



# Bole bryophyte diversity and distribution patterns along three altitudinal gradients in Yunnan, China

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## Keywords

Altitude; Biodiversity hotspot; Conservation; Epiphyte; Hump-shaped; Life form; Liverwort; Local rarity; Moss; Species richness; Subtropical; Tropical

## Abbreviations

CCA = canonical correspondence analysis; IV = importance value; MDE = mid-domain effect; MDS-2D = multi-dimensional scaling in two dimensions;  $R_{cov}$  = relative coverage;  $R_{fre}$  = relative frequency.

## Nomenclature

Crosby et al. (1999); Gao & Cao (2000); Li (2002, 2005)

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## Abstract

**Question:** We investigated the bryophyte communities on tree boles along three altitudinal gradients located within different types of forested area to answer the following questions: (1) how many bole epiphytic bryophyte species are there; (2) what are the dominant species; (3) what are the richness patterns of epiphytic bryophyte communities along the altitudinal gradients; and (4) what are the major drivers and conservation implications of these patterns?

**Location:** Three protected forested areas in sub-montane (Mengla transect: 800–1400 m), montane (Zhenyuan transect: 2000–2600 m) and sub-alpine (Lijiang transect: 3200–3800 m) regions in Yunnan, SW China.

**Method:** Sixty 20 m × 20 m sampling plots were established, five at each of 12 altitudes at 200-m intervals along the transects. Species composition and cover of bryophytes were investigated from 594 subplots (each 400 cm<sup>2</sup>) on large tree boles of these plots. One-way ANOVAs were adopted to test for differences in species diversity among different transects. Multi-dimensional scaling in two dimension (MDS-2D) ordinations were conducted to assess similarity of bryophyte communities among study transects and altitudes. Canonical correspondence analysis (CCA) was applied to relate species composition to selected environmental variables.

**Results:** The three protected forests in Yunnan harboured 226 epiphytic bryophyte species belonging to 101 genera and 46 families, which were essential components of biodiversity of the entire forest ecosystem. In total, 99% of bryophyte species (224 species) showed varying degrees of local rarity. Smooth mat, fan and turf dominated in the sub-montane, montane and sub-alpine forests, respectively. Significantly lower bryophyte species richness was detected in the sub-montane area, which may be partly attributed to higher temperature, limited water availability and more frequent human disturbance. Epiphytic bryophytes exhibited a hump-shaped species richness pattern with increasing altitude. Peak richness coincided with highest moisture levels at ca. 2600 m.

**Conclusions:** Based on the presence of a high diversity of bryophytes and a high percentage (99%) of locally rare species growing on tree boles, this study emphasizes the importance of conserving these forests in Yunnan. Additionally, the regional pattern of lower epiphytic bryophyte diversity in warmer, drier areas shown in this study reveals how emerging climate change threatens Yunnan's epiphytic bryophytes.

## Introduction

With more than 20 000 species recorded worldwide, bryophytes are no doubt one of the earliest and most diversified groups of land plant (Mishler 2001; Gensel 2008). Bryophytes are poikilohydric, and lack roots and an outer waxy cuticle; they take up water and nutrients directly throughout their surface (Gignac 2001). Based on the close relationship between bryophytes, especially corticolous ones, and the atmosphere, these organisms are considered sensitive to environmental change (Gignac 2001; Song et al. 2012a,b). Changes in microclimate and host characteristics associated with altitudinal and latitudinal gradients and vegetation types are suggested to alter distribution of epiphytic bryophytes (Holz & Gradstein 2005; Ariyanti et al. 2008; Song et al. 2011). As bryophytes are particularly sensitive to climatic conditions (Gignac 2001) and usually have wide geographic distributions (Schofield 1992), they have been advocated as useful organisms to describe altitudinal zonation of mountain forests (Frahm & Gradstein 1991; Kessler 2000; dos Santos & da Costa 2010). The species richness of epiphytic bryophyte communities may indicate forest quality and integrity in terms of forest structure and resource availability (Frego 2007; Song et al. 2011). Additionally, most bryophyte species usually exhibit clonal or colonial life forms (Bates 1998). Bryophyte life forms, which can be interpreted as recurring arrangements of photosynthetic tissues that minimize evaporative water loss and maximize primary production, rather than individual shoots or thalli, are therefore the ecologically functional unit (Bates 1998).

Knowing the species composition and richness in forest ecosystems and understanding their major drivers has long been of interest and will provide crucial information for ecologists, biogeographers, conservationists and forest managers (Raabe et al. 2010). Since the last century, botanists and ecologists have focused on patterns of species richness along altitudinal gradients as an important issue. Species richness was thought to decrease with increasing altitude (Stevens 1992), but recent evidence suggests that this trend is generally not monotonic, although species richness does decrease at high altitudes (Rahbek 2005; Cardelús et al. 2006). The species richness of bryophytes along altitudinal gradients has three major patterns: increasing richness (Gradstein et al. 1989), decreasing richness with increasing altitude (Tusiime et al. 2007) or hump-shaped distribution (Wolf 1993; Ah-Peng et al. 2012). It has also been reported that bryophyte species richness does not show any clear altitude trend (Andrew et al. 2003; Sun et al. 2013). Even though factors associated with these patterns of species distribution vary from study to study, it is generally agreed that bryophyte diversity peaks at the altitude having optimum environmental

conditions, including suitable microclimate and substrate (Ah-Peng et al. 2007; Sun et al. 2013).

Although studies on epiphytic bryophyte ecology began almost a century ago (Olsen 1917; Barkman 1958; Iwatsuki 1960), our knowledge of the diversity and distribution of epiphytic bryophytes remains incomplete in many regions (Pharo et al. 1999; Ah-Peng et al. 2007; Gehrig-Downie et al. 2013). In Yunnan Province of southwestern China, for example, only a few small-scale bryophyte studies have been conducted (Wu 1992; Ma et al. 2009), despite this region supporting an estimated 70% (1500 spp.) of the Chinese bryophyte flora (Yang et al. 2004). The species composition and distribution patterns of epiphytic bryophytes along altitudinal gradients in Yunnan and their links to environmental variables remain little studied, although this would provide fundamental information related to bryophyte ecology and might provide valuable insights into biological conservation in this biodiversity hotspot under climate change.

In this study, bryophytes on tree boles were investigated along three altitudinal gradients in three representative forest areas in Yunnan. The goals of the study were to: (1) determine species composition and distribution patterns of epiphytic bryophytes of these poorly-studied protected forest areas in Yunnan; (2) understand similarity and diversity patterns of epiphytic bryophyte communities in different forests and along altitudinal gradients; and (3) assess the major drivers and the conservation implications of these patterns.

## Methods

### Study area

This study was conducted in Yunnan, an inland province of ca. 394 000 km<sup>2</sup> (21°09'–29°15' N, 97°32'–106°12' E) in SW China (Yang et al. 2004). Yunnan is located at a point of overlap of three geographic regions: the Tibetan plateau region, the eastern Asia monsoon region and the tropical monsoon region of southern Asia and Indo-China (Yang et al. 2004). Yunnan is a province with a vast mountainous plateau area, which declines in altitude from northwest to southeast. The province exhibits a series of three topographic 'steps': (1) northwest Yunnan is the most northerly and highest step, ca. 3000–4000 m a.s.l.; (2) middle Yunnan at ca. 2000–2500 m a.s.l.; and (3) south Yunnan, the most southerly and lowest step at ca. 600–1500 m a.s.l. (Kunming Ecological Institute & Yunnan Agricultural Regional Planning Committee Office 1994). A monsoon climate prevails over Yunnan, with cold-moist summers and dry-warm winters. In winter, a dry continental wind prevails but this is hindered by the Qinghai-Tibet Plateau, while in summer southwest and southeast marine monsoonal winds dominates (Kunming

Ecological Institute & Yunnan Agricultural Regional Planning Committee Office 1994). The region spans seven climatic zones (three major zones divided into seven climate zones), a northern tropical climate, a subtropical climate (north, mid, south) and a temperate climate (north, mid, south) based on differences in temperature (Cheng et al. 2009).

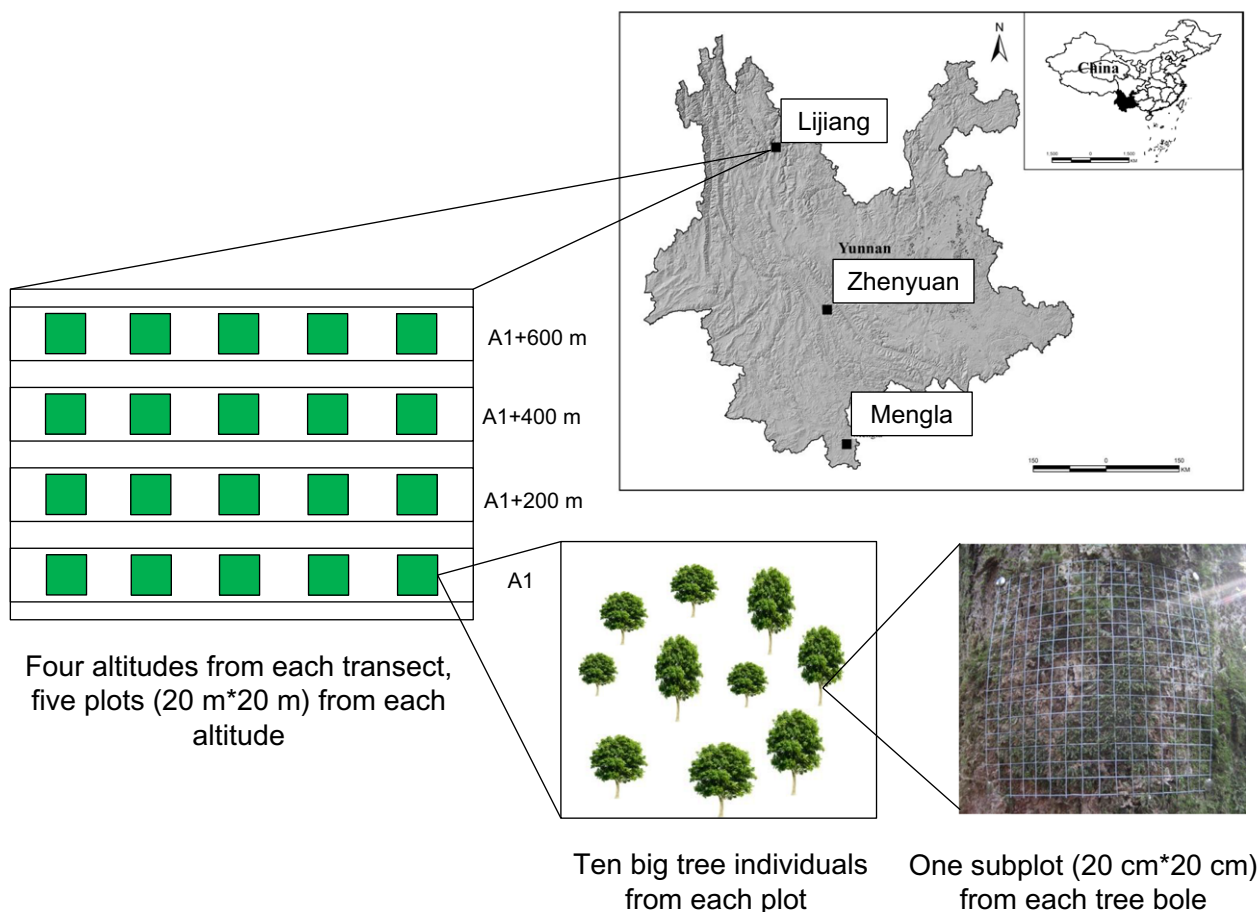
With the synergistic effect of horizontal latitude change and vertical altitude change, the landscape experiences almost all climate zones and land ecosystem types and consequently harbours a very high diversity of organisms (Li & Walker 1986; Yang et al. 2004). Yunnan is famous throughout the world as a 'Wildlife Kingdom', and Southern Yunnan has been included in the Indo-Burma biodiversity hotspot (Yang et al. 2004; Ah-Peng et al. 2007). More than 18 000 species of higher plant (51.6% of China's total) and 1836 vertebrate species (54.8% of China's total) have been recorded in Yunnan, a relatively small land area that accounts for only 4.1% of China's total area (Yang et al. 2004).

In 2010, three protected forested areas in Mengla, Zhenyuan and Lijiang were chosen as sampling transects

as part of the Queensland–Chinese Academy of Sciences Biotechnology Project. These transects are located in the three different climatic zones (tropical, subtropical and temperate) with elevational ranges that do not overlap (Fig. 1). At each transect, five plots (20 m × 20 m) were established at each of four elevations located at 200-m altitudinal intervals, as suggested by Gradstein et al. (1996) (Fig. 1). Details of the three studied protected forested areas are given in Table 1.

### Field survey and identification

Bryophyte field surveys and collections were carried out from May 2011 to November 2012, and bryophyte specimens were identified using a microscope (BH-2; Olympus, Tokyo, JP) in the laboratory from March to August 2013. Host (phorophyte) tree species can be an important factor influencing the distribution and composition patterns of bryophytes (Studlar 1982; Kuusinen 1996). However, it was impossible to control for host tree species across the three transects because they each support different vegetation types dominated by different tree species (Table 1). To



**Fig. 1.** Study sites and sampling methods.

**Table 1.** Environmental conditions of the three altitudinal transects in Yunnan, China. Sources: Huang (1984), Wu & Zhu (1987), Hijmans et al. (2005), Song et al. (2012b), Li et al. (2013), and data gathered during the Queensland–Chinese Academy of Sciences Biotechnology Project.

	Mengla	Zhenyuan	Lijiang
Annual Mean Temperature (°C)	21.9	11.1	8.4
Annual Precipitation (mm)	1575	1874	934
Latitude and Longitude	21°35' N, 101°33' E	24°16' N, 101°16' E	27°08' N, 100°14' E
Altitude Range (m)	800–1400	2000–2600	3200–3800
Forest Type	Tropical seasonal rain forest, monsoon evergreen broad-leaved forest	Sub-tropical montane moist evergreen broad-leaved forest	Sub-alpine coniferous forest
Human Disturbance	Monsoon evergreen broad-leaved forests located at 1200–1400 m were selectively logged in the 1960s, but tropical seasonal rain forest located at 800–1000 m has been well protected	Nearly no human disturbance	Nearly no human disturbance
Stand Age (yr)	50–100	>300	100–200
Dominant Tree Species	<i>Castanopsis mekongensis</i> , <i>Parashorea chinensis</i> , <i>Lithocarpus truncatus</i>	<i>Lithocarpus xylocarpus</i> , <i>Castanopsis wattii</i> , <i>Rhododendron leptothrium</i>	<i>Abies georgei</i> , <i>Abies forrestii</i> , <i>Quercus pannosa</i>
Canopy Closure (%)	80–85	89–95	85–90
Canopy Height (m)	45–60	25–30	30–40
Mean DBH (cm)	24.9	15.7	25.8
Tree Density (individuals·ha <sup>-1</sup> )	1296	1405	776
Total Number of Tree Species	150	75	25
Number of Sampled Host Species	59	37	10
Number of Sampled Host Individuals	201	195	198

obtain a representative sample of the bole bryophyte diversity, about ten large trees (most with DBH  $\geq 20$  cm) were sampled in each 20 m  $\times$  20-m plot (Fig. 1), giving a total of 201, 195 and 198 tree individuals belonging to 59, 37 and 10 host species in the Mengla, Zhenyuan and Lijiang transects, respectively. It has long been recognized that the species composition of epiphytic bryophyte communities changes over the vertical gradient of a tree (Barkman 1958; Kenkel & Bradfield 1986; Mota de Oliveira et al. 2009). In addition, exposure of the plots may affect bryophyte species composition because of microclimate differences of the windward and leeward sides of the bole (González-Mancebo et al. 2003; Song et al. 2011). We thus investigated epiphytic bryophytes at a similar height (ca. 1.5 m) and exposure (southwest) using a subplot consisting of a 20 cm  $\times$  20 cm metal frame quadrat with 256 equal-sized standard grids (Fig. 1) for each individual tree so that samples from different transects and altitudes were comparable (Song et al. 2011). For each subplot, observers recorded all bryophyte species and number of grid cells occupied by each species. L. Song, W.Z. Ma and Y.L. Yao identified most of specimens to species. Nomenclature follows *Flora Yunnanica* Vol. 17 to Vol. 19 (Gao & Cao 2000; Li 2002, 2005) and *A Checklist of Mosses* (Crosby et al. 1999). Life forms of bryophytes were classified and recorded according to Ma et al. (2009).

For all hosts sampled, DBH was measured with a DBH tape at 1.3 m from the ground. The bark roughness of each subplot was determined using a 1–9 scale (1 = very

smooth; 3 = smooth but with fissures; 5 = shallowly furrowed; 7 = deeply fissured; 9 = with abundant crevices across the surface; while 2, 4, 6 and 8 were intermediate conditions; Male & Roberts 2005). We tried to use a pH meter (PHB-1; Shanghai San-Xin Instrumentation, Inc., Shanghai, China) to measure bark pH in the field, but the values were unstable and thus were not adopted.

#### Data analysis

In each subplot, the cover of each species of epiphytic bryophyte was calculated as a percentage of the 256 grid cells occupied.

In each transect, importance value of epiphytic bryophytes was calculated using the following formula (Song et al. 2011):

$$IV = (R_{cov} + R_{fre})/2 \times 100\%.$$

Rabinowitz (1981) suggested that a species could be classed as rare if its distribution fits one of three criteria: narrow geographic range; high habitat specificity/low frequency; or consistently small population size. Unlike Rabinowitz, we use only our own plot data to assign rarity classes to bryophyte species, which we refer to 'local rarity'. In this study, species occurring at only one of the three transects were defined as having a narrow geographic range. Following Vanderpoorten & Engels (2003), species occurring in <10% of the subplots were considered as low

frequency. Species with maximum cover <10% were defined as small population size.

Epiphytic bryophyte diversity was evaluated using (1)  $\alpha$ -diversity, including average species richness, Margalef, Shannon-Weiner and Simpson indices per plot; (2)  $\gamma$ -diversity, the total species number in each study transect following Li et al. (2013); (3)  $\beta$ -diversity, Whittaker index calculated as  $\gamma/\alpha - 1$ . Species richness pattern along altitudes was fitted using peak regressions based on a log normal distribution with four parameters.

Before conducting further statistical analysis, all data were checked for normality using the Shapiro-Wilks test and homogeneity of variances using Bartlett's test. Differences in diversity of bryophyte species among altitudinal transects were tested using one-way ANOVAs, and Tukey's HSD and Games-Howell for multiple pair-wise comparisons in SPSS 16.0 (SPSS, Chicago, IL, US).

Multi-dimensional scaling in two dimensions (MDS-2D) ordination of samples was conducted using Primer 6 (PRIMER-E, Plymouth, UK). Canonical correspondence analysis (CCA) was applied to relate species composition to the selected environmental variables (ter Braak 1986). We performed this with the CANOCO package (Microcomputer Power, Ithaca, NY, US), and all analyses were conducted with 'automatic selection' (forward selection). CCA was run with abundance data (cover of each epiphytic bryophyte species in each subplot) and the environmental data including transect (three nominal variables), altitude, host DBH and roughness data. Data related to species in less than three of the subplots were removed from the analysis to lessen the disproportionate effects of rare species on transect scores.

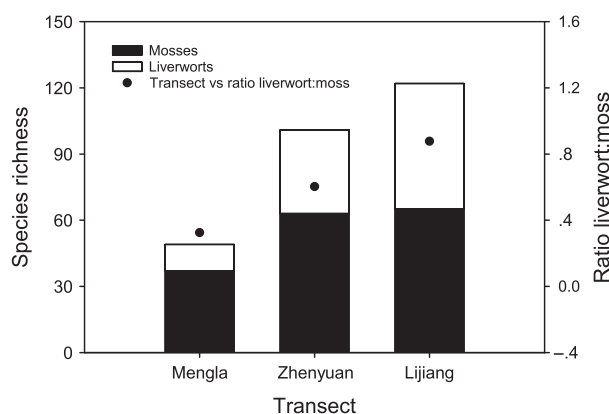
## Results

### Species composition

Protected forests in Yunnan harbour an abundant epiphytic bryo-flora. Overall bryophyte richness ranged from 0 to 16 species per subplot (20 cm × 20 cm) and from 0 to 38 per plot (20 m × 20 m). In total, 226 bryophyte species (140 mosses and 86 liverworts) belonging to 101 genera and 46 families were recorded (App. S1). The richest moss and liverwort families were Sematophyllaceae (21 species) and Plagiochilaceae (15 species; App. S1). In total, 99% of the epiphytic bryophyte species (224 species) was considered locally rare (Table 2). Of the locally rare species, species with narrow geographic range, low frequency and small population size accounted for 83.2%, 95.6% and 46.9% of the total number of species, respectively (Table 2). Interestingly, the ratio of the total number of liverwort species to the total number of moss species increased from 0.32 in the Mengla transect to 0.60 in the

**Table 2.** Local rarity analysis of bole bryophytes from the three altitudinal transects in Yunnan. Values are the number within the different categories with the corresponding percentages in parentheses.

	Geographic Range			
	Wide		Narrow	
	High Frequency	Low Frequency	High Frequency	Low Frequency
Population Size				
Somewhere Large	2 (0.9)	22 (9.7)	8 (3.5)	88 (38.9)
Everywhere Small	0 (0.0)	14 (6.2)	0 (0.0)	92 (40.7)



**Fig. 2.** Comparisons of species richness of mosses, liverworts and ratio of liverwort to moss species richness among the three altitudinal transects in Yunnan. Species richness per transect was pooled from twenty 20 m × 20 m plots.

Zhenyuan transect and 0.88 in the Lijiang transect (Fig. 2).

The three most common species recorded in the Mengla transect were *Sematophyllum subhumile* (C. Muell.) Fleisch. (relative frequency,  $R_{\text{fre}}$ : 15.9%, relative cover,  $R_{\text{cov}}$ : 32.0%), *Calymperes fasciculatum* Dozy et Molk. ( $R_{\text{fre}}$ : 11.3%,  $R_{\text{cov}}$ : 13.3%) and *Leucobryum chlorophyllosum* Müll. Hal. ( $R_{\text{fre}}$ : 13.3%,  $R_{\text{cov}}$ : 7.2%), while *Plagiochila assamica* Steph. ( $R_{\text{fre}}$ : 5.9%,  $R_{\text{cov}}$ : 20.1%), *Syrrhopodon gardneri* (Hook.) Schwaegr. ( $R_{\text{fre}}$ : 6.3%,  $R_{\text{cov}}$ : 11.0%) and *Homaliodendron flabellatum* (Sm.) Fleisch ( $R_{\text{fre}}$ : 8.0%,  $R_{\text{cov}}$ : 8.7%) were dominant species in the Zhenyuan transect (App. S1). In the Lijiang transect, dominant species included *Herbertus giraldianus* (Steph.) Nicholson ( $R_{\text{fre}}$ : 8.5%,  $R_{\text{cov}}$ : 22.9%), *Dicranodontium denudatum* (Brid.) Britt. ( $R_{\text{fre}}$ : 9.6%,  $R_{\text{cov}}$ : 12.3%) and *Orthotrichum ibukiense* Toyama ( $R_{\text{fre}}$ : 9.2%,  $R_{\text{cov}}$ : 9.7%).

### Life form composition

The Mengla transect was dominated by smooth mat bryophytes at all altitudes, except 800 m, which was

dominated by fan life forms. Fan was also the most common life form in the Zhenyuan transect, while turf bryophytes dominated the Lijiang transect (Fig. 3). In addition, the most dominant species at Mengla, *S. subhumile*, is a smooth mat bryophyte. Two of the three most dominant species in the Zhenyuan transect (*P. assamica* and *H. flabellatum*) are fan bryophytes, whereas all three most dominant species in the Lijiang transect (*H. giraldianus*, *D. denudatum* and *O. ibukiense*) are turf bryophytes (App. S1).

### Similarity

The bryophyte fauna of the Zhenyuan and Lijiang transects was most similar, whereas fauna of the Mengla and Lijiang transects were least similar (Table 3). Although different transects shared some species, epiphytic bryophyte species composition varied significantly between the transects (App. S1). This was clearly supported by the MDS-2D ordinations, which showed clear clustering of the plots within each of the three transects (Fig. 4).

### Diversity patterns

Nested ANOVA results indicated significant differences of bryophyte species richness among transects ( $F_{2,48} = 136.105$ ,  $P < 0.001$ ) and altitudes nested within transects ( $F_{9,48} = 3.525$ ,  $P = 0.002$ ). Both the Zhenyuan and Lijiang transects had significantly higher  $\alpha$ - and  $\gamma$ -diversity compared with the Mengla transect, whereas the latter had the

highest  $\beta$ -diversity (Table 4). Bryophyte species richness showed an increasing trend with increasing altitude, ranging between 800 and 2400 m, reached a mid-altitudinal peak at ca. 2600 m, and then declined at higher altitudes from 3200 to 3800 m (Fig. 5).

### Species composition and environmental variables

The CCA ordination of all sample plots and bryophyte species indicated that variation in the species composition of bryophytes was mainly explained by the transect locations and altitude, and partly by host characteristics such as bark roughness and DBH (Fig. 6).

## Discussion

### Abundant epiphytic bryophytes in Yunnan

In this study, 226 bryophyte species were recorded from 594 subplots of 20 cm × 20 cm on tree boles within 60 plots of 0.04 ha across the three protected forested areas in Yunnan. Similarly, in a study of tree bole communities in Central Sulawesi, Ariyanti et al. (2008) found 168 bryophyte species from 12 0.25 ha sites in three forest types. In another study in Réunion Island, Ah-Peng et al. (2012) recorded 265 bryophyte species from tree trunks along an altitudinal gradient across eight different vegetation types. In the Canary Islands, an inventory of 140 quadrats (each 625 cm<sup>2</sup>) on different substrates from three forest types along an altitudinal gradient yielded 86 bryophyte species

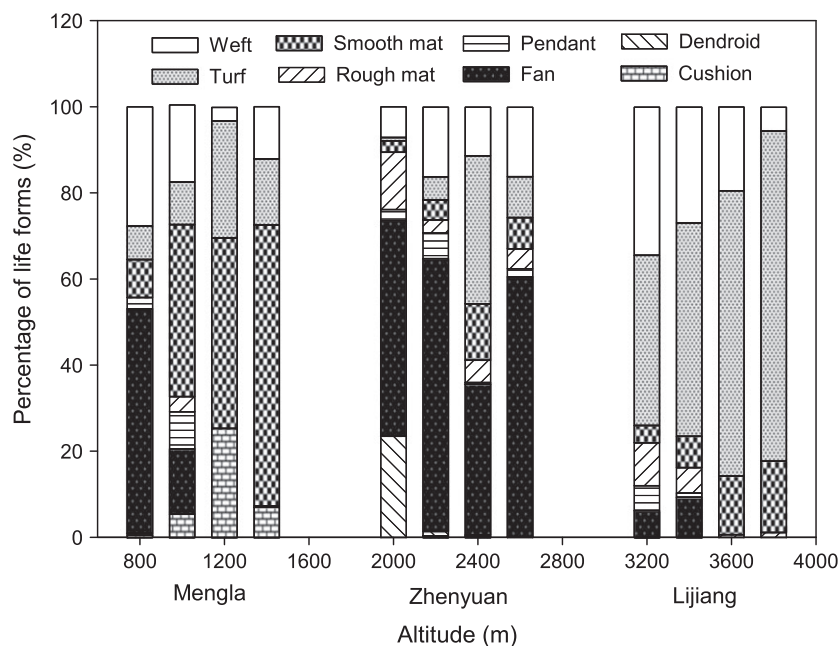


Fig. 3. Compositional patterns of bole bryophyte life forms across the three altitudinal transects in Yunnan.

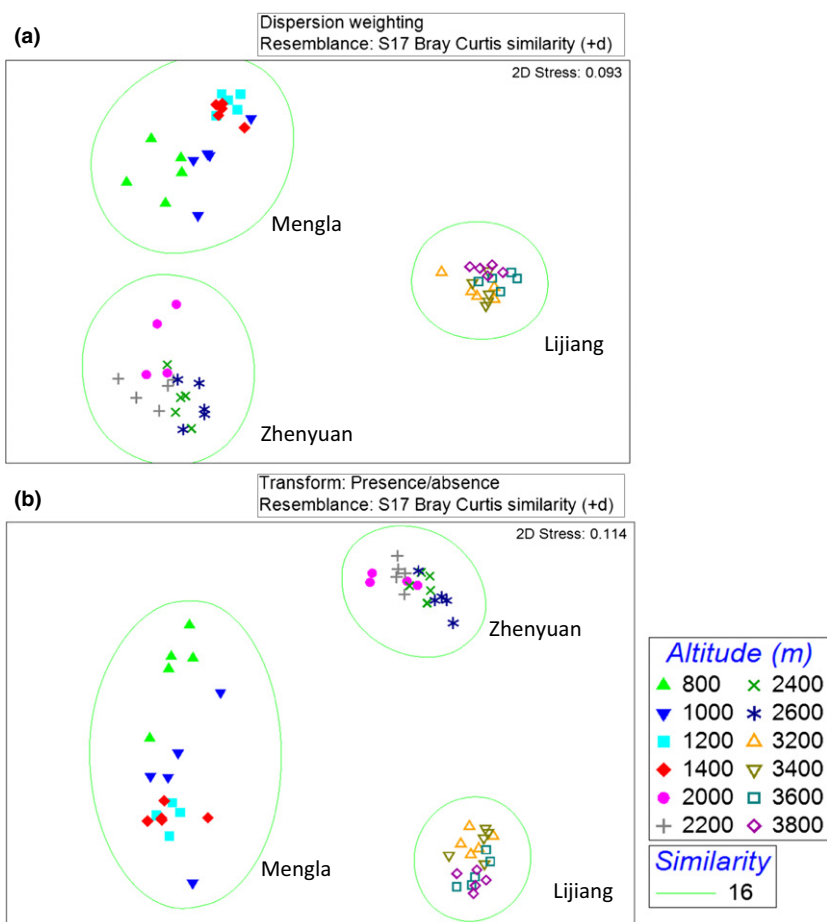
**Table 3.** Shared species (upper right) and Sørensen similarity index values (lower left) between the three altitudinal transects in Yunnan.

	Mengla	Zhenyuan	Lijiang
Number of Shared Species			
Mengla	–	15	10
Zhenyuan	0.201	–	28
Lijiang	0.118	0.250	–
Sørensen similarity index			

(González-Mancebo & Hernández-García 1996). In Costa Rican upper montane oak forests, a complete inventory of about 6 ha of forest yielded 206 bryophyte species (Holz et al. 2002). The species richness of epiphytic bryophytes in our study is among the highest ever reported for tropical and subtropical forests, and underlines the importance of the Yunnan region as a global biodiversity hotspot. Diverse terrain and moist climate mentioned in the section of 'Study area' are suggested to be the two major drivers of bryophyte diversity.

### Diversity patterns and drivers

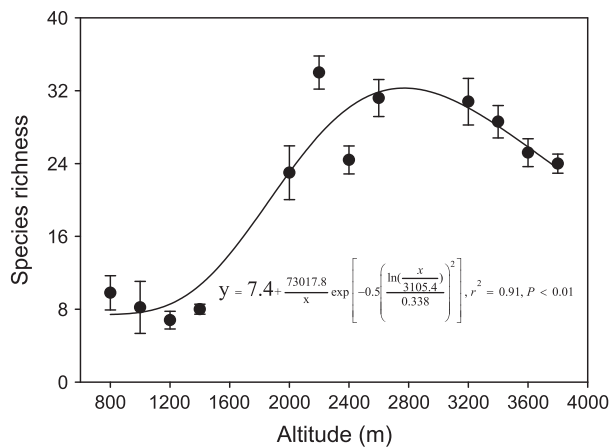
This is the first study to document epiphytic bryophyte communities in SW China across a wide geographical area from forests in sub-montane (Mengla, 21°35' N) Xishu-angbanna, montane (Zhenyuan, 24°16' N) Ailao Mountain and sub-alpine (Lijiang, 27°08' N) Jade Dragon Snow Mountain. Each of the three forested areas had a very distinctive epiphytic bryo-flora, although they shared some species. Bryophyte species richness was not significantly different between the Lijiang and Zhenyuan transects but was significantly lower in the Mengla transect (Table 4). The poor development of bryophytes at the low altitudes observed in this study confirmed the findings of Pócs (1980), Wolf (1993), Ah-Peng et al. (2007) and Bader et al. (2013). The Mengla transect, however, had the highest richness of tree species among the three transects, which, it could be suggested, might create more niches leading to increased diversity of bryophyte species. Nevertheless, other factors, including higher temperature,



**Fig. 4.** MDS-2D ordinations based on (a) bryophyte cover and (b) presence/absence data. We laid clusters over the MDS-2D ordination graph (indicated as green lines) to more clearly show the similarity of bryophyte communities from different transects. 'Similarity' in the box means resemblance level of clusters using S17 Bray-Curtis similarity (+d).

**Table 4.** Mean ( $\pm$ SE) values of  $\alpha$ -diversity components using multiple diversity indices across the three altitudinal transects in Yunnan, with summary results of ANOVA showing  $F$ - and  $P$ -values. Different letters indicate significant differences based on *post-hoc* tests ( $P < 0.05$ ).  $\beta$ - and  $\gamma$ -diversity for each transect are also shown.

	Study Transects			$F$	$P$ -value
	Mengla	Zhenyuan	Lijiang		
$\alpha$ -Diversity					
Species Richness	8.63 $\pm$ 0.78a	28.42 $\pm$ 1.49b	27.15 $\pm$ 1.04b	93.45	<0.001
Margalef Index	1.46 $\pm$ 0.16a	4.22 $\pm$ 0.22b	3.93 $\pm$ 0.14b	71.96	<0.001
Shannon–Weiner Index	0.70 $\pm$ 0.03a	0.83 $\pm$ 0.01b	0.86 $\pm$ 0.01b	19.22	<0.001
Simpson Index	2.05 $\pm$ 0.13a	3.20 $\pm$ 0.09b	3.42 $\pm$ 0.10b	45.85	<0.001
$\beta$ -Diversity	4.68	2.55	3.49		
$\gamma$ -Diversity	49	101	122		

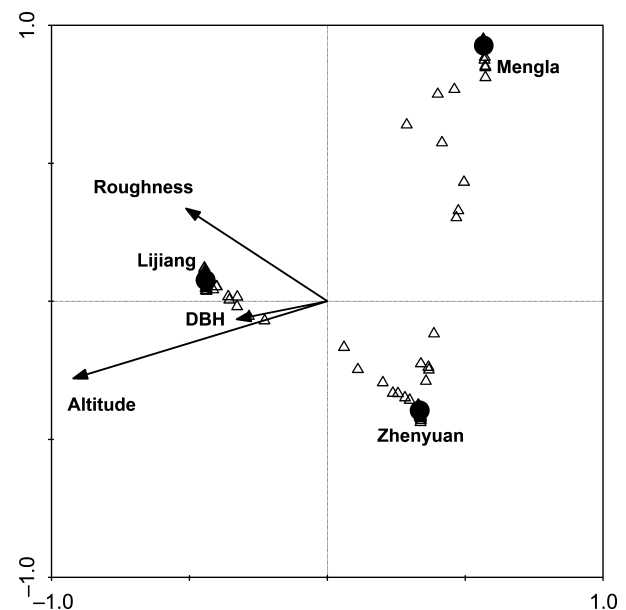


**Fig. 5.** Average ( $\pm$ SE) species richness of bole bryophytes along altitudinal gradients in Yunnan. Peak regression equation is also provided with  $r^2$  and  $P$ -values.

limited water availability and more frequent human disturbances (Table 1) may have limited development of diverse bryophyte communities in the Mengla transect.

Measurements of carbon exchange dependence on light, temperature and thallus water content, combined with modelling exercises such as moisture-dependent activity patterns during the day, indicate that net carbon gain may indeed be critically low in lower montane bryophyte species (Wagner et al. 2013). In sub-montane and lowland areas, high temperature causes high nocturnal respiration and, in combination with low diurnal carbon gain, this may result in a carbon budget imbalance for these bryophytes compared to those of montane areas. In addition, high temperature may lead to high evaporation rates, resulting in water stress to the carbon balance of bryophytes (Wagner et al. 2013). These together may exclude many montane bryophyte species from the warm lower altitudes (Richards 1984; Zotz 1999).

In addition to temperature, sub-montane and lowland areas are generally different from montane areas in



**Fig. 6.** CCA ordination: biplot of bryophyte species and environmental variables for the first two canonical axes (with eigenvalues in brackets). Cumulative percentage variance explained by the first two axes is 74.1%. Open triangles present different bryophyte species. Arrows refer to different environmental variables. Closed circles represent centroids of categorical variables (transect locations).

terms of precipitation patterns (Bader et al. 2013). While precipitation tends to occur as heavy showers in the lowlands, there are generally lighter and longer-lasting rains in montane areas with frequent occurrence of lateral precipitation from clouds and fog (Cavelier et al. 1996; Richards 1996). This creates markedly different conditions for poikilohydric organisms such as bryophytes. Bader et al. (2013) thus presented an alternative hypothesis based on the limited desiccation tolerance of montane species to explain the observed altitudinal pattern of bryophyte species richness, although their results failed to validate this hypothesis (Bader et al. 2013).



Our results on the altitudinal distribution of two different bryophyte life forms, however, provide support for Bader's hypothesis. Fan, a life form usually found in wet shady habitats (Bates 1998; Ma et al. 2009), is the most dominant life form in the montane forest (Zhenyuan). Smooth mat, a life form adapted to relatively dry conditions (Bates 1998), dominated in the sub-montane forests (Mengla). Moreover, the lower ratio of liverworts to mosses and the lower drought tolerance of liverworts further implies water stress in bryophytes of the sub-montane forests (Frahm & Ohlemüller 2001).

Host specificity of epiphytic bryophytes had been demonstrated in a large number of studies in various temperate and boreal regions (Barkman 1958; Studlar 1982; Kuusinen 1996). This phenomenon was observed in the tropical forests in this study, e.g. bryophyte species *Neckeropsis exserta* (Hook. ex Schwägr.) Broth. only occurred on *Parashorea chinensis* Wang Hsie. in the Mengla transect. Physico-chemical characteristics of hosts such as diameter (size), height, exposure, bark physical and chemical properties (e.g. bark roughness, bark pH) may explain the distribution and composition patterns of epiphytic bryophyte communities (Barkman 1958; Cornelissen & Steege 1989; González-Mancebo et al. 2003; Mota de Oliveira et al. 2009; Gradstein & Culmsee 2010; Song et al. 2011; de Oliveira & ter Steege 2013). To make samples from different transects and altitudes more comparable, epiphytic bryophytes were investigated at a similar height (ca. 1.5 m) and exposure (SW) for each tree in this study. The results suggested that host characteristics including bark roughness and DBH might directly affect diversity patterns (Fig. 6), while both stand age and forest type affect host characteristics and act on diversity patterns indirectly. Bark chemistry is another important factor that significantly influences diversity patterns of epiphytic bryophytes (Barkman 1958; Gustafsson & Eriksson 1995). In boreal forests, for example, unique and rich bryophyte communities are generally found on *Populus tremula*, which has relatively high bark pH compared with other host species (Kuusinen 1996). Unfortunately, we unable to record the bark pH of host trees.

In this study, epiphytic bryophytes exhibited a hump-shaped species richness pattern (Fig. 5), which is consistent with results of similar studies by Wolf (1993), Frahm & Ohlemüller (2001) and Ah-Peng et al. (2012). We suggest that water availability, the most important factor determining epiphytic bryophyte growth and diversity (Van Reenen & Gradstein 1983; Sillett & Antoine 2004; Song et al. 2012b), is the main factor that explains the mid-altitude peak, because peak richness coincided with the highest moisture levels in our study. The mid-altitudes (Zhenyuan) had the highest annual precipitation compared with the other two transects

(Table 1). In addition, Song et al. (2012b) reported a trend of increasing relative humidity from 2300 m to 2550 m in the montane moist evergreen broad-leaved forest in the Ailao Mountains. Bryophyte species richness peaked at ca. 2600 m, which matches the altitude with maximum water availability.

### Implications for conservation

Publications such as the European Red Data Book of Bryophytes have indicated the ecological importance of bryophytes and shown that conservation of these small plants deserves more attention (Vitt & Belland 1997). This study is the first assessment of species composition and diversity patterns of epiphytic bryophytes on a geographical scale in SW China, and provides fundamental data allowing an evaluation of biodiversity in Yunnan Province. In a previous study, it was reported that the number of bryophyte species in Yunnan as a whole reached ca. 1500 (Yang et al. 2004). The number of epiphytic bryophytes recorded in this study (226 species belonging to 101 genera, 46 families), therefore, accounts for about one-sixth of the Yunnan bryo-flora, and is close to the total number of tree species (246 species, Z.H. Sun & M. Cao, unpublished data) in the same study region. If we consider bryophytes that grow on tree branches, the forest floor and rocks, bryophyte species richness would probably be substantially higher. Forest bryophytes are suggested to be extremely sensitive to anthropogenic disturbance and could be used as potential indicators of forest quality and integrity (Frego 2007). The flourishing bryophyte communities on tree boles and the presence of large trees (Z.H. Sun & M. Cao, unpublished data) suggest that the three studied forest areas in Yunnan have generally been well protected, although lower bryophyte diversity in the Mengla transect indicates relatively poorer forest quality due to either unsuitable climatic conditions or human disturbance. Additionally, our results indicate that bryophytes are one of the key components of the Indo-Burma biodiversity hotspot, emphasizing their importance in biodiversity conservation.

In this study, we determined that almost all of the epiphytic bryophyte species (99%) were considered locally rare. Closer examination indicated that most of the locally rare species were those with low frequency (accounted for 95.6% of total species richness), which probably implied high habitat specificity of these species. These distribution patterns suggest that for bryophytes as a whole, special habitats may be more important than dispersal ability (Vitt & Belland 1997; Birks et al. 1998; Soderstrom & During 2005). This contrasts with the results of Laaka-Lindberg et al. (2000), who found that for some dioecious species,

rarity was strongly linked to low or absent sporophyte production, suggesting dispersal limitation. Rare bryophytes have recently attracted attention of conservationists and bryologists (Vitt & Belland 1997), such species being increasingly endangered due to either frequent human activities such as timber harvesting and the side effects of fossil fuel combustion, or local ecological and climatological fluctuations (Vellak et al. 2007). Considering the high percentage of locally rare species, their importance in maintaining biodiversity (Chapin et al. 2000; Lyons et al. 2005) and their high vulnerability to environmental changes, particular conservation attention should be paid to these organisms.

As large climatic variations occur within short geographic distances, altitudinal gradients provide a classical framework to study the relationship between species distribution and climate (Lloret & González-Mancebo 2011). Water availability and temperature are suggested to be two major drivers of the distributions of bole bryophytes along altitudinal gradients in these study areas. It has been suggested that bryophytes are threatened by climate changes, with higher water deficits associated with increasing temperatures, more frequent climatic extremes or reduced water inputs from clouds in tropical mountain forests (Still et al. 1999; IPCC 2007; Lloret & González-Mancebo 2011; Song et al. 2012b). The regional pattern of lower epiphytic bryophyte diversity in warmer, drier areas shown in this study suggests that epiphytic bryophytes in Yunnan are also sensitive to climate change. During the last four decades annual temperatures over the Yunnan Plateau have increased, while evapotranspiration rates and relative humidity have decreased (Fan et al. 2011; Fan & Thomas 2013). In accordance with a recent transplantation experiment in the same study region (Song et al. 2012b), our results reveal the imminent risk to epiphytic bryophyte communities of the emerging climate changes in Yunnan.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** List of bole bryophytes recorded in the three experimental transects in Yunnan, China.