlich, 2008).

### *Spider diversity*

Pinkus-Rendón *et al.* (2006) found that spider diversity increases as habitats become more complex and heterogeneous. Our results, however, show that the highest spider

alpha diversity occurs in moderately disturbed AYP, rather than in the less altered, and more complex and diverse TSRF (Table 2). Tsai *et al.* (2006) also showed that cultivated woodlands subjected to an intermediate level of disturbance exhibited the highest spider diversity. Oxbrough *et al.* (2012) showed that mixed stands do not always possess higher biodiversity than monoculture stands. The highest beta diversity found in TSRF in our study indicates that species turnover between replicates of natural stands is higher than in the three forest plantations (Table 2). Beta diversity of spiders has been shown to be positively related to environmental heterogeneity (Jiménez-Valverde *et al.*, 2010). These results demonstrate that replacement plantations cannot match the composition and structure of the original forests, thus potentially having dire consequences for spider diversity.

Our stepwise linear regression results indicate that herbs and shrubs in plantations are important factors affecting bark-dwelling spider diversity. Most of the bark-dwelling spider species have not been found to exclusively use bark habitats (Pinzón & Spence, 2010). As a consequence, surrounding vegetation likely affects the diversity of bark-dwelling spiders. In our study, the relatively open canopies of AYP permit development of herbs and shrubs that our stepwise linear regression and RDA results (Fig. 5) also confirm to be important to bark-dwelling spiders. Intensive management, however, has altered vegetation structure, influencing bark-dwelling assemblages, similar to that shown in canopy spiders of rubber plantations in Xishuangbanna (Zheng *et al.*, 2015). Vegetation structure was shown to be a major driver of spider diversity (Greenstone, 1984; Malumbres-Olarte *et al.*, 2013) and the loss of some structural elements could have severe negative effects on native species (Fischer & Lindenmayer, 2007). RTM and RP have similar canopy cover as AYP in the rainy season, and RTM has higher shrub cover than AYP. Both are heavily managed and, thus, resulted in a more simplified vegetation structure. Therefore, these plantations, and particularly RP, show the lowest spider richness.

Strong seasonal changes have been shown in arthropods in tropical rainforests (Wolda, 1992; Novotny & Basset, 1998). Insect abundance was shown to increase in the summer–wet season in the tropical region (Aide, 1993; Novotny & Basset, 1998). Consistent with previous studies, our mean catch is highly sensitive to seasonal change, decreasing significantly in the rainy season. We speculate that too frequent rainfall suppresses spider activity on tree trunks. Seasonal changes most affect mean catch of bark-dwelling spiders in RP, which has the simplest vegetation structure, while seasonal changes less affect spiders in natural forests and plantations that retain shrubs or herbs.

### *Relationships with environmental variables*

Spider assemblages depend on both local conditions and features of surrounding landscapes. Therefore, land-

use type and understory vegetation play important roles for bark-dwelling spiders. The intensity of management determines vegetation complexity, such as herbs and shrubs in plantations in this area, and thus strongly influences bark-dwelling spider assemblages. Previous studies showed that canopy cover (Oxbrough *et al.*, 2005), herb cover (Ziesche & Roth, 2008; Purchart *et al.*, 2013; Zheng *et al.*, 2015) and shrub cover (Zheng *et al.*, 2009) were key factors affecting ground-dwelling spider assemblages. In Xishuangbanna, understory vegetation cover (herbs and shrubs) is more important to bark-dwelling spiders in the dry season. RDA shows that canopy cover, herb cover and shrub cover were key factors explaining spider assemblages in the dry season (Fig. 5), whereas in the rainy season only canopy cover significantly explains these assemblages (Fig. 6). Thus, we hypothesise that frequent cloudy and rainy weather during the rainy season has a greater influence on the composition of bark-dwelling spiders than the variation in understory vegetation. In the dry season, however, microhabitats on exposed tree trunks in the daytime in plantations may not be suitable for spiders due to higher temperature and solar radiation, and lower humidity. Therefore, shrubs and leaf litter may offer refuge to bark-dwelling spiders. Local dynamics, such as niche availability may drive bark-dwelling spider assemblage diversity and species composition (Larrivée & Buddle, 2010). Zheng *et al.* (2009) also showed that shade tea could promote the development of a diverse fauna of ground-dwelling spiders. The small, densely packed leaves of tea trees provided more space for arthropods, such as spiders and their prey, as well as more complexity and moister microhabitats for spiders.

## Conclusions

Altered vegetation structure of forests affects bark-dwelling spider assemblages in Xishuangbanna. Large areas of rubber monoculture exist in Xishuangbanna (Li *et al.*, 2007) and across Southeast Asia (Ziegler *et al.*, 2009). Replacing natural rainforest with *H. brasiliensis* plantations leads to a simplification of not only the landscape and plant assemblages but also the spider fauna (Zheng *et al.*, 2009, 2015). We suggest that local government and plantation managers encourage the planting of tea trees and preserve the herb layer in RP because these factors can increase spider diversity (Zheng *et al.*, 2009, 2015) and improve biological pest control in plantations. Secondly, the forestry administrative department should supply effective guidance to conserve the remnant natural areas. Further, detailed data on long-term system variability, spatial distribution and diversity for this important group will be essential for developing effective conservation plans. Further research is necessary to interpret the effects of whole-tree architecture and its relationships with other forest strata. This will help to clarify the role of tree trunks in forest ecosystems.

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