

# Structure and composition of the understory treelets in a non-dipterocarp forest of tropical Asia

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## ABSTRACT

Species richness, floristic composition, and structure of understory treelets were investigated in three 1-ha plots, distributed in the undisturbed tropical seasonal rain forest of Xishuangbanna, SW China. We investigated all the woody species except lianas in these plots, compared the differences of species diversity of trees and treelets in these plots and the differences of understory structure between this forest and the typical dipterocarp forests in SE Asia. We found 5089 individuals belonging to 356 species, 189 genera, and 63 families in the three plots. The five most important families were Rubiaceae, Euphorbiaceae, Lauraceae, Meliaceae, and Annonaceae. The treelet layer was much more diverse than the tree layer, indicating that result based only on trees may be not an appropriate representation of the diversity status of a particular tropical forest type. The three plots were more similar when the treelet layer was considered than when tree layer was considered. In contrast with the dipterocarp forests in SE Asia, the understory of tropical seasonal rain forest was mainly composed of the trees with small and middle stature at maturity classes. These results indicate that the structure of tropical forest understory may differ not only among continents but also within continent.

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## 1. Introduction

Tropical rain forests are among the most species rich communities on the Earth (Carson and Schnitzer, 2008). Most studies carried out on vascular plants have focused on the trees with diameter at breast height (DBH)  $\geq 10$  cm (Phillips et al., 1994), despite the fact that the understory is responsible for a high percentage of total diversity in the tropical forests (Tchouto et al., 2006). The species richness of small trees and shrubs is usually higher than that of the large trees (DBH  $\geq 10$  cm) in different tropical forests (Gentry and Dodson, 1987). It has been found that shrub layer ( $1.5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) is significantly more diverse and species-rich than the tree (DBH  $\geq 10 \text{ cm}$ ) and herbaceous layers, accounting for eighty per cent species of tropical forests in Cameroon (Tchouto et al., 2006). The understory plants provide food resources for many species of insects, birds, and mammals. The composition of understory is usually different from that of the canopy (Gentry and Emmons, 1987), and thus supports a different fauna than does the canopy. Furthermore, the understory plays an important role in the nutrient cycling and conservation of the forest and is an important component of the aesthetics of forests (Bauhus et al., 2001). This important group of small trees has received limited attention,

which may however be caused both by their limited interest for foresters and the difficulties to identify them.

Although tropical forests in different areas may appear similar in tree number (with 400–500 stems of trees  $\geq 10 \text{ cm}$  DBH per hectare), basal area ( $30\text{--}45 \text{ m}^2 \text{ ha}^{-1}$ ), and taxonomic composition of canopy trees (dominated by Fabaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Annonaceae, and so on) (Gentry, 1988), they may show contrasting structure and composition of the understory (LaFrankie et al., 2006). In a study carried out in six different tropical forests of three continents, LaFrankie et al. (2006) found that the saplings of species with DBH  $\geq 40 \text{ cm}$  stature at maturity (SAM) comprised 18–34% of the 1–2 cm DBH stems, which were generally higher than those of the African and American forests. Notably, Dipterocarpaceae is the dominant family in the three Asian sites, comprising about 14% of the 1–2 cm DBH trees in Asian forests and dominating the largest SAM class (Losos and Leigh, 2004; LaFrankie et al., 2006). Though available evidence shows that non-dipterocarp forests of Asia differ a lot from dipterocarp forests with respect to forest structure, species diversity and taxonomic composition of overstorey trees (Cao and Zhang, 1997; Hamann et al., 1999; Kessler et al., 2005; Zheng et al., 2006), we still know little about the patterns of understory in the non-dipterocarp forests of tropical Asia except for some studies carried out in tropical evergreen forest of India (Rasingam and Parthasarathy, 2009). Consequently, our knowledge on the understory of tropical forests in Asia may be biased, more data from different areas are critically needed.

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The rate of deforestation due to agriculture, human habitation and industrial development in the tropical area is accelerating, which causes rapid changes in community composition and ecosystem functioning of the tropical forests (Rudel et al., 2009; Ziegler et al., 2009; Klanderud et al., 2010). These perturbations have a direct influence on stem density, species diversity, and composition of overstory (Zhu et al., 2004; Kessler et al., 2005), and consequently, on the quantity and quality of light reaching the understory, and the competition of resources between overstory and understory (Dupuy and Chazdon, 2006). Thus, trees with smaller DBH classes must be given appropriate attention when considering species changes resulting from habitat fragmentation (Page et al., 2010). It has been found that small canopy gaps may exert important influence on plant distributions in the tropical forest understory (Svenning, 2000). In contrast to the clear worldwide trends in tropical forest fragmentation and degradation, global patterns of understory composition are not well understood. Given that forest fragmentation may influence understory composition and dynamics, it is important to investigate the patterns of understory in primary tropical forests of different regions to help understand to what extent understory may change facing forest fragmentation.

We simultaneously made a biodiversity inventory of all woody species ( $\text{DBH} \geq 2 \text{ cm}$ ) in three 1-ha replicated plots of tropical seasonal rain forest, which are located in different areas of Xishuangbanna, southwest China. The results of tree ( $\text{DBH} \geq 10 \text{ cm}$ ) and liana diversity ( $\text{DBH} \geq 2 \text{ cm}$ ) are already available (Lü et al., 2009; Lü and Tang, in press). All the results show that the composition and diversity of both overstory trees and lianas differ greatly from the typical dipterocarp forests in Southeast Asia (Lü et al., 2009; Lü and Tang, in press). The objectives of this study were to describe the species diversity, taxonomic composition, and structure of treelets in the understory of the tropical seasonal rain forests. Specific questions addressed here include: (1) How does understory differ from overstory in the same plots with respect to taxonomic composition and species diversity? (2) How do species composition, diversity, and abundance of the understory differ among different plots of the same forest types? (3) How do the composition and structure of understory in tropical seasonal rain forest differ from those of other tropical forests in Asia?

## 2. Materials and methods

### 2.1. Study area

The study was conducted in Xishuangbanna ( $21^{\circ}08' - 22^{\circ}36' \text{ N}$  and  $99^{\circ}56' - 101^{\circ}50' \text{ E}$ ), SW China. It borders Myanmar in the southwest and Laos in the southeast, and has mountainous topography, with mountain ridges running in a north–south direction, decreasing in elevation southward (Cao and Zhang, 1997). Climatological data (1959–2002) from the Xishuangbanna Tropical Rainforest Ecosystem Station ( $21^{\circ}55' \text{ N}$ ,  $101^{\circ}15' \text{ E}$ , 600 m asl) reveal a mean annual temperature of  $21.7^{\circ}\text{C}$  (minimum  $15.9^{\circ}\text{C}$  and maximum  $25.7^{\circ}\text{C}$ ) and a mean annual precipitation of 1539 mm (of which 87% occurs in the rainy season and 13% in the dry season). The soil is classified as latosol (pH 4.5–5.5) developed from purple sandstone.

Three replicated 1-ha ( $100 \text{ m} \times 100 \text{ m}$ ) plots, located in three different places, were selected from primary forest sites to investigate the diversity of woody plants. We refer these plots as: Menglun ( $21^{\circ}57' \text{ N}$ ,  $101^{\circ}12' \text{ E}$ ; 730 m), Mengla ( $21^{\circ}32' \text{ N}$ ,  $101^{\circ}33' \text{ E}$ ; 581 m) and Manyang ( $21^{\circ}27' \text{ N}$ ,  $101^{\circ}36' \text{ E}$ ; 643 m). Detailed information of the three plots can be found in Lü and Tang (in press).

### 2.2. Field census

For the convenience of inventory, each plot was divided into subplots of  $10 \text{ m} \times 10 \text{ m}$ . Within each subplot, we marked all trees with a  $\text{DBH} \geq 2 \text{ cm}$  with aluminum tags. For the measurement of DBH, the point of measurement was at 1.3 m, except for trees with buttresses, which were measured above the buttress according to the protocol of Chinese Ecosystem Research Network (CERN). We identified the species and voucher specimens of the trees were collected and deposited at the Herbarium of Xishuangbanna Tropical Botanical Garden. Nomenclature follows *Lists of Plants in Xishuangbanna* (Li et al., 1996). All the fieldwork was conducted between December 2004 and April 2005.

### 2.3. Data analysis

In this study, we focused on the treelets with  $2 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ . We quantified basal area, relative density, relative frequency, relative dominance, and importance value index (IVI) for all species following Curtis and Cottam (1962). The family importance value (FIV) was calculated according to Mori et al. (1983). To determine species richness, we added up the number of tree species registered for each plot. We calculated Margalef's index, Fisher's  $\alpha$ , Simpson's index, Shannon–Wiener index, Pielou's measure of evenness and Hill diversity numbers following Magurran (1988) and assessed similarity between the plots using Jaccard's coefficient of similarity and Sorenson index (SI) of similarity (Magurran, 1988; Small et al., 2004). Two-sided, paired *t*-test was used to compare the difference of species diversity indices between understory and overstory. Two-way ANOVA was used to detect the effects of tree stature classes (treelets vs trees) and taxonomic units (family, genera, and species levels) on beta diversity of the three plots. Because of small sample sizes and the inherent variability of the diversity indices among different plots, the significance level was set at  $\alpha = 0.10$  for some statistical comparisons. Analysis was conducted with SPSS (SPSS 13.0 for windows, SPSS Inc., Chicago, IL, USA.). Stature at maturity was determined for species with  $\geq 10$  individuals in each plot by dropping the largest DBH and taking the mean of the next three largest DBHs. The SAM classes were determined at the following DBH intervals using the method revised from LaFrankie et al. (2006): (1) 2–5 cm; (2) >5–10 cm; (3) >10–20 cm; (4) >20–40 cm; (5) >40–80 cm; and (6)  $\geq 80 \text{ cm}$ .

## 3. Results

### 3.1. Species richness and diversity

A total of 356 species of small trees ( $2 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) that belonged to 184 genera and 63 families was enumerated in the three 1-ha plots. Species richness as well as other diversity indices varied greatly among the three plots (Table 1). Menglun plot, with 241 species was the most, diverse than Mengla and Manyang plot (150 and 160 species, respectively).

The similarity indices ranged from 0.817 to 0.866 (SI) and from 0.691 to 0.764 (Jaccard's Coefficient) at family level for all individuals of small trees (Table 2). The similarity at family level was much higher than those at genera and species level (Table 2).

### 3.2. Stand structure and floristic composition

The diameter class distribution pattern for small trees was a negative exponential distribution in each of the three plots (Fig. 1). The total density of small trees in Menglun plot was the highest, with 2048 stems. In contrast, there were only 1520 and 1521 individuals in Mengla and Manyang plots, respectively. The three

**Table 1**

Abundance and species diversity indices for treelets of 2 cm  $\leq$  DBH < 10 cm in the three 1-ha plots of tropical seasonal rain forest in Xishuangbanna.

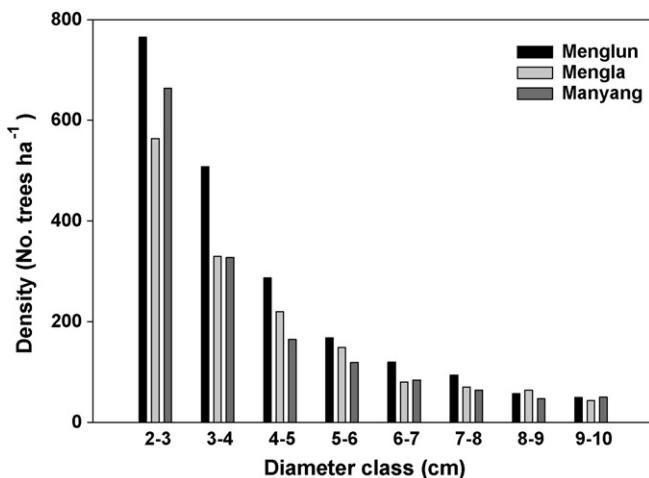
	Menglun	Mengla	Manyang
$N$ (stems $\text{ha}^{-1}$ )	2048	1520	1521
$S$ (species $\text{ha}^{-1}$ )	241	150	160
$H'$	4.54	4.17	4.07
$D$	31.61	20.34	21.7
$N1$	94.50	64.79	58.38
$N2$	51.22	43.33	33.32
Fisher's $\alpha$	70.95	41.29	45.10
$E$	0.83	0.83	0.80
$\lambda$	0.02	0.02	0.03
$S/N$	0.12	0.10	0.11

$N$  is the number of individuals registered.  $S$  is the total number of species censused.  $H'$  is the Shannon–Wiener index,  $H' = -\sum (n_i/N_i) \ln(n_i/N_i)$ .  $D$  is the Margalef's index of species richness,  $D = (S - 1)/\ln N$ .  $N1$  is the Number 1 of Hill diversity indices,  $N1 = e^{H'}$ .  $N2$  is the Number 2 of Hill diversity indices,  $N2 = 1/\lambda$ .  $\alpha$  is Fisher's index of diversity,  $S = \alpha \ln(1 + N/\alpha)$ .  $E$  is the Pielou's evenness index,  $E = H'/\ln S$ .  $\lambda$  is the Simpson's concentration index,  $\lambda = \sum (n_i/N_i)^2$ .  $S/N$  is the rate of species increase per individual recorded.

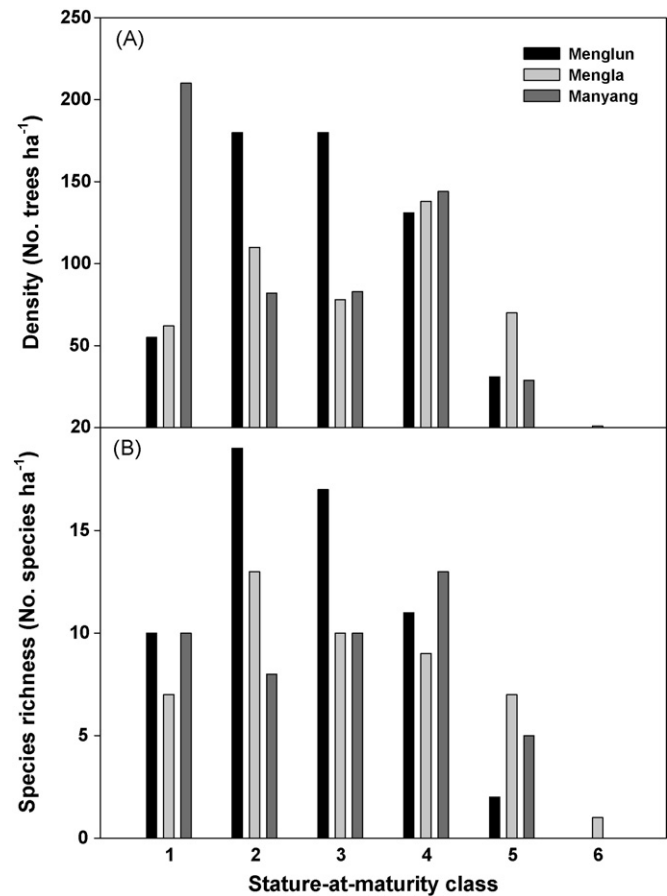
smallest diameter classes contributed to the higher small trees density, especially in the Menglun plot (Fig. 1).

The 10 most important species accounted for 30–40% of the combined importance value in each plot (Appendix A). *Mezzettiposis creaghii* and *Diospyros xishuangbannaensis*, both with the highest stems, frequency, and basal area, and consequently, were the most important species in Menglun and Mengla plots (Appendix A). *Myristica yunnanensis* was the most important species in Manyang plot, due to the highest frequency and basal area and the second highest number of stems. No single species clearly dominated each plot. About half of the species were represented by only one or two individuals in each plot. Three species in Menglun, two species in Manyang, and no species in Mengla had more than 100 individuals.

The ten most important families accounted for about 60 percent of the combined FIV in each plot (Table 3). Averaged across the three plots, Rubiaceae, Euphorbiaceae, Lauraceae, Meliaceae, and Annonaceae were the top five important families. Euphorbiaceae was the most important family in both Menglun and Mengla plots due to the higher species richness and larger basal area (Table 3). Rubiaceae was the most important one in Manyang due to the highest number of individuals, the second one in Menglun and the fifth important in Mengla plot. Lauraceae was the most diverse family in both Menglun (25 species) and Manyang (23 species), whereas Euphorbiaceae (20 species) was the most diverse one in Mengla plot.



**Fig. 1.** Diameter class distribution of treelets (2 cm  $\leq$  DBH < 10 cm) for the three tropical forest plots in Xishuangbanna, SW China.



**Fig. 2.** Density (A) and species richness (B) of treelets 2–3 cm DBH (No.  $\text{ha}^{-1}$ ) by stature at maturity (SAM) class in the tropical seasonal rain forests in Xishuangbanna, SW China. The SAM classes were determined at the following DBH intervals: (1) 2–5 cm; (2) >5–10 cm; (3) >10–20 cm; (4) >20–40 cm; (5) >40–80 cm; (6)  $\geq$  80 cm.

### 3.3. Representation of stature classes in the understory

According to our criterion, 59 species from Menglun, 47 species from Mengla and 46 species from Manyang were selected to determine the SAM of treelets in each plot. The mode of SAM differed among these plots: class 2 and 3 were most abundant and diverse in Menglun; class 4 was most abundant while class 2 was most diverse in Mengla; class 1 was most abundant and class 4 was most diverse in Manyang (Fig. 2A and B). Averaged across the three plots, the small (class 1 and 2) and middle classes (class 3 and 4) were more abundant and diverse than the large classes (class 5 and 6) (Fig. 2), in that >90% of the individuals and species were located in classes 1–4.

### 3.4. Comparison of diversity between understory and overstory

Species richness of small trees was much higher in the understory than that of overstory (241 vs 106 in Menglun; 150 vs 94 in Mengla; 160 vs 84 in Manyang) in each plot. Furthermore, across the three plots, the understory was more diverse than the overstory indicated by the higher values of several diversity indices (Fig. 3A–E). The fisher's  $\alpha$  index of the understory was not significantly higher than the overstory ( $P = 0.21$ ; Fig. 3F). This index of the understory was much higher than the overstory in both Menglun (71 vs 50) and Manyang (45 vs 32), but not in Mengla (41 vs 41). The evenness of understory and overstory was similar (Fig. 3G). The Simpson's diversity index ( $\lambda$ ) was lower in the understory than the overstory (Fig. 3H), indicating more diverse or heterogeneous pat-

**Table 2**Sorensen Index (SI) and Jaccard's Coefficient (*J*) between any two plots of the three tropical seasonal rain forest plots for treelets in Xishuangbanna, SW China.

Plots	SI			<i>J</i>		
	Family	Genera	Species	Family	Genera	Species
Menglun–Mengla	0.824	0.656	0.446	0.700	0.488	0.287
Menglun–Manyang	0.865	0.644	0.440	0.764	0.475	0.282
Mengla–Manyang	0.817	0.596	0.406	0.691	0.425	0.255

tern. However, the change of  $\lambda$  was not statistically significant due to the large variation of the values in overstory (0.03–0.08). In contrast, the rate of species increase per individual recorded (*S/N*) in the understory was lower than the overstory (Fig. 3I).

Results of two-way ANOVAs show that the similarity of diversity pattern of understory was significantly higher than that of the overstory at family, genera, and species levels (Fig. 4). The similarity of any two of the three plots was highest at family level and lowest at species level (Fig. 4).

#### 4. Discussion

The understory treelet species richness of total 356 species enumerated in the three 1-ha plots and 150–240 species in each plot reflect a high treelets diversity status of tropical seasonal rain forest of Xishuangbanna. The species richness of treelets in our plots was higher than tropical montane forest in Doi Inthanon of Thailand (105 species  $\text{ha}^{-1}$ ;  $\text{DBH} \geq 1$  cm) and seasonal dry evergreen forest in Huai Kha Khaeng of Thailand (96 species  $\text{ha}^{-1}$ ;  $\text{DBH} \geq 1$  cm) (Losos and Leigh, 2004), whereas lower than the tropical dipterocarp forest in Lambir (618 species  $\text{ha}^{-1}$ ;  $\text{DBH} \geq 1$  cm) and Pasoh (495 species  $\text{ha}^{-1}$ ;  $\text{DBH} \geq 1$  cm) of Malaysia (Losos and Leigh, 2004) and the Campo-Ma'an rain forest in Cameroon (231–413 species  $\text{ha}^{-1}$ ;  $1.5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) (Tchouto et al., 2006). Lower rainfall and higher seasonality in Xishuangbanna may contribute to the

lower woody species diversity enumerated in this study compared with the forests located near the equator. These two factors are among the important ones that would be the causes of gradients in tropical tree diversity (Givnish, 1999).

The five most important families in the understory of tropical seasonal rain forests in Xishuangbanna were Rubiaceae, Euphorbiaceae, Lauraceae, Meliaceae, and Annonaceae. Similarly, all these families are the dominant ones in Doi Inthanon forest and Huai Kha Khaeng forest of Thailand (Losos and Leigh, 2004). The Rubiaceae was ranked first in FIV averaged across the three plots and ranked first in abundance of treelets in both Menglun and Manyang (Table 3), whereas there were only seven stems of trees with  $\text{DBH} \geq 10$  cm in either Menglun or Manyang plot (Lü and Tang, in press). This contrasting pattern of the Rubiaceae between understory and overstory indicates that most species and individuals of Rubiaceae are smaller ones in the understory. The Lauraceae and Euphorbiaceae were the two most diverse families either when only treelets or when only trees ( $\text{DBH} \geq 10$  cm) (Lü and Tang, in press) were considered, indicating these two families contribute a lot to the woody species richness in both understory and overstory of the tropical seasonal rainforests. There was no species that belonged to Dipterocarpaceae were enumerated in our study. Though there is *Shorea wangtianshuea* formation of tropical seasonal rain forest in this area, it is located in limited areas and *Terminalia myriocarpa*

**Table 3**The top 10 families with the highest importance values of the treelets ( $2 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) in three plots in Xishuangbanna, SW China. Number of species (NS), number of individuals in a family (NI), basal area (BA,  $\text{cm}^2$ ), relative diversity (RDi), relative density (RDe), relative dominance (RDo), Family Importance Value (FIV).

Plot	Family	NS	NI	BA	RDi	RDe	RDo	FIV
Menglun	Euphorbiaceae	23	232	3473	9.5	11.3	10.9	31.8
	Rubiaceae	14	233	2762	5.8	11.4	8.7	25.9
	Annonaceae	8	228	3403	3.3	11.1	10.7	25.1
	Lauraceae	25	108	1971	10.4	5.3	6.2	21.8
	Meliaceae	13	162	2342	5.4	7.9	7.4	20.7
	Myrsinaceae	4	139	2100	1.7	6.8	6.6	15.0
	Moraceae	14	61	1079	5.8	3.0	3.4	12.2
	Sapindaceae	6	91	1164	2.5	4.4	3.7	10.6
	Papilionaceae	3	67	1490	1.2	3.3	4.7	9.2
	Icacinaeae	3	72	1077	1.2	3.5	3.4	8.1
Mengla	Euphorbiaceae	20	123	2318	13.2	8.1	9.2	30.1
	Meliaceae	8	158	2334	5.3	10.4	9.3	24.9
	Ebenaceae	3	164	2724	2.0	10.8	10.8	23.6
	Annonaceae	8	107	1837	5.3	7.0	7.3	19.6
	Rubiaceae	11	62	829	7.2	4.1	3.3	14.6
	Sapindaceae	4	77	1434	2.6	5.1	5.7	13.4
	Moraceae	5	66	1113	3.3	4.3	4.4	12.0
	Lauraceae	7	49	855	4.6	3.2	3.4	11.2
	Anacardiaceae	3	69	1140	2.0	4.5	4.5	11.0
	Papilionaceae	6	59	657	3.9	3.9	2.6	10.4
Manyang	Rubiaceae	17	287	3796	10.6	18.9	16.2	45.7
	Lauraceae	23	140	2035	14.4	9.2	8.7	32.2
	Myristicaceae	4	140	3118	2.5	9.2	13.3	25.0
	Euphorbiaceae	14	82	1093	8.8	5.4	4.7	18.8
	Moraceae	10	75	1030	6.3	4.9	4.4	15.6
	Meliaceae	6	76	1133	3.8	5.0	4.8	13.6
	Myrsinaceae	4	98	745	2.5	6.4	3.2	12.1
	Lecythidaceae	1	62	1602	0.6	4.1	6.8	11.5
	Annonaceae	4	52	1004	2.5	3.4	4.3	10.2
	Symplocaceae	2	58	991	1.3	3.8	4.2	9.3



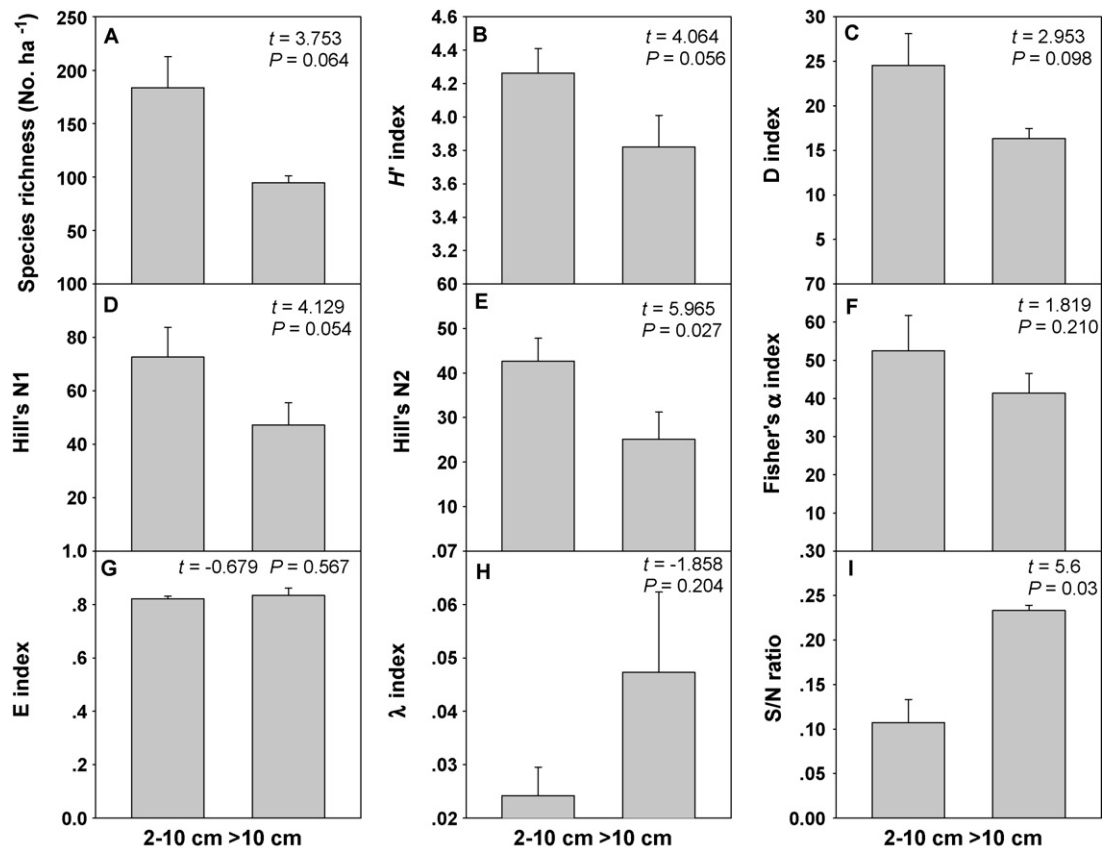


Fig. 3. The differences of species richness (A), Shannon–Wiener index (B), Margalef's index (C), Number 1 (D) and Number 2 (E) of Hill diversity indices, Fisher's  $\alpha$  index (F), Pielou's evenness index (G), Simpson's concentration index (H), and the rate of species increase per individual recorded (I) between treelets (2–10 cm) and trees (DBH > 10 cm) averaged across the three plots of the tropical seasonal rain forests in Xishuangbanna, SW China.

and *Pometia tomentosa* formations occupy largest areas (Zheng et al., 2006). It is different from the typical tropical forests in SE Asia where Dipterocarpaceae is the predominant family with emergent canopy trees and large quantities of understory trees (Losos and Leigh, 2004; LaFrankie et al., 2006).

Our results showed that the three plots of tropical seasonal rain forest were similar to each other in the extremely low representation of large SAM classes and high representation of small and middle (1–4) classes in the understory. This contrasts with the results from the dipterocarp forests of tropical Asia, in which the understory shows a high representation of middle and large SAM (3–6) classes but not of small SAM classes (LaFrankie et al., 2006). The difference in floristic composition of forests in Xishuangbanna and the forests in SE Asia may contribute to the different SAM patterns. The family Dipterocarpaceae, dominant in SE Asia, contributes a lot to the density of 1–2 cm DBH trees in these plots and dominates stature class 6. However, there was no existence of individuals that belonged to Dipterocarpaceae in our plots. In addition, Pitman et al. (2002) suggest that the climatic differences may be accounted for the varied composition of understory in different tropical forests. The three plots of SE Asia included in LaFrankie's study located near the equator, where the climate (higher mean annual temperature and higher mean annual precipitation) is more hospitable for growth of canopy trees. This can be partly revealed by the higher density of canopy trees (DBH  $\geq$  10 cm) in these forests (554–637 stems ha<sup>-1</sup>) (LaFrankie et al., 2006) than in our plots (393–467 stems ha<sup>-1</sup>) (Lü and Tang, in press). More closing canopy means lower available light to the understory. Although it has been suggested that greater penetration of light into gaps and favorable conditions for growth may allow more smaller-statured species to coexist with canopy trees in tropical vs. temperate forests (King

et al., 2006b), the dipterocarp forest tends to be darker and more stable than tropical forests in Africa and Amazon probably due to the morphological characteristics of dominant trees and a tendency toward lower wind speeds in tropical Asia (Primack and Corlett, 2005). We suspect that poor light condition may have negative effects on the germination and growth of the species within small SAM classes, because understory plants with small stature of adults occur preferentially in the brighter parts of the understory (Svenning, 2000). In all, our results suggest that the understory pattern may vary greatly not only among continents, such as the contrasting pattern among tropical forests in Africa, Asia, and South America found by LaFrankie et al. (2006), but also within continent.

Our results are based on inventories of all stems with 2 cm  $\leq$  DBH < 10 cm on three 1 ha plots and the definition of the SAM for each species with more than 10 individuals per plot as the mean DBH of the second and fourth largest tree, whereas LaFrankie et al. (2006) carried out their research with inventories of all stems 1 cm  $\leq$  DBH < 10 cm in plots with the area ranged from 15 to 50 ha and they defined SAM for each species with more than 30 individuals per plot as the mean DBH of the second and fourth largest tree. However, it should be notable that there were some unavoidable uncertainties in the comparisons between this study and LaFrankie et al. (2006). Method used here may yield larger diameters for more abundant species as suggested by King et al. (2006a). In addition, there would be some avoidable biases when comparing samples drawn from smaller plots (such as in this study) with the larger plots of LaFrankie et al. (2006). The choice of the second and fourth largest trees in small plots may underestimate the numbers of species of large trees, especially those with the stem abundance of  $\leq$  1 individual ha<sup>-1</sup>. Average across the three plots, we found only one species with a SAM of >80 cm. If the area of plots was enlarged,

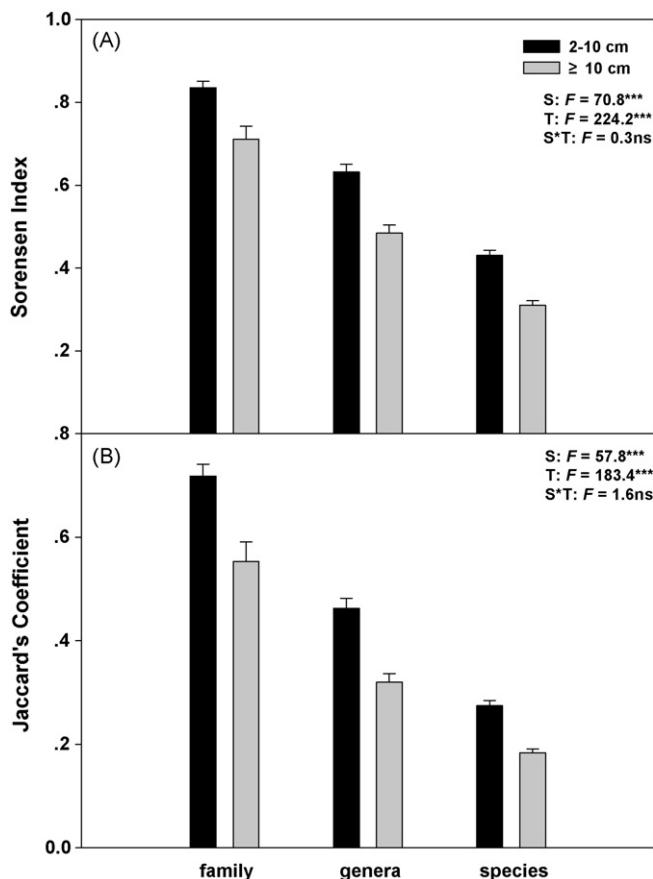


Fig. 4. The effects of tree stature (S; 2–10 cm vs  $\geq 10$  cm) and taxonomic units (T) on Sørensen Index (A) and Jaccard's coefficient (B) for the tropical seasonal rain forests in Xishuangbanna, SW China. \*\*\*  $P < 0.001$ ; ns,  $P > 0.1$ .

however, there are probably some other large species among the 2–10 cm DBH classes studied here that would have been identified. In spite of all these uncertainties, our study did make an important contribution to our understanding of the variation among tropical forests within tropical Asia and it did show that sapling of large trees were less common in Xishuangbanna than in the well-known dipterocarp forests of SE Asia.

The treelet layer was much more diverse than tree layer with respect to species richness and other diversity indices (Fig. 3), indicating that the size limit of 10 cm DBH in most of the forest inventories may exclude many understory trees. Similar results have been reported by Tchouto et al. (2006) in African tropical forest, that the shrub layer ( $1.5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$ ) was the most species-rich, holding a higher number of species and a higher Shannon diversity index than the tree and the herb layer. In their study, the shrub layer accounted for 82% of tree species, 90% of shrubs, 78% of lianas and 70% of herbaceous species. Moreover, only small part of the diversity of small trees, shrubs, and herbs could be explained by the diversity of large and medium sized trees in the same forest type (Tchouto et al., 2006). In addition, as an integral and important part of forest community, the understory provides foods for many species of insects, birds, and mammals (Gentry and Emmons, 1987). It plays an important role in the food web and nutrient cycling of forest ecosystems. Thus, all vascular plants with  $\text{DBH} \geq 1$  or 2 cm

(but not only trees with  $\text{DBH} \geq 10 \text{ cm}$ ) will constitute more appropriate sampling method for biodiversity conservation purposes, as what have been done in the long-term, large-scale research on forests by Center for Tropical Forest Science (Losos and Leigh, 2004).

Natural and anthropogenic disturbances can affect the diversity and composition of understory in different forests (Hart and Chen, 2008; Lin and Cao, 2009; Rasingam and Parthasarathy, 2009), which may have great implications for succession, dynamics, and ecosystem function and services of forest (Royo and Carson, 2006). The tropical seasonal rain forests in Xishuangbanna are being rapidly destroyed due to human population growth, traditional slash-and-burn agricultural activities, and the most important one, rubber plantation expansion (Ziegler et al., 2009). Tropical forest degradation and fragmentation has caused losses of tree species diversity (Zhu et al., 2004), changes of soil seedbanks (Lin and Cao, 2009), habitat alteration of Asian elephants (Zhang and Wang, 2003), reduction of fog formation and duration (Liu et al., 2007), and reduction of carbon storage (Li et al., 2008) in this region. Given the important role the understory species play in the tropical forests, we should pay more attention on the pattern and ecological consequences of the changes of understory in face of forest clearance and fragmentation in this area.

## 5. Conclusions

Our knowledge about the species diversity of tropical forest communities is heavily biased, because most of the related studies focused on trees with  $\text{DBH} \geq 10 \text{ cm}$ . However, our study has demonstrated that the species diversity of treelets ( $2 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) is much higher than that of the trees ( $\text{DBH} \geq 10 \text{ cm}$ ) in the tropical seasonal rain forest in Xishuangbanna. The species richness and floristic composition were similar with tropical forests in northern Thailand, but differed from the dipterocarp forests in SE Asia. Moreover, the representation of SAM classes in this non-dipterocarp forest differed significantly from the typical dipterocarp forests in Malaysia and Philippines, in that the understory of Xishuangbanna was mainly composed of trees within small and middle SAM classes whereas saplings of large canopy trees contribute a lot to the density of understory trees in the dipterocarp forests (LaFrankie et al., 2006). Considering tropical forests in this area are facing pressure from rubber plantation and other human activities, special priority should be given to conserve not only the tree layer but also the treelet layer of tropical forest in this region.

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## Appendix A.

Comparison of density ( $D$ ), frequency ( $F$ ), basal area ( $BA$ ,  $\text{cm}^2$ ), relative density ( $RDe$ ), relative frequency ( $RF$ ), relative dominance ( $RDo$ ) and importance values ( $IVI$ ) of the 10 most important species ( $2 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) in three tropical seasonal rain forest plots in Xishuangbanna, SW China.

Plot	Species	$D$	$F$	$BA$	$RDe$	$RF$	$RDo$	$IVI$
Menglun	<i>Mezzettipsia creaghii</i>	120	49	1974	5.9	3.6	6.2	15.7
	<i>Ardisia tenera</i>	118	41	1912	5.8	3.0	6.0	14.8
	<i>Saprosma ternatum</i>	104	43	1052	5.1	3.2	3.3	11.5

Plot	Species	D	F	BA	RDe	RF	RDo	IVI
Mengla	<i>Chisocheton siamensis</i>	71	37	1254	3.5	2.7	3.9	10.1
	<i>Millettia leptobotrya</i>	63	25	1436	3.1	1.84	4.5	9.4
	<i>Randia acuminatissima</i>	57	29	991	2.8	2.1	3.1	8.0
	<i>Barringtonia macrostachya</i>	46	34	990	2.2	2.5	3.1	7.9
	<i>Pittosporopsis kerrii</i>	55	24	710	2.7	1.8	2.2	6.7
	<i>Dichapetalum gelonioides</i>	35	31	743	1.7	2.2	2.3	6.3
	<i>Gironniera subaequalis</i>	32	21	989	1.6	1.5	3.1	6.2
	<i>Diospyros xishuangbannaensis</i>	93	48	1705	6.1	4.5	6.8	17.4
	<i>Pseuduvaria indochinensis</i>	71	44	1147	4.7	4.1	4.6	13.4
	<i>Dichapetalum gelonioides</i>	52	38	1381	3.4	3.6	5.5	12.5
	<i>Semecarpus reticulata</i>	63	35	1062	4.1	3.3	4.2	11.6
	<i>Walsura robusta</i>	56	36	942	3.7	3.4	3.7	10.8
	<i>Diospyros nigrocartex</i>	57	33	806	3.8	3.1	3.2	10.0
	<i>Knema furfuracea</i>	57	32	652	3.8	3.0	2.6	9.3
	<i>Aglaia parviridia</i>	50	31	657	3.3	2.9	2.7	8.8
	<i>Syzygium latilimbium</i>	40	27	690	2.6	2.5	2.7	7.9
	<i>Millettia pachycarpa</i>	43	28	442	2.8	2.6	1.8	7.2
Manyang	<i>Myristica yunnanensis</i>	105	48	2500	6.9	5.1	10.6	22.6
	<i>Randia acuminatissima</i>	92	40	1653	6.0	4.2	7.0	17.3
	<i>Barringtonia macrostachya</i>	62	43	1602	4.1	4.5	6.8	15.4
	<i>Lasianthus attenuatus</i>	108	42	690	7.1	4.4	2.9	14.5
	<i>Ardisia depressa</i>	95	37	713	6.2	3.9	3.0	13.2
	<i>Symplocos macrophylla</i>	57	32	925	3.7	3.4	3.9	11.1
	<i>Walsura robusta</i>	57	28	870	3.7	3.0	3.7	10.4
	<i>Cinnamomum bejolghota</i>	52	33	714	3.4	3.5	3.0	9.9
	<i>Ixora amplexicaulis</i>	41	27	839	2.7	2.9	3.6	9.1
	<i>Mezzettipsis sinensis</i>	43	25	781	2.8	2.6	3.3	8.8

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