LIANA COMMUNITIES IN THREE TROPICAL FOREST TYPES IN XISHUANGBANNA, SOUTH-WEST CHINA

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CAI ZQ, SCHNITZER SA, WEN B, CHEN YJ & BONGERS F. 2009. Liana communities in three tropical forest types in Xishuangbanna, south-west China. Lianas are an important growth form in tropical forests around the world. However, they are relatively unknown in south-east Asia. We identified, measured and determined the climbing and dispersal modes for lianas in five 0.1-ha plots in three common forest types at the tropical-temperate transitional zone in Xishuangbanna, SW China, namely, montane forest, evergreen broad-leaved forest and seasonally wet forest. Liana diversity in the three forests combined was high; we found a total of 147 liana species, representing 48 families and 75 genera. The mean density of lianas was 3407 ha^{-1} and varied significantly between the three forests, with 445, 276 and 301 individuals 0.1 ha^{-1} in the seasonally wet, montane and evergreen forests respectively. Similarity coefficients between the forests were low and mean species richness varied among different forests, indicating that species turnover among the forests was high. In all three forests, most lianas were stem twiners and scramblers, with relatively few hook, tendril and root climbers. Liana species were mostly wind dispersed in the evergreen forest but were animal and gravity dispersed in the other two forests. Compared with other Asian tropical forests, the diversity and abundance of lianas are relatively high in Xishuangbanna, which may be due to the warm climate as well as high seasonal rainfall and high rates of disturbance and forest fragmentation.

Keywords: Abundance, diversity, mechanism of climbing, mode of dispersal

CAI ZQ, SCHNITZER SA, WEN B, CHEN YJ & BONGERS F. 2009. Komuniti liana di tiga jenis hutan tropika di Xishuangbanna, barat daya China. Liana merupakan tumbuhan yang penting di hutan tropika seluruh dunia. Bagaimanapun, tidak banyak yang diketahui tentang tumbuhan ini di tenggara Asia. Kami mengenal pasti, mengukur serta menentukan kaedah memanjat dan penyebaran liana di lima plot, setiap satunya bersaiz 0.1 ha, yang terletak di tiga jenis hutan utama di zon peralihan tropika-temperat di Xishuangbanna, barat daya China. Hutan tersebut ialah hutan gunung, hutan berdaun lebar malar hijau dan hutan lembap bermusim. Apabila digabungkan, kepelbagaian liana di ketiga-tiga hutan adalah tinggi iaitu terdapat 147 spesies liana yang tergolong dalam 48 famili dan 75 genus. Ketumpatan min liana ialah 3407 ha^{-1}. Ketumpatan di ketiga-tiga jenis hutan berkenaan berbeza secara signifikan dan nilainya adalah masing-masing sebanyak 445, 276 and 301 individu 0.1 ha^{-1} di hutan lembap bermusim, hutan gunung dan hutan malar hijau. Pekali keserupaan antara hutan adalah rendah dan min kekayaan spesies berbeza-beza antara jenis hutan. Ini menunjukkan pusing ganti spesies adalah tinggi di ketiga-tiga hutan tersebut. Kebanyakan liana di ketiga-tiga hutan ialah jenis pelilit dan pepanjat batang dan hanya sebilangan kecil merupakan jenis yang memanjat menggunakan cangkuk, sulur paut dan akar. Kebanyakan liana di hutan malar hijau disebarkan melalui angin namun di dua hutan yang lain, cara sebaran utama adalah melalui haiwan serta graviti. Berbanding hutan tropika Asia yang lain, kepelbagaian serta kelimpahan liana di Xishuangbanna adalah agak tinggi. Ini mungkin dikaitkan dengan iklim panas di kawasan ini serta hujan bermusim yang tinggi dan kadar gangguan serta fragmentasi hutan yang juga tinggi.

INTRODUCTION

Lianas (woody climbers) are an abundant and diverse life-form in most tropical forests and their presence is often a key physiognomic feature differentiating tropical from temperate forests (Putz & Mooney 1991, Schnitzer & Bongers 2002). Lianas contribute substantially to the floristic, structural and functional diversity of tropical forests. Lianas compete with other vegetation for above- and belowground resources, substantially decreasing the growth rates and

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fecundity of adult trees, retarding regeneration of tree seedlings and saplings and also increasing the number of trees damaged or killed in treefalls (Stevens 1987, Allen *et al.* 1997, Schnitzer *et al.* 2000, 2005, Pérez-Salicrup 2001, Grauel & Putz 2004, Kainer *et al.* 2006). On the other hand, lianas can also have positive effects on forests; they provide valuable food resources, habitat and connections among tree canopies that are used as pathways by arboreal animals (Emmons & Gentry 1983, Ødegaard 2000). At the ecosystem level, lianas may contribute to tropical forest carbon budgets, representing as much as 10% of fresh aboveground biomass (Putz 1984). However, when lianas become abundant they may displace trees and actually reduce the ability of forests to sequester carbon (Laurance *et al.* 2001, Phillips *et al.* 2002, Wright *et al.* 2004). Determining the abundance and dynamics of lianas in tropical forests is particularly timely because lianas appear to be increasing in abundance, possibly due to global climate change (Phillips *et al.* 2002, Wright *et al.* 2004, Swaine & Grace 2007).

Liana abundance in forests outside of the tropics, however, are not increasing because cold winter temperatures at higher latitudes may be the overriding factor that limits liana abundance (Schnitzer 2005), although this may not account for changes at lower temperate latitudes (Bragg 2004, Allen *et al.* 2007). Liana abundance and diversity are more likely to increase at the transition zone between tropical and temperate forests, where small increases in temperature may reduce the number of days below freezing (Londré & Schnitzer 2006, Allen *et al.* 2007). Liana communities in the tropical-temperate transition zone, however, are poorly studied (but see Allen *et al.* 1997, 2005, 2007) and before we can test the hypothesis that lianas are increasing in abundance in this zone, we need to describe, in detail, liana communities that are situated there.

The forests in the tropical-temperate transitional zone at Xishuangbanna, south-west China differ from typical lowland rain forests in equatorial areas, in part, by having many deciduous trees in the canopy layer, fewer megaphanerophytes and epiphytes, as well as more species of microphylls (Zhu *et al.* 2006). However, little is known about the liana communities of this region and, thus, here we provide the first detailed study of lianas. We examined the liana communities in this region by describing their abundance, basal area, size class distributions, species richness and species composition in three different, but common forest types in Xishuangbanna. We also describe liana climbing modes and dispersal syndromes and analyse whether these factors vary predictably among the forest types.

MATERIALS AND METHODS

Study area and site description

The study was conducted in Xishuangbanna (21° 09'–22° 33' N, 99° 58'–101° 50' E), which is located at the northern margin of mainland south-east Asia and the southern end of the Hengduan Mountains (part of the Himalayas). Lying in the east Asian monsoon region, Xishuangbanna is dominated by warm–wet air masses from the Indian Ocean in summer and continental air masses from the subtropical regions in winter, which result in an alternation of rainy (May–October) and dry (November–April) seasons (Cao *et al.* 2006). Due to the barrier of the Himalayas in the north, this region is sheltered from northerly cold air masses. Average annual temperature in the tropical forests in Xishuangbanna is 21.4 °C and average annual rainfall is 1539 mm, of which about 82% occurs in the rainy season, while heavy fog in winter partially compensates for the rainfall shortage during the dry season.

The four main tropical forest types in the area are: (1) seasonally wet forest (hereafter referred to as 'seasonal forest'), which consists of a combination of evergreen and deciduous broad-leaved trees, (2) evergreen broad-leaved forest ('evergreen forest'), (3) montane forest ('montane forest'), and (4) monsoon forest over limestone ('monsoon forest') (Cao *et al.* 2006, Zhu *et al.* 2006). The combination of these four forest types contributes to the relatively high tree species diversity of this region. The seasonal and evergreen forests constitute the majority of forests in this region, while the montane forest contributes significantly less (Zhu *et al.* 2006) (Table 1). We sampled one forest from three of these major forest types, omitting the monsoon forest because these forests contribute only a very small area of all forest types and are exceptionally difficult to traverse due to their steep slopes.

Table 1 A summary of key abiotic factors describing the three study sites

Location	Forest type	Geographical location	Altitude (m asl)	pH value	Organic matter (%)
Mengsong	Montane forest	21° 27' N, 100° 25' E	1650	4.5	4.5
Nangongshan	Evergreen broad-leaved forest	21° 37' N, 101° 27' E	1300	4.9	1.4
Baka	Seasonally wet forest	21° 50' N, 101° 12' E	750	3.7	2.7

The soil type of the three forests studied was lateritic red soil.

Sampling procedures

We surveyed lianas between September and November 2004 in 15 plots measuring 20 × 50 m (0.1 ha), with five replicates in each of the three forest types. The selected sites were representative of the forest types. In each forest, randomly selected plots were separated by a minimum distance of 50 m and were at least 100 m from the forest edge. In each plot, we enumerated and measured the diameter of all free-standing and climbing liana individuals (≥ 0.2 cm). For lianas ≥ 1 cm in diameter, we measured the stems at 130 cm from the roots (Gerwing *et al.* 2006). For smaller lianas (0.2–1 cm), we measured their diameter at 10 cm stem above ground. We defined lianas as woody climbers rooted in the ground; thus, we excluded herbaceous vines, epiphytes and hemiepiphtes. When a single liana individual had multiple vegetative offshoots connected to the main stem, we included only the largest diameter stem and excluded all multiple vegetative offshoots (methods follow those of Mascaro *et al.* 2004, Schnitzer *et al.* 2006). We also measured and enumerated all trees (dbh ≥ 5 cm) that were rooted in the plot.

We identified lianas in the field and collected voucher samples, including flower and diaspore type, from each individual. Species were identified using the regional floras (*Yunnan Flora*, Volumes 1–15), and confirmed at the Xishuangbanna herbarium. Local taxonomists verified all species identification using herbarium specimens at Xishuangbanna Tropical Botanical Garden. We classified flower type based on the size and colour of flowers (Gentry 1982, 1991b). We distinguished inconspicuous flowers (those with white or green colours and smaller than 1 cm in length) from conspicuous flowers (those with bright colours and flower lengths generally longer than 1 cm). Diaspores are the structures that aid in seed dispersal, including fruits, seeds or seeds with some part of the fruit that remains attached. Based on diaspore morphology, three dispersal syndromes are commonly classified: anemochory (wind-dispersed fruits or seeds with plumose appendages or scarious wing-like appendages), zoochory (animal-dispersed fruits with soft and fleshy outer layers or seeds with arils), and barochory (heavy fruits that fall near the maternal plant). We categorized liana species into one of five potential climbing types: (1) scramblers, (2) twiners, (3) root climbers, (4) tendril climbers, and (5) hook climbers following methods by Putz and Chai (1987) and DeWalt *et al.* (2000).

Data analysis

We quantified the liana community in each of the three forests by calculating mean liana density (number of individuals per plot), liana basal area (sum of all lianas ≥ 0.2 cm diameter), liana basal area as percentage of tree (≥ 5 cm dbh) basal area, species richness (number of species per plot) and Fisher's log series α (Fisher's α) for each forest, using plot as the unit of replication. Additionally we calculated species mean relative abundance (MRA) and basal area (MBA) by dividing the abundance or basal area of the focal species per plot by the abundance and basal area of all the individuals in the plots respectively, and then taking the average of the plots. The relative importance value (RIV) is the sum of the MRA and MBA divided by two (Hartshorn & Hammel 1994, Mascaro *et al.* 2004).

We included Fisher's α as an index of diversity because it varies relatively little with sample size and thus facilitates comparisons of diversity among sites that differ in abundance (Magurran 2004). Fisher's α is calculated using the equation:

$$S = \alpha * \ln(1 + n/\alpha)$$

where

S = number of species

n = number of individuals
α = alpha.

We used analysis of variance (ANOVA) to examine differences among the three forest types as an estimate of turnover among forest types. We determined how similar species composition was both within- and among-sites using Morisita-Horn similarity index (C_{MH}), which is robust to differences in sample size and species number (Magurran 2004) using the equation:

$$C_{MH} = 2\sum(a_i * b_i) / (d_a + d_b) * N_a * N_b$$

where

N_a (or N_b) = total number of individuals in site A (or B)
a_i (or b_i) = number of individuals in ith species in site A (or B)
d_a = $\sum a_i^2/N_a^2$; d_b = $\sum b_i^2/N_b^2$

We plotted randomized species accumulation curves for each of the sites using EstimateS version7.5 (Colwell *et al.* 2004). EstimateS is a freely distributed simulation software (http://purl.oclc.org/estimates) that allows for the calculation of species-accumulation curves based on empirically sampled data.

RESULTS

Lianas were abundant in the Xishuangbanna forests. The mean density of lianas (≥ 1 cm diameter) per 0.1 ha differed significantly among the three forests ($F = 32.7$, $p < 0.001$, Table 2) with the seasonal forest having the highest (189.4) and the montane forest the lowest values (57). Likewise, both mean liana basal area and proportional basal area (based on the ratio of lianas to trees) were the highest in the seasonal forest ($F = 8.3$, $p = 0.015$ and $F = 8.2$, $p = 0.007$ respectively), while there were no significant differences between montane and evergreen forest. The mean density of small lianas (< 1 cm) was > 200 individuals per plot and the stem number did not differ significantly among the three forest types ($F = 1.2$, $p > 0.05$). More than 75% of liana individuals were smaller than 4 cm in diameter in all forests (Table 3), while large lianas (dbh > 10 cm, *sensu* Phillips *et al.* 2002) were sparse. The largest liana in all plots measured 42 cm in diameter (*Craspedolobium schochii)* and was found in the montane forest. More trees carried at least one liana in the seasonal than in the evergreen forest (log-transformed, $F = 7.2$, $p = 0.028$, Table 2). Tree basal area was negatively correlated to liana basal area, but the correlations were rather weak and not significant (log-transformed, $r^2 = 0.22$, $p > 0.05$, $n = 15$).

Species richness, diversity and dominance

In all 15 plots combined, we found a total of 147 liana species belonging to 75 genera and 48 families (see Appendix). Of these 43, 68 and 114 species were found in the montane, evergreen and seasonal forest plots respectively. In the montane forest, the most diverse families, in terms of the number of species, were Fabaceae (Papilionaceae) (8) and Apocynaceae (8), which when combined contributed 37.2% of the total species richness. In evergreen forest, Fabaceae (8) and Rubiaceae (4) were well represented, contributing 17.6% of the total species. The seasonal forest contained 44 families and 74 genera, and the Fabaceae (11), Rubiaceae (11) and Apocynaceae (8) were the most speciose families.

Species richness in the three forest types ranged from 21.4 to 40.4 species per 0.1 ha. The seasonal forest plots had significantly more species than montane and evergreen forest plots ($F = 22.8$, $p < 0.0001$) while montane and evergreen forests were not significantly different from each other (Table 2, Figure 1). Species diversity estimated using Fisher's α was two times higher in the seasonal forest compared with evergreen forest, while montane forest was intermediate ($F = 19.9$, $p < 0.0001$, Table 2). Because Fisher's α is relatively insensitive to sample size, the high diversity in the seasonal forest is likely to be independent of the high stem density in this forest (Mascaro *et al.* 2004).

The evergreen forest plots had highest among-plot similarities compared with the other two forest types (two *t*-tests, each $p < 0.0001$), suggesting that species composition was the least variable among plots in the evergreen forest, while the seasonal and montane forests were both lower but equal in among-plot similarities (Table 4, *t*-test, $p > 0.05$). Similarities within forests were much higher than similarities among forests. Plots in evergreen and seasonal forests were more alike than the other forests combinations (two *t*-tests, each $p < 0.0001$), while the similarities between evergreen and montane and between

Table 2 Mean liana density, species richness, basal areas and Fisher's α of lianas in three forests in Xishuangbanna, SW China

Forest type	Liana species richness (0.1 ha)	Total species number (0.5 ha)	Liana density 0.2 cm < dbh < 1 cm (0.1 ha)	Liana density dbh ≥1 cm (0.1 ha)	Liana basal area (cm^2/0.1 ha)	% of trees with at least one liana (0.1 ha)	Liana/tree basal area (%) (0.1 ha)	Fisher's α
Montane forest	26 (0.9) a	68	218.8 (27.5) a	57 (15.9) a	1004.0 (135.5) a	–	2.7 (0.4) a	7.1(0.3) b
Evergreen broad-leaved forest	21.4 (3.4) a	43	211.8 (26.5) a	89.2(15.5) b	663.8(54.5) a	36.1 (6.8) a	2.0 (0.3) a	5.3(0.6) a
Seasonally wet forest	40.4 (3.3) b	114	255.8 (36.0) a	189.4 (13.7) c	1637.7(127.6) b	61.9 (5.7) b	10.7 (2.7) b	10.5 (0.9) c

The data (means ± SE, n = 5) with different letters were significantly different between sites (ANOVA, $p < 0.05$); liana basal area was calculated as the sum of all lianas ≥ 0.2 cm dbh; liana/tree basal area (%) was calculated by dividing liana basal area by basal areas of trees ≥ 5 cm dbh.

Table 3 Size-class distribution of lianas in each plot (0.1 ha) in three forests at Xishuangbanna, SW China

Dbh (cm)	Montane forest	Evergreen broad-leaved forest	Seasonally wet forest
0.2–0.5	123.3 ± 43.0 a	98.0 ± 48.7 b	104.4 ± 49.9 ab
0.5–1.0	100.9 ± 34.2 b	113.8 ± 36.0 b	151.4 ± 22.1 a
1–2	51.9 ± 28.5 b	59.8 ± 15.2 b	105.2 ± 21.8 a
2–5	18.8 ± 16.5 b	23.0 ± 12.1 b	65.8 ± 8.24 a
5–10	6.6 ± 4.0 b	5.0 ± 1.9 b	17.8 ± 3.0 a
> 10	2.1 ± 2.3 a	1.4 ± 1.9 b	0.6 ± 0.8 c

Different letters within the same row indicate significant difference between the forests (ANOVA, $p < 0.05$).

Table 4 Morisita-Horn similarity values among plots, both within forests and among forests

	Montane forest	Evergreen broad-leaved forest	Seasonally wet forest
Montane forest	0.55 ± 0.22	0.10 ± 0.05	0.10 ± 0.07
Evergreen broad-leaved forest		0.78 ± 0.11	0.27 ± 0.11
Seasonally wet forest			0.59 ± 0.17

Mean values and SD are given. Numbers of comparisons were 10 for within forests and 25 for among forest.

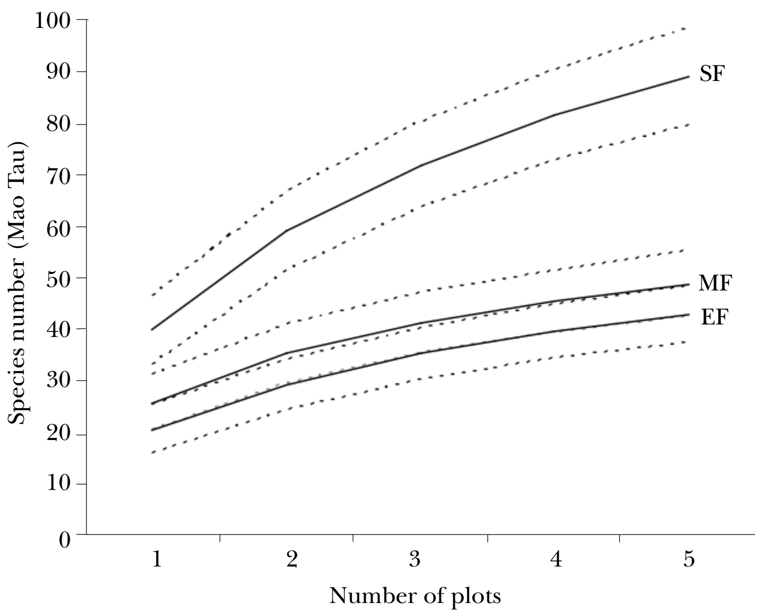

Figure 1 Species–sample curves for liana species in seasonal (SF), montane (MF), and evergreen (EF) forests in Xishuangbanna, China. Species number is the number of species expected in the pooled samples, given the empirical data (Colwell *et al.* 2004) and their 95% confidence intervals. Values are computed using EstimateS Version 7.5.

rainforest and montane were equal (*t*-test, $p > 0.05$).

The top 10 species accounted for more than 75% of the total importance values of all liana species in evergreen and montane forests; they were less than 50% of the total importance values in seasonal forest (Table 5). *Celastrus monospermus* was the most dominant liana species in the seasonal forest, with an importance value of 11.9%. *Craspedolobium schochii* was the most abundant species in evergreen and montane forests, with importance values of 16.8 and 22.7% respectively. The relative basal area of *C. schochii* was exceptionally variable in evergreen forest, ranging from 7.8 to 74.5% per plot. Only one of the top 10 species (*C. monospermus*) was shared between the montane and seasonal forests, while four species (*Dalbergia stipulacea, Smilax hypoglauca, C. monospermus, Bauhinia aurea)* were shared between the evergreen and seasonal forests. Only one rattan species (*Calamus nambariensis*) was found among these top 10 dominant species, exclusively in the montane forest (see Appendix).

Climbing mechanisms, flower and dispersal syndromes

Liana climbing mechanisms did not differ significantly among the three forest types (log-transformed, $F = 0.03$, $p > 0.05$, Figure 2). Twining was the predominant climbing mechanism in all forests in terms of species richness (43.1–52.4%), followed by scramblers (20–26.2%). The other three types of climbing mechanism were less common and varied in abundance among the forest types. There were more conspicuous than inconspicuous flowers in all three forest types but differences were less pronounced in the seasonal forest (Figure 3a). Lianas displayed a wide range of diaspore types, namely, wind-dispersed, animal-dispersed and autochorous (Figure 3b). The proportion of diaspore types was essentially the same in montane and seasonal forests (log-transformed, $F = 0.02$, $p < 0.05$). However, the evergreen forest differed significantly from the other two forest types due to the predominance (61.5%) of wind-dispersed species.

DISCUSSION

Liana abundance and diversity is variable among sites throughout the tropics (Putz 1984, Gentry 1991a, Muthuramkumar & Parthasarathy 2000, Pérez-Salicrup *et al.* 2001, Mascaro *et al.* 2004, Parthasarathy *et al.* 2004, DeWalt *et al.* 2006), and lianas commonly compose 10–45% of the woody individuals and species in tropical forests. In liana-dense tropical forests, such as those in the Bolivian Amazon, lianas can reach an average of 2471 lianas ha^{-1} (≥ 2 cm dbh) and they can constitute as much as 44% of the woody species (Pérez-Salicrup *et al.* 2001). In one temperate forest lianas made up 5–15% of all woody stems (> 2.5 cm dbh, Allen *et al.* 2007). Compared with many published studies, we found relatively high liana abundance and diversity in the three Xishuangbanna forests. With a mean abundance of 1118 lianas (≥ 0.2 cm dbh) and 75 species 0.5 ha^{-1} among each of the forests, liana abundance and diversity in Xishuangbanna was similar to, or higher than that of other tropical Asian forests. For example, at Lambir Hills in Sarawak, north-western Borneo, mean liana abundance was 348 and 164 liana individuals (diameter ≥ 2 cm) ha^{-1} in valley and hilltop sites respectively, with a total of 79 species ha^{-1} (Putz & Chai 1987). In the Danum Valley Conservation Area in Sabah, north-eastern Borneo, Campbell and Newbery (1993) found 882 individuals per ha (diameter ≥ 2 cm) in two 4-ha plots of lowland dipterocarp forest. In five forests in southern India, there were an average of 345 lianas ha^{-1} (> 1.6 cm) and 148 species in a total sample area of 47 ha (Muthuramkumar & Parthasarathy 2000, Parthasarathy *et al.* 2004). At Sepilok Forest Reserve, Malaysia, DeWalt *et al.* (2006) found an average of 258 lianas ha^{-1} (≥ 2 cm) in three forest types. In comparison, we found a mean density of 470 lianas ≥ 2 cm for the three forests. The liana density in Xishuangbanna is similar to that of La Selva Biological Station in Costa Rica, which has approximately 473 lianas ≥ 2 cm diameter and 1493 lianas ≥ 0.2 cm diameter (Mascaro *et al.* 2004).

Our finding that liana abundance was highest in the seasonal forest is consistent with the documented pattern that lianas peak in abundance with decreasing rainfall and increasing seasonality (Schnitzer 2005). The seasonality index, i.e. the sum of the absolute deviations of mean monthly rainfalls from the overall monthly mean divided by the mean annual rainfall (Walsh & Lawler 1981) was relatively high (0.77) in the seasonal forest in Xishuangbanna. Furthermore, our findings that liana abundance and diversity were lowest in the montane forests are consistent with published data (reviewed by Schnitzer & Bongers 2002).

Table 5 Ten most abundant liana species according to the density and basal area, arranged in order of decreasing relative importance value

Montane forest				Evergreen broad-leaved forest				Seasonally wet forest			
Dominant species	MRA	MBA	RIV (%)	Dominant species	MRA	MBA	RIV (%)	Dominant species	MRA	MBA	RIV (%)
Craspedolobium schochii	12.3 (1.3)	21.3 (8.6)	16.8	*Craspedolobium schochii*	14.8 (4.0)	30.6 (15.2)	22.7	*Celastrus monospermus*	14.1 (0.9)	9.7 (1.1)	11.9
Millettia pachycarpa	11.8 (1.2)	20.2 (5.5)	16.0	*Bauhinia griffithiana*	11.0 (2.8)	15.6 (5.1)	13.3	*Dalbergia stipulacea*	4.4 (0.6)	15.9 (1.1)	10.1
Bousigonia angustifolia	11.4 (2.0)	15.0 (11.3)	13.2	*Smilax hypoglauca*	17.6 (8.8)	5.5 (1.7)	11.6	*Gnetum parvifolium*	3.3 (1.0)	6.1 (0.5)	4.7
Spatholobus suberectus	7.9 (1.0)	16.9 (6.7)	12.4	*Dalbergia stipulacea*	9.6 (7.2)	11.6 (6.6)	10.6	*Combretum latifolium*	2.7 (0.5)	6.1 (0.4)	4.4
Parabarium linearicarpum	9.2 (0.5)	4.2 (1.9)	6.7	*Connarus paniculatus*	9.8 (3.1)	11.3 (9.2)	10.6	*Byttneria grandifolia*	4.1 (0.6)	3.8 (0.4)	3.9
Calamus nambariensis	9.8 (2.0)	0.7 (0.4)	5.3	*Smilax microphylla*	13.5 (2.8)	1.2 (0.5)	7.3	*Mussaenda hossei*	5.8 (0.8)	1.6 (0.6)	3.7
Celastrus monospermus	3.7 (0.8)	2.6 (2.1)	3.2	*Mussaenda hossei*	4.8 (1.8)	3.2 (2.5)	4.0	*Marsdenia tinctoria*	4.4 (0.1)	0.3 (0.0)	2.3
Dalbergia pinnata	2.1 (0.3)	0.5 (0.3)	1.3	*Celastrus monospermus*	2.5 (1.5)	1.9 (1.2)	2.1	*Smilax hypoglauca*	3.4 (0.8)	0.8 (0.1)	2.1
Piper flaviflorum	1.1 (0.2)	0.1 (0.1)	0.6	*Smilax corbularia*	1.0 (0)	0.1 (0.0)	0.5	*Pristimera arborea*	2.6 (0.2)	1.1 (0.1)	1.8
Salacia aurantiaca	0.9 (0.3)	0.1 (0.0)	0.5	*Spatholobus suberectus*	0.5 (0.5)	0.1 (0.1)	0.3	*Erycibe glaucescens*	1.3 (0.2)	0.3 (0.0)	0.8
Sum	70.2	81.6	75.9		85.1	81.1	83.1		46.3	45.8	46.1

MRA = mean relative abundance; MBA = mean basal area; RIV = relative importance value; values in parantheses are standard errors.

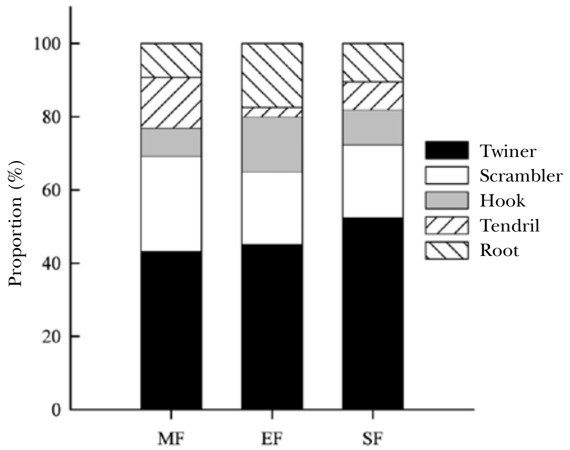

Figure 2 The proportion of each climbing mechanism of liana species in montane forest (MF), evergreen broad-leaved forest (EF) and seasonally wet forest (SF) in Xishuangbanna, China

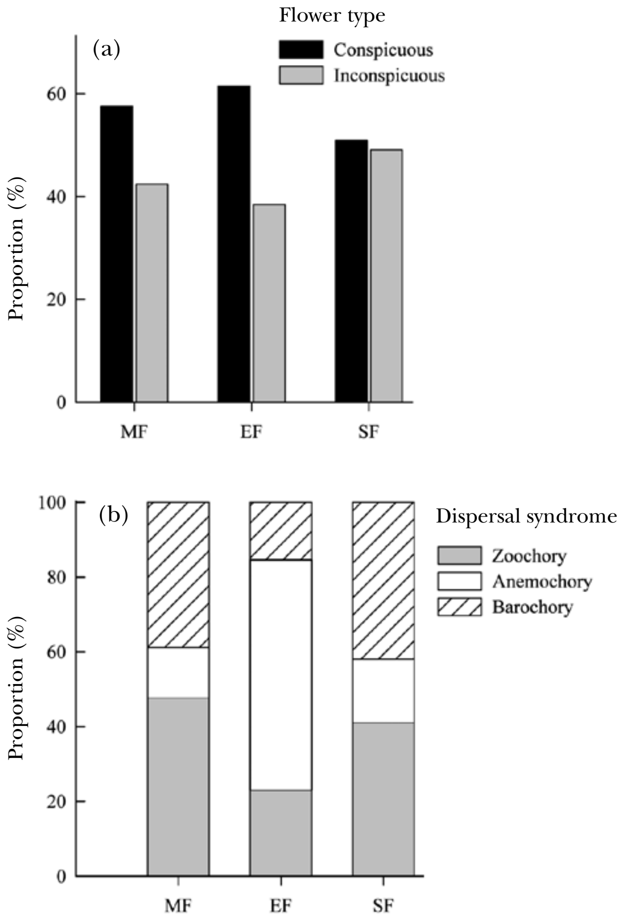

Figure 3 The proportion of the flower type(a) and dispersal syndrome (b) of liana species in the montane forest (MF), evergreen broad-leaved forest (EF) and seasonally wet forest (SF) in Xishuangbanna, China

However, because these forests (seasonal and montane) both differed in rainfall and elevation, we cannot be certain, based on our data, whether one factor is more important than the other.

Liana abundance and diversity decrease with increasing latitude (Gentry 1991a, Schnitzer & Bongers 2002, Schnitzer 2005). However, whether this change is linear or a step-function is not well established. For example, Schnitzer (2005) suggested that liana abundance will drop abruptly at the tropical-temperate transition because of the inability of most lianas to cope with freezing temperatures. Alternative, lianas may decrease linearly with increasing latitude (Gentry 1991a, Parthasarathy *et al.* 2004). Since liana abundance in this study is similar to, or even exceeds the abundance and diversity from a variety of tropical forest studies (Campbell & Newbery 1993, Muthuramkumar & Parthasarathy 2000, Mascaro *et al.* 2004, Parthasarathy *et al.* 2004), our data support the hypothesis that liana abundance may not be a strict linear decrease with increasing latitude. Rather, liana abundance and diversity may drop abruptly at higher latitudes, where the prevalence of winter freezing occurs. Another possible explanation for the relatively high abundance of lianas in Xishuangbanna is the legacy of forest disturbance. Half of the primary forest in Xishuangbanna was lost during the last 50 years (Zhu *et al.* 2004). In south-west China in general, large areas of tropical forests were replaced by rubber plantations in the 1960s, leaving smaller forest remnants near local villages. Although these forest remnants remain mostly undisturbed for religious reasons (Liu *et al.* 2002, Zhu *et al.* 2004), previous disturbance and higher propagule pressure from prolific liana growth on the forest edges may have resulted in increased liana abundance in these forests (DeWalt *et al.* 2000, Schnitzer *et al.* 2000, Zhu *et al.* 2004). We tried to avoid biases in forest age by selecting sites in forests with little recent disturbance and that were at least 100 m from the forest edge. Nonetheless, it is possible that human disturbance may, to some degree, explain the relative high abundance of lianas found in this study compared with other forests in this region.

Species dominance was high compared with other studies. In our study, *C. schochii* was the most dominant liana species in the montane and evergreen forests, and one of the top three liana species accounting for over 10% of relative abundance in these two forests. In a chronosequence study in central Panama, DeWalt *et al.* (2000) found that *Maripa panamensis* composed approximately 11% of liana stems and was found in all stands in secondary and primary forests in Panama. Similarly, in eastern Ecuador, Burnham (2002) reported that the most dominant liana, *Machaerium cuspidatum*, represented approximately 11% of the liana stems. There was an extremely high dominance in a tropical wet forest at La Selva Biological Station in Costa Rica, where the 10 top species accounted for more than 70% of all species and the most dominant liana species, *Moutabea aculeata* constituted 17% of all individuals (Mascaro *et al.* 2004). Combined with these published reports, our finding of 12 and 15% relative abundances of *C. schochii* in the montane and evergreen forests respectively, and 14% of *C. monospermus* in the seasonal forest suggests that strong species dominance may be a general characteristic of liana communities world-wide.

Of the five climbing mechanisms distinguished in this study, twining around the host tree was the most common, followed by scrambling. These climbing mechanisms were 3–5 times more common than tendril, root and hook climbers, which were relatively rare (Figure 3). Our findings are consistent with other studies which reported that twining was found to be dominant (Jongkind & Hawthorne 2005, Kuzee & Bongers 2005), especially in older forests (DeWalt *et al.* 2000). Other studies, however, reported that tendril climbers were more abundant in early secondary forests compared with old growth forests (Hegarty 1988, DeWalt *et al.* 2000). The high ratio of stem twiners to tendril climbers in our study may indicate that the forests are in a relatively late stage of succession.

Seed dispersal syndromes are often correlated with seasonality and precipitation, with wind-dispersed seeds common in highly seasonal forests and far less common in aseasonal forests (Gentry 1982, 1991b). In our study, wind-dispersal was prevalent only in the evergreen forest, where > 60% of the species were wind dispersed. In contrast, wind dispersed seeds were only 17 and 13.4% in the seasonal and montane forests respectively. Our findings are similar to those in semi-evergreen and dry evergreen forests in India (Muthuramkumar & Parthasarathy 2000, Parthasarathy *et al.* 2004) and in a seasonally dry tropical forest in Mexico (Solorzano *et al.* 2002). The prevalence of succulent diaspores in montane and seasonal forests in Xishuangbanna indicates the possible faunal dependence of many liana species. The prevalence of zoochory suggests that a holistic, whole-forest approach to conservation strategies is necessary to maintain forest diversity because plants such as lianas are dependent on animal fauna for dispersal. In turn, lianas may be a valuable food source for many forest animals. Overall, our findings demonstrate that lianas can be abundant and diverse even in the tropical–subtropical transition zone and, thus, the importance of lianas for forest diversity, dynamics and functioning likely extends into this zone as well.

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APPENDIX

Complete list of climbing and free-standing lianas identified in the 15 0.1-ha plots in three forests in Xishuangbanna. 'M, E, SF' in parentheses represent the distribution of liana species, namely, montane, evergreen broad-leaved and seasonally wet rainforest respectively.

Annonaceae: *Artabotrya hongkongensis* Hance [E, M], *Fissistigma acuminatissimum* Merr. [M], *Fissistigma latifolium* (Dun.) Merr. [SF] *Fissistigma polyanthoides* (A. DC.) Merr. [SF], *Fissistigma polyanthum* (Hook.f.et Thoms.) Merr. [M], **Apocynaceae**: *Aralia armata* (Wall.) Seem. [SF], *Tupidanthus calyptratus* Hook.f. et Thoms [M], *Aganosma harmandiana* Pierre [E, SF, M], *Alyxia menglongensis* Tsiang et P.T. Li [SF], *Alyxia simensis* Craib [M], *Amalocalyx yunnanensis* Tsiang [E, SF], *Beaumontia grandiflora* Wall [SF], *Bousigonia angustifolia* Pierre [E, SF, M], *Ecdysanthera rosea* Hook. Et Arn. [SF], *Epigynum auritum*(Scheid.) Tsiang et P.T.Li. [M], *Melodinus henryi* Craib [SF], *Melodinus tenuicaudatus* Tsiang et P.T.Li [M], *Parabarium linearicarpum* (Pierre) Pichon [E, M], *Trachelospermum jasminoides* (Lindl.) Lem. [M], *Pottsia laxiflora* (Bl.) O. Kuntze [SF, M], **Araceae:** *Pothos chinensis* (Raf.) Merr. [M], *Rhaphidophora hongkongensis* Schott [M], *Rhaphidophora luchunensis* H. Li. [SF], **Aristolochiaceae:** *Aristolochia tagala* Champ [E], **Asclepiadaceae:** *Gymnema sylvestre* (Retz.) Schult. [SF], *Marsdenia balansae* Cost [SF], *Marsdenia tinctoria* R. Br. [SF], **Bambusoideae:** *Ampelocalmus menglaensis* Hsuehe F.Du [M], *Dinochloa multiramora* Hsueh etHui. [M], *Gigantochloa nigrocoliata* (Buse) Kurz [SF], **Caesalpiniacea:** *Bauhinia aurea* Levl. [E, M], *Bauhinia claviflora* L.Chen [M], *Bauhinia griffithiana* (Benth.) Prain [M], *Caesalpinia tsoongii* Merr [M], **Capparidaceae:** *Stixis suaveolens* (Roxb.) Pierre [W, FM], **Caprifoliaceae:** *Viburnum foetidum* Wall. var. *rectangulatum* (Graebm. Rehd.) [SF], **Cardiopteridaceae:** *Peripterygium quinquelobum* Hassk [SF], **Celastraceae:** *Celastrus angulatus* Maxim. [M], *Celastrus monospermus* Roxb. [SF, M], *Celastrus paniculatus* Willd [SF], *Euonymus acanthocarpus* Franch [M], **Combretaceae:** *Combretum latifolium* Bl. [SF], *Quisqualis caudata* Craib [SF], **Compositae:** *Vernonia cumingiana* Benth. [M], *Vernonia solanifolia* Benth [SF], **Connaraceae:** *Connarus paniculatus* Roxb. [SF, M], *Rourea minor* (Gaertn.) Leenh [SF], **Convolvulaceae:** *Erycibe glaucescens* Wall. Ex Choisy [E, SF], *Argyreia nervosa* (Burm. f.) Bojer [M], **Dilleniaceae:** *Tetracera asiatica* (Lour.) Hoogl. [SF], **Dioscoreaceae:** *Dioscorea alata* Linn. [SF], *Dioscorea hispida* Dennst. [SF, M], *Dioscorea glabra* Roxb. [E, SF], **Euphorbiaceae:** *Phyllanthus reticulatus* Poir. [SF], **Gnetaceae:** *Gnetum parvifolium* (Warb.) C.Y. Cheng ex Chun [E, SF], *Gnetum pendulum* C.Y. Cheng [M], **Hernadiaceae:** *Illigera parviflora* Dunn [SF], *Illigera rhodantha* Hance [SF, M], **Hippocrateacaea:** *Pristimera arborea* (Roxb.) A.C.Sm.[E], *Salacia aurantiaca* C.y.Wu et S.Y. Bao.[E, SF, M], **Icacinaceae:** *Iodes vitiginea* (Hance) Hemsl [SF, M], **Leguminosae:** *Uraria crinita* (Linn.) Desv.ex DC [E], **Lygodiaceae:** *Akebia quinata* (Thunb.) Decne [E], *Lygodium conforme* C. Chr. [E, SF], **Malpighiaceae:** *Hiptage benghalensis* (Linn.) Kurz [SF, M], **Menispermaceae:** *Cyclea racemosa* Oliv. [M], *Diploclisia glaucescens* (Bl.) Diels [SF], *Pericampylus glauca* (Lam.) Merr. [SF], *Stephania hernandifolia* (Willd.) Walp [E, M], **Mimosaceae:** *Acacia megaladena* Desv., *Acacia pennata* (Linn.) Willd. ex Del. [E, SF], *Entada phaseoloides* (Linn.) Merr [SF], **Moraceae:** *Cudrania fruticosa* (Roxb.)Wigth ex Kurz [SF], *Ficus sarmentosa* var. *duclouxii* (Lerl. Et Vant.) Corner [SF], *Ficus sarmentosa* var. *lacrymans* (Levl.) Corner [M], **Myrsinaceae:** *Embelia oblongifolia* Hemsl. [SF], *Embelia parviflora* Wall [SF], *Embelia scandens* (Lour.) Merr. [SF], *Embelia subcoriacea* (C.B. Clarke) Mez [SF], *Embelia* var. *ribes* Burm.f. [E, SF, M], **Rhamnaceae:** *Ventilago calyculata* Tul. [SF], *Zizyphus apetala* Hook.f. [SF], *Zizyphus oenoplia* (Linn.) Mill. [E, SF], **Oleaceae:** *Jasminum coarctatum* Roxb. [SF] *Jasminum polyanthum* Fr. [M], *Jasminum robustifolium* Kobuski. [E, SF, M], **Palmae:** *Calamus nambariensis* Becc. var. *xishuangbannaensis* S.J.pei et S.Y.Chen [M], *Caryota monostachys* Becc.[SF], *Caryota ochlandra* Hance [SF], **Papilionaceae:** *Craspedolobium schochii* Harms [E, SF, M], *Dalbergia pinnata* (Lour.) Prain [E, SF, M], *Dalbergia rimosa* Poxb. [E, SF], *Dalbergia stipulacea* Roxb [E, SF, M], *Millettia dielsiana* Harms [SF, M], *Millettia lantsangensis* Z.Wei [M], *Millettia oosperma* Dunn [SF], *Millettia pachycarpa* Benth.[SF, M], *Mucuna macrobotrya* Hance [SF], *Pueraria colletti* Prain [E, SF], *Pueraria stricta* Kurz [E, SF], *Spatholobus suberectus* Dunn [E, SF], *Whitfordendron filipes* (Dunn) Dunn [M], **Passifloraceae:** *Adenia parviflora* (Blanco) Cusset [E, SF], *Passiflora altebilobata* Hemsl. [SF], *Passiflora siamica* Craib [SF], **Piperaceae:** *Piper betle* Linn. [SF, M], *Piper magen* B.C. Cheng [SF], *Piper flaviflorum* C.DC. [SF, M], *Gynostemma pubescens* (Gagnep.) C.Y.Wu ex C.Y.Wu et S.K.Chen [M], *Neoalsomitra integrifoliola* (Cogn.) Hutch [E, SF], **Polygalaceae:** *Securidaca inappendiculata* Hassk [SF], **Ranunculaceae:** *Clematis menglaensis* M.C. Chang [E, SF], **Rosaceae:** *Rubus alceaefolius* Poir. [E, SF], *Rubus rufus* Focke var. *palmatifidus* Card [M], **Rubiaceae:** *Hedyotis hedyotidea* DC, *Mussaenda erosa* Champ [E, SF], *Mussaenda hossei* Craib [E, SF], *Mussaenda pubescens* Ait. f. [E, SF, M], *Randia bispinosa* (Griff.) Craib [SF], *Randia sinensis* (Lour.) Merr. [SF], *Uncaria hirsuta* Haril. [SF], *Uncaria laevigata* Wall. [SF], *Uncaria lancifolia* Hutch. [SF], *Uncaria macrophylla* Wall. [E, SF], **Rutaceae:** *Paramignya retispina* Craib[M], *Toddalia asiatica* (Linn.) Lam. [E], *Zanthoxylum cuspidatum* Champ. [SF], **Schizandraceae:** *Kadsura anamosma* Ker [M], *Kadsura coccinea* (Lem.) A.C. [M], *Schizandra henryi* C.B. Clarke [SF], *Schizandra henryi* C.B. Clarke var. *yunnanensis* A.C.Sm [SF, M], *Schizandra plena* A.C.Sm. [SF], **Smilacaceae:** *Smilax cocculoides* Warb [SF, M], *Smilax corbularia* Kunth [E, M], *Smilax hypoglauca* Benth.[E, SF, M], *Smilax indica* Vitm.[SF], *Smilax microphylla* C.H. Wright [E], **Sterculiaceae:** *Byttneria grandifolia* DC. [SF], **Vitaceae:** *Ampelocalmus delavayana* Planch. ex Fr.[M, SF], *Cayratia mekongensis* C.Y.Wu ex W.T. Wang [M], *Cayratia tenuifolia* (Wang et Arm.) Gagnap [SF], *Cissus jarana* DC. [E, SF], *Cissus kerrii* Craib [E, SF], *Cissus subtetragona* DC. [SF], *Tetrastigma obovatum* (Wall.) Planch. [M], *Tetrastigma planicaulum* (Hook.f.) Gagnep. [M].