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# Species richness and vertical stratification of epiphytic lichens in subtropical primary and secondary forests in southwest China

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## ABSTRACT

An entire-tree investigation was conducted in two primary and three secondary forest types in the subtropical Ailao Mountains of southwest China to determine whether species richness and vertical stratification of epiphytic lichens responded to forest type and host attributes. Lichen species number, composition and cover differed significantly among forest types and tree species, while tree diameter and tree height had a modest influence. Epiphytic lichen species and functional groups showed clear vertical stratification. Epiphytic lichens were richer in canopies than on trunks and exhibited a great preference for the intermediate zones of trees, while five lichen groups showed distinct vertical diversification. The stratification patterns are clearly related to forest type and may reflect the microclimatic requirements of individual species, e.g. light availability and humidity.

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## Introduction

Epiphytic lichens are a widespread and significant component of forest structure and play a vital role in biodiversity conservation, environmental monitoring and nutrient transformation in tropical, subtropical, temperate and boreal forests (Ellis, 2012; Li et al., 2013a,b; Sillett and Antoine, 2004; Wang et al., 2008). The distribution of epiphytic lichens varies based on horizontal and vertical gradients (Ellis, 2012;

Sillett and Antoine, 2004); however, while the horizontal distribution of lichens has received more attention (Ellis and Coppins, 2006; Hedenás and Ericson, 2000, 2004; Wolseley and Aguirre-Hudson, 1997), equivalent information on the vertical distribution patterns of epiphytic lichens remains rare.

The available evidence shows that the vertical stratification of non-vascular and vascular epiphytes is related to microhabitat gradients created by tree height; that is,

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temperature, light availability and wind speed increase from the tree base to the tip, while moisture and nutrient availability simultaneously decrease (Barkman, 1958; Johansson, 1974; Meinzer and Goldstein, 1996). Light availability is better than moisture in explaining the vertical distribution of epiphytes (Richards, 1996). Forest type (Acebey et al., 2003; Arévalo and Betancur, 2006; Cascante-Marín et al., 2006; Normann et al., 2010; ter Steege and Cornelissen, 1989) and host species (Ellyson and Sillett, 2003; Lyons et al., 2000; McCune et al., 1997; Pike et al., 1975; Williams and Sillett, 2007) also have important effects on epiphyte distribution. For example, the vertical patterns of epiphytes are affected by the canopy conditions among forest types (de Souza Werneck and do Espírito-Santo, 2002).

Species richness of epiphytic lichens increases with tree height in various forest ecosystems (Fritz, 2009; Normann et al., 2010; Sillett and Rambo, 2000; Williams and Sillett, 2007). Moreover, lichen functional groups exhibit a strong preference for specific vertical zones, which can occur at different heights and locations in diverse forests and reflect the sensitivity of epiphytes to desiccation and excessive irradiation (Barkman, 1958; McCune, 1993). For example, cyanolichens prefer the basal and more humid part of trunks in aspen stands (Ellis and Coppins, 2006; Hedenås and Ericson, 2000, 2004), whereas they are most abundant in middle/upper zones in old-growth conifer forests (Ellyson and Sillett, 2003; Lyons et al., 2000; McCune, 1993; McCune et al., 1997; Sillett and Rambo, 2000). Fruticose lichens with green algae are generally restricted to higher zones or open forests, in accordance with their well-known tolerance to high light intensities (Barkman, 1958; Hale, 1967). To date, the majority of the few, limited studies addressing the vertical distribution of epiphytic lichens have been conducted in tropical forests (Cornelissen and ter Steege, 1989; Komposch and Hafellner, 2000; Normann et al., 2010), cool temperate rainforests (Ford et al., 2000; Jarman and Kantvilas, 1995) and coniferous forests (Ellyson and Sillett, 2003; Lyons et al., 2000; McCune et al., 1997; Sillett and Rambo, 2000; Williams and Sillett, 2007). In the southwestern subtropics of China, little quantitative information is available on the vertical distribution of epiphytic lichens, despite the high number of species present (Li et al., 2013b). An interesting, unanswered question remains: do epiphytic lichens exhibit similar patterns in vertical stratification within the diverse ecosystems that make up broad-leaved evergreen subtropical forests?

In subtropical China, epiphytes have received little attention and are largely ignored in forest protection and management (Li et al., 2013b). Now, epiphytic lichens are receiving increasing attention in some subtropical forests, but the available data are still too limited in this field. While epiphytic lichens have been studied among the primary and secondary forests of the Ailao Mountains, a major feature of southwestern China (Li et al., 2007, 2011, 2013a,b), very little is known about their vertical stratification. In the Ailao Mountains, trees are frequently blown down during the wet-dry transition period. Newly fallen trees (treefalls) can offer an opportunity to study epiphytic lichens along the entire tree, as has been done previously (Aptroot, 2001; Fritz, 2009; Jarman and Kantvilas, 1995; Milne and Louwhoff, 1999). In the present study, the vertical stratification of epiphytic lichens was

analyzed in two primary and three secondary forests in the Ailao Mountains, based on the combined surveying of recent treefalls and standing living trees. Our study specifically addresses two questions: (1) how do epiphytic lichen species and functional groups change with tree height in subtropical forests? and (2) how do forest type, host species, height and diameter influence their stratification?

## Methods

### Study area

The study was conducted in the Xujiaba region (2 000–2 750 m a.s.l.), a core area of the Ailao Mountains National Nature Reserve in south central Yunnan (23°35′–24°44′ N, 100°54′–101°30′ E), China. The mountain range is part of the Indo-Burma biodiversity hotspot (Myers et al., 2000). The National Nature Reserve, with an area of 677 km<sup>2</sup>, forms one of the largest tracts of natural evergreen broad-leaved forest in China (Zhu and Yan, 2009). The core area covers 5 100 ha on the northern crest of the Ailao Mountains, and the forest landscape is characterized by an extensive area of continuous primary forests (84.6 % of the total area), archipelagos of small secondary forest fragments (<16 %) and high forest connectivity (Li et al., 2013b; You, 1983). The forests have been protected since the foundation of the reserve, and branch and trunk surfaces of trees are occupied by more than 600 epiphytic species (Li et al., 2013b). The mean annual precipitation is 1 947 mm, with 85 % falling in the rainy season from May to Oct.. The annual mean temperature is 11.3 °C, and the mean relative humidity is 85 % (Li et al., 2011). Details of the meteorology and forest structure can be found in Li et al. (2013a,b) and Ma et al. (2009).

### Sampling method

Five forest types were studied: primary *Lithocarpus* forest (also called primary montane moist evergreen broad-leaved forest, PLF), primary dwarf mossy forest (PDMF), middle-aged oak secondary forest (MOSF), *Populus bonatii* secondary forest (PBSF) and *Ternstroemia gymnanthera* secondary forest (TGSF). Fieldwork was relatively easy to carry out in these forests owing to tree architecture and surrounding topography. Based on data for lichens on different host species (Li et al., 2007, 2013a), only dominant tree species, which hosted typical lichen species assemblages and/or had relatively abundant lichen species within each forest type, were selected for sampling (Table 1). In particular, nine additional trees of various species were also sampled to represent the other co-dominant tree species in the PLF.

Fieldwork was conducted between April 2009 and Dec. 2010. To ensure that collected epiphytic lichens were representative of the community, two sampling methods were used to examine the vertical distribution of epiphytic lichens. Firstly, newly fallen trees, which were blown down by intense wind events during the wet-dry season transition (April–May and Oct.–Nov. in 2009–2010), were selected. Most of them had not fallen completely to the ground. The treefalls were accessible for lichen surveying and offered the opportunity to

**Table 1 – Description of sampled trees in five forest types in the Ailao Mountains, southwest China**

Forest type	Sample method and tree number	Tree species	Diameter (cm, range)	Height (m, range)
PDMF	Climbing (14)	<i>Lithocarpus crassifolius</i> (7)	15.7 (12.8–20.4)	4.7 (4.0–5.0)
		<i>Rhododendron irroratum</i> (7)	14.7 (8.9–20.2)	5.1 (5.0–6.0)
PLF	Treefall (28)	<i>Lithocarpus hancei</i> (9)	45.2 (12.1–122.5)	17.4 (8.0–24.0)
		<i>Ilex corallina</i> (5)	19.2 (6.5–28.3)	12.4 (8.0–16.0)
		<i>Vaccinium duclouxii</i> (5)	15.9 (10.2–21.5)	11.0 (9.0–13.0)
		Others (9)	24.0 (14.4–62.4)	15.9 (10.0–24.0)
MOSF	Climbing (14)	<i>Lithocarpus hancei</i> (7)	15.6 (11.1–20.5)	8.0 (8.0–8.0)
		<i>Vaccinium duclouxii</i> (7)	10.6 (6.5–14.0)	7.0 (6.0–8.0)
PBSF	Treefall (10)	<i>Populus bonatii</i> (10)	11.9 (5.8–25.4)	8.2 (5.0–16.0)
TGSF	Climbing (7)	<i>Ternstroemia gymnanthera</i> (7)	4.9 (2.7–6.8)	3.9 (3.0–5.0)

study epiphytes along the entire tree (Aptroot, 2001; Fritz, 2009; Jarman and Kantvilas, 1995; Milne and Louwhoff, 1999), e.g. in the PLF and the PBSF, in which treefalls often occurred. Secondly, standing living trees of low-canopy forests were accessed using an extendable aluminum ladder or by free-climbing, e.g. in the PDMF, the MOSF and the TGSF, whose few treefalls were found. In each forest type, the distance between the sampled hosts was greater than 50 m, and each host served as one survey unit. Based on the situation of fallen trees and species richness of lichens on different tree species in five forest types, 5–10 treefalls of each host species were sampled in the PLF and PBSF, and 7 trees of each host species in other three forests. A total of 73 trees were sampled (Table 1). For each tree, the diameter at breast height (dbh), height and species were recorded.

Each tree was divided into 2-m segments (absolute height), and the basal trunk (0–2 m) was further divided into three height intervals (0–0.5, 0.5–1.3 and 1.3–2 m) for comparative studies, as has been done previously (Li et al., 2013a). Branches were counted to determine the number of sampled branches (usually 1–6, accounting for 30–100 % of the total branches) in each segment.

Based on the segment division and tree architecture (tree height, trunk length and canopy structure), each tree was also schematically divided into six vertical zones (relative height): (I) basal trunk, (IIa) lower trunk, (IIb) upper trunk, (IIIa) lower canopy, (IIIb) middle canopy and (IIIc) upper canopy, designed to correspond to natural zones of environmental conditions (modified from Cornelissen and ter Steege, 1989; Johansson, 1974). Because some trunks and canopies were less than 2 m tall, six division zones were not necessary and their schematic stratification was, therefore, less.

Epiphytic lichen species were divided into five functional groups according to growth form and photobiont: crustose lichens (CRL), cyanolichens (CYL), fruticose lichens (FRL), broadly-lobed foliose lichens with green algae (BFL) and narrowly-lobed foliose lichens with green algae (NFL) (Li et al., 2013a; McCune, 1993; Nimis and Martellos, 2008).

On each segment, the presence/absence of lichen species on trunks and branches was recorded, and one 20-cm-long cylindrat was placed at the midpoint of the trunk and/or was randomly located on each sampled branch. The cylindrat size varied depending on the stem/branch diameter. The cover of each lichen species was estimated in each cylindrat; the data were then transformed to percentage values to reduce sampling errors associated with cylindrat size. Moreover, in

stranding trees, branches that were difficult to access directly (mostly zones IIIb and IIIc), were carefully removed and lowered to the ground for lichen sampling. To capture the maximum possible richness, a lichen survey was performed at each segment until no additional species were found within 10–20 min. The time spent on each tree was 4–20 hr, based on the tree size and lichen species richness. Vouchers were deposited in the laboratory of the Kunming Division of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Lichen species taxonomy followed Li et al. (2013b, see Appendix 2).

#### Data analysis

Species accumulation curves were created so that expected species richness could be determined to assess whether cumulative lichen richness differed among forest types (Colwell et al., 2004). In each forest type, species number and cover of epiphytic lichens and their average values in each segment were calculated for the same segments at the whole tree level. For each lichen functional group, the absolute values and the percent contribution to total species richness and cover were considered in each vertical zone.

One-way ANOVA was carried out to test differences in both lichen cover and species number among forest types and among host species. A multiple Tukey's HSD test was applied when significant differences were found. Before the analysis, all data were checked for normality and homogeneity of variance using Shapiro–Wilk and Bartlett's tests, respectively. When these assumptions could not be satisfied after transformation, a non-parametric Kruskal–Wallis rank-sum test followed by a Wilcoxon rank-sum test was carried out.

Two generalized linear models (GLMs) were used to analyze correlations between lichen species number and tree characteristics (height and dbh): a GLM with a logarithmic link function and Poisson distribution of errors and a GLM with an identity link function (linear regression model). The correlations between lichen cover and host characteristics, and the interaction between host height and dbh were calculated with a GLM with an identity link function. Because the  $R^2$  is not applicable in GLMs, an adjusted pseudo- $R^2$  measure ( $R^2_{\text{dev.}} = 1 - [(\text{Residual deviance} + k/2)/\text{Null deviance}]$ , where  $k$  is the number of variables in the model) was used to compare the different models (Mittlböck and Waldhör, 2000).

Additionally, nonmetric multidimensional scaling (NMDS) based on Bray–Curtis distance index was performed with the

metaMDS function in the package *vegan* (Oksanen et al., 2014) to estimate lichen species similarities among tree species and among vertical zones. Stress values lower than 20 % generally lead to usable interpretations.

The similarity in lichen composition among vertical zones in five forest types was also visualized using a cluster dendrogram. Bray–Curtis Similarity Coefficient and average linkage clustering (UPGMA) were used to reduce distortion in the initial matrix for the generation of the dendrogram. This analysis was realized using the *hclust* function in *vegan* (Oksanen et al., 2014).

Statistical analyses were implemented using the R 2.15.3 statistical package (R Development Core Team, 2014).

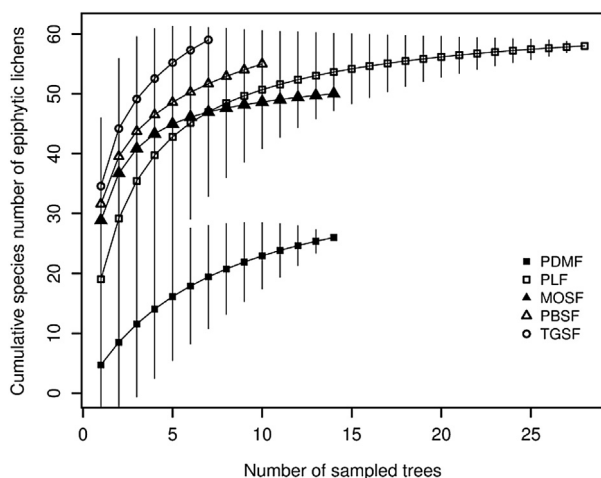
## Results

### Species richness, cover and composition

A total of 77 epiphytic lichen species were recorded on 73 entire trees in five forest types (Appendix A). Fifty-nine species occurred in the TGSF, followed by the PLF (58), the PBSF (55), the MOSF (50) and the PDMF (26). Species-accumulation curves showed similar results for lichen species; however, species richness was far from being completely recorded in the TGSF (Fig 1).

At the tree level, epiphytic lichen species number (Kruskal–Wallis  $\chi^2 = 34.17$ ,  $df = 4$ ,  $P < 0.001$ ) and cover ( $\chi^2 = 54.76$ ,  $df = 4$ ,  $P < 0.001$ ) differed significantly among forest types. Secondary forests had more species and higher cover, while the PDMF had the lowest values (Fig 2A and C).

Similarly, lichen species number ( $\chi^2 = 54.59$ ,  $df = 7$ ,  $P < 0.001$ ) and cover per tree ( $\chi^2 = 55.97$ ,  $df = 7$ ,  $P < 0.001$ ) varied significantly among host species. *Lithocarpus hancei* hosted the highest species number and *P. bonatii* had the greatest coverage, whereas *Rhododendron irroratum* had the lowest values (Appendix A; Fig 2B and D). Moreover, the NMDS ordination showed distinct lichen assemblages on different host species (Fig 3).



**Fig 1** – Species accumulation curves for epiphytic lichens in five forest types in the Ailao Mountains, southwest China. The vertical lines show standard deviations.

For all hosts, lichen species number had positive and significant correlations with host dbh and height, while lichen cover was negatively correlated with host dbh and height (Table 2). For each tree species, significant correlations between lichen distribution and tree characteristics were only found on *Lithocarpus crassifolius*, *L. hancei*, others and *Vaccinium duclouxii*. The interactions between host dbh and height were significant for total trees, *L. crassifolius* and *V. duclouxii*.

### Vertical distribution among height segments

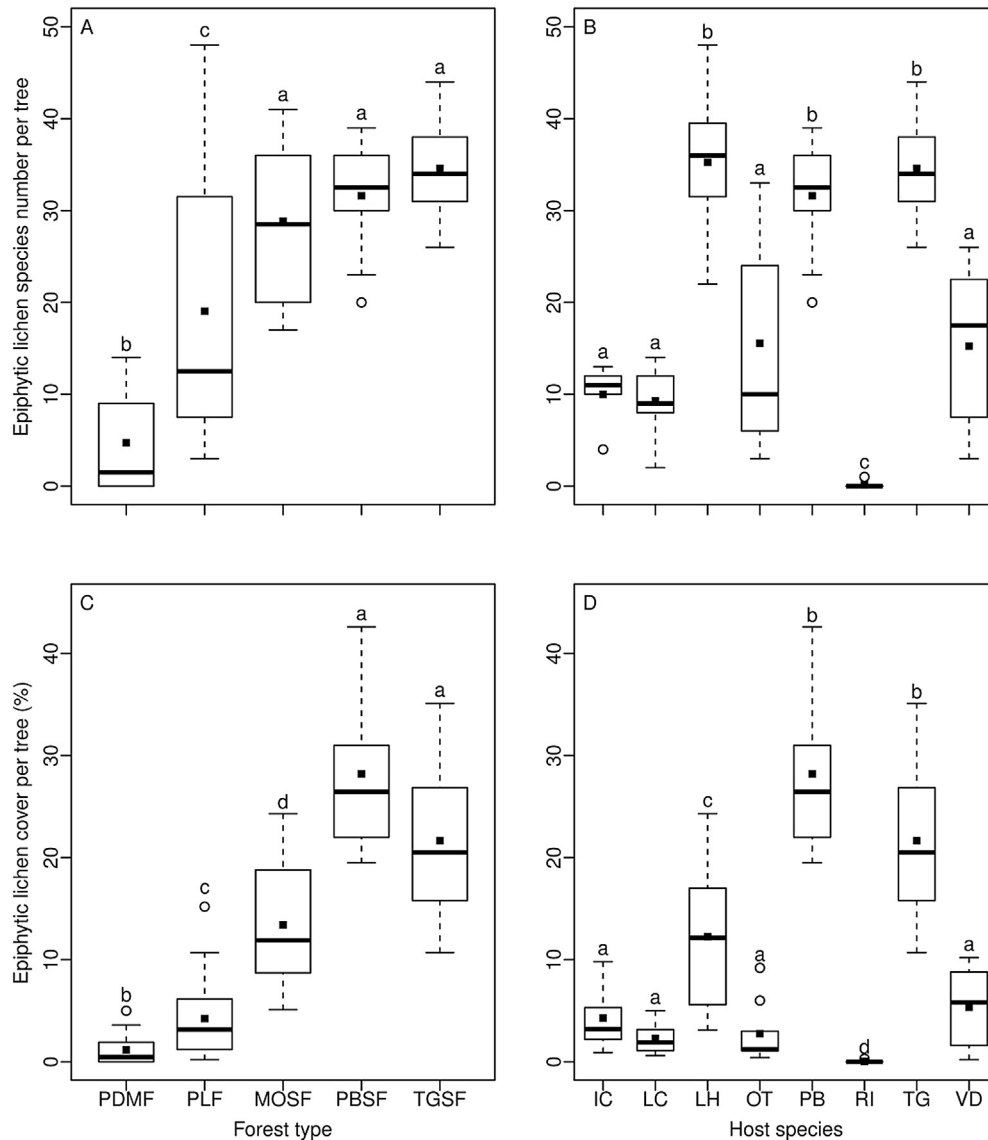
The distribution pattern of epiphytic lichens, in terms of total species number, mean species number and cover, along the tree height differed among forest types (Fig 4). In the PDMF, the richest segment was 2–4 m and almost all lichen species occurred in this segment, while no species were found at 0–1.3 m. In the PLF, lichen abundance tended to increase with tree height, and was the most pronounced for the mean species number and cover. The total number remained constant above 6 m. In the MOSF, the total, mean species number and cover of epiphytic lichens were highest at 4, 6 and 8 m, respectively. In the PBSF, higher values occurred at 2–14 m. In the TGSF, 1.3–2 m was the richest segment. In the three secondary forests, 0–2 m also supported higher lichen species number and cover.

### Vertical distribution among vertical zones

Species number and cover of epiphytic lichens differed considerably among vertical zones within forests. Canopies were richer in lichen species and cover than trunks in all studied forests (Fig 5). IIIa was the species-richest zone in most forests, but slightly lower than IIIb in the PLF. The species-poorest zone was I in the PLF and PBSF, IIa in the PDMF and MOSF, and IIIc in the PBSF and TGSF. Lichen cover seemed to exhibit similar patterns. However, cluster analysis (Fig 6) and NMDS (Appendix B) also indicated that variation in species composition tended to be more influenced by forest type than by vertical zone.

For lichen functional groups, species number was stratified vertically within forests (Fig 5A and B). The broadly-lobed foliose group first increased and then decreased with height, with the highest value in the PLF and the MOSF observed in zones IIIb (10) and IIIa (8), respectively. The crustose group was more frequent in zones IIIa–IIIc in primary forests, while it remained constant in different zones in secondary forests. The species number of cyanolichens remained relatively constant (5–8) with tree height in the PLF, while they were found at higher frequencies in zones I (6) and IIIa (8) in the MOSF and I–IIIa (11–12) in the PBSF. The fruticose group was most abundant in zones IIIa–IIIc of the PLF (5–6) and MOSF (4–6), IIa–IIIb (6–8) of the PBSF and I (4) of the TGSF. Species of the narrowly-lobed foliose group were often richer in zones IIIa–IIIc (6–18). The cover of each lichen group also showed similar patterns. In particular, the cover of fruticose lichens increased greatly from the tree base (0.87 %) to the tip (16.30 %) in the PBSF.

The vertical pattern of the changes in the percentage of each lichen group at any particular zone also differed among forest types (Fig 5C and D). The percent richness of the



**Fig 2 – Species richness and cover per tree of epiphytic lichens on eight host species in five forest types in the Ailao Mountains, southwest China. Different letters with bars represent significant differences ( $P < 0.05$ ). The “■” inside the box symbolizes the mean value. IC: *Ilex corallina*, LC: *Lithocarpus crassifolius*, LH: *Lithocarpus hancei*, OT: Others, PB: *Populus bonatii*, RI: *Rhododendron irroratum*, TG: *Ternstroemia gymnanthera*, VD: *Vaccinium duclouxii*.**

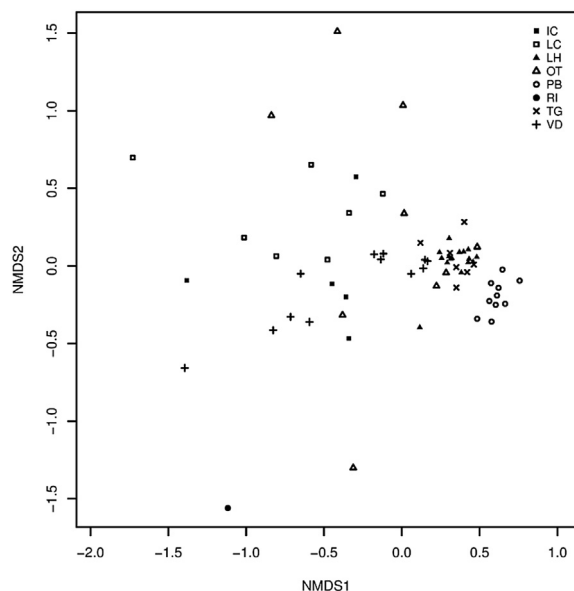
broadly-lobed foliose group increased from 7.69 % in zone I to 18.31 % in IIIc in the PLF and from 10.81 % to 18.92 % in the PBSF, while the crustose group decreased with increasing tree height from 30.77 % to 20.41 % in the PLF and from 28.26 % to 25.00 % in the TGSF. Cyanolichens also decreased with height in the PLF (from 38.46 % to 16.33%) and the PBSF (from 32.43 % to 16.22 %) and were higher in zones I (18.18 %) and IIIa (16.33 %) in the MOSF. The fruticose group had higher percentages in all zones but I in the PLF (10.20–12.50 %) and the MOSF (10.00–15.79 %). The change of the richness contribution of the narrowly-lobed foliose group was similar to the change of its species richness with tree height. For cover contribution, the broadly-lobed foliose group increased with height from 1.86 % to 26.45 % in the PLF and decreased from 46.77 % to 14.91 % in the PBSF and from 37.86 % to 14.52 % in the TGSF. The cover contribution of the crustose group

decreased with height in the PLF (from 86.56 % to 14.34 %) and the MOSF (from 30.06 % to 13.66 %). The variations of the cyanolichens and narrowly-lobed foliose group were similar to those of their respective richness contribution. The cover contribution of the fruticose group increased from 0 to 13.18 % in the PLF and from 5.78 % to 38.28 % in the PBSF.

## Discussion

### Species richness and composition

Our first entire-tree survey for epiphytic lichens in the subtropical forests in southwest China showed that the PLF and three secondary forests had more abundant lichen flora, in terms of species richness and cover, while the PDMF had the



**Fig 3 – Similarity of epiphytic lichen species on 73 trees in five forest types in the Ailao Mountains, southwest China. Two-dimensional scatterplot of NMDS based on Bray–Curtis distance index (stress = 14.5 %).**

lowest values. The results agree with our earlier studies on the horizontal distribution of lichens in this area (Li et al., 2013a,b), which may be the result of a combination of habitat variables. The lowest lichen richness of the PMDF may be due in part to its higher elevation, while epiphytic lichens of

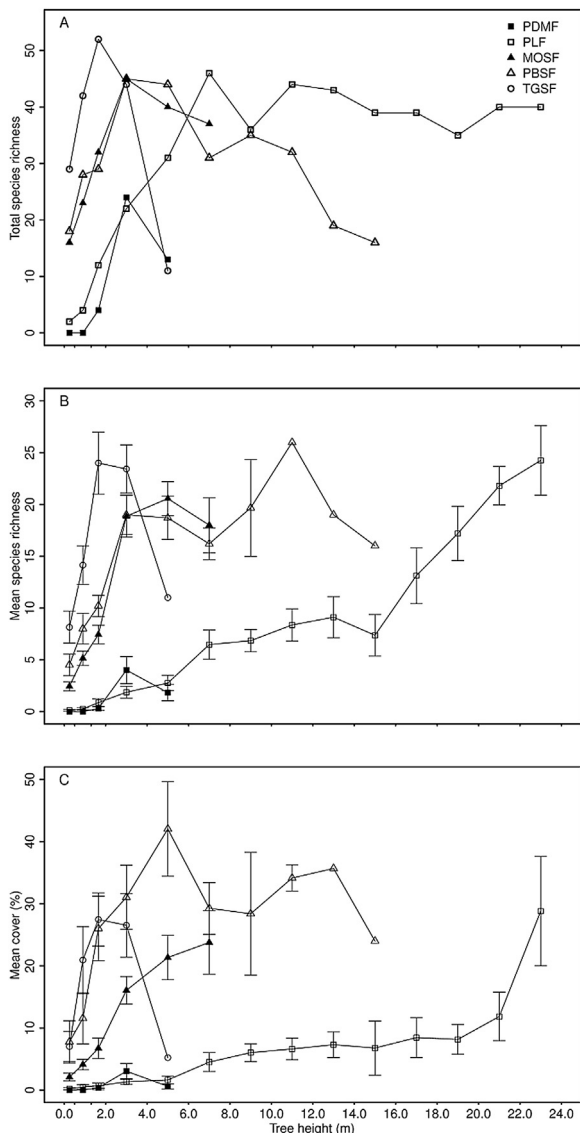
secondary forests benefit from landscape characteristics such as extensive primary forests, small secondary forest fragments and high forest connectivity (Li et al., 2011, 2013a,b).

This study emphasized the importance of host species on the coverage, species richness and composition of epiphytic lichens, agreeing with previous observations in temperate and boreal forests (Ellis, 2012; Juriado et al., 2003). Variations in the characteristics of host species are likely to affect the distribution of epiphytic lichens (Sillett and Antoine, 2004). The dominant trees *L. hancei*, *P. bonatii* and *T. gymnanthera* supported an abundant lichen flora, indicating that these tree species make an important contribution to the lichen flora in subtropical forests (Li et al., 2011, 2013a,b). In contrast, the low number of lichen species found in the PMDF may reflect the small contribution of the dominant trees *L. crassifolius* and *R. irroratum* to the lichen flora (Li et al., 2013b). The tree-level lichen distribution on *L. hancei* and *V. duclouxii* in the PLF and the MOSF also shows that the influence of forest type on the lichen community cannot be ignored. Additionally, the whole-tree lichen richness in our study was considerably lower than that found on *Sequoia sempervirens* (183 species, Williams and Sillett, 2007) and fallen *Elaeocarpus* sp. (173 species, Aptroot, 2001), similar to that on fallen *Lagarostrobos franklinii* (76 species, Jarman and Kantvilas, 1995), *Picea sitchensis* (72 species, Ellyson and Sillett, 2003) and *Fagus sylvatica* (76 species, Fritz, 2009), and higher than that on fallen *Nothofagus cunninghamii* (36 species, Milne and Louwhoff, 1999) and *P. sitchensis* (39 species, Coote et al., 2007).

In common with our earlier studies (Li et al., 2011, 2013a,b) and in contrast to studies in temperate and boreal regions (Ellis, 2012; McMullin et al., 2010; Ranius et al., 2008; Rogers and Ryel, 2008), host diameter and height had a minor influence on epiphytic lichens in the subtropical forests. The

**Table 2 – Relationship between tree characteristics and species number and cover of epiphytic lichens in the Ailao Mountains, southwest China.  $R^2_{adj}$  values are from GLMs with an identity link function and  $R^2_{dev}$  from GLMs with logarithmic link function and Poisson distribution of errors. ns: not significant; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . (+): positive trend; (–): negative trend**

		Lichen species number			Lichen cover		
		Dbh	Height	Dbh × height	Dbh	Height	Dbh × height
Total	$R^2_{adj}$	ns	ns	0.148**	0.059* (–)	0.055* (–)	0.202***
	$R^2_{dev}$	0.031*** (+)	0.033*** (+)				
<i>Ilex corallina</i>	$R^2_{adj}$	ns	ns	ns	ns	ns	ns
	$R^2_{dev}$	ns	ns				
<i>Lithocarpus crassifolius</i>	$R^2_{adj}$	ns	ns	0.806*	ns	ns	ns
	$R^2_{dev}$	0.332* (–)	ns				
<i>Lithocarpus hancei</i>	$R^2_{adj}$	ns	ns	ns	0.261* (–)	0.407** (–)	ns
	$R^2_{dev}$	ns	ns				
Others	$R^2_{adj}$	ns	ns	ns	ns	ns	ns
	$R^2_{dev}$	0.185*** (+)	0.178*** (+)				
<i>Populus bonatii</i>	$R^2_{adj}$	ns	ns	ns	ns	ns	ns
	$R^2_{dev}$	ns	ns				
<i>Rhododendron irroratum</i>	$R^2_{adj}$	ns	ns	ns	ns	ns	ns
	$R^2_{dev}$	ns	ns				
<i>Ternstroemia gymnanthera</i>	$R^2_{adj}$	ns	ns	ns	ns	ns	ns
	$R^2_{dev}$	ns	ns				
<i>Vaccinium duclouxii</i>	$R^2_{adj}$	ns	0.575** (–)	0.671**	ns	0.611** (–)	0.598*
	$R^2_{dev}$	0.135** (–)	0.616*** (–)				



**Fig 4 – Total, mean species number and mean cover of epiphytic lichens at each height segment in five forest types in the Ailao Mountains, southwest China.**

importance of host size was generally considered to be largely weakened by the landscape characteristics, which can also promote the establishment of lichens on young trees and in secondary forests in this area (Li et al., 2011, 2013a,b). Alternatively, these primary forests generally have small average tree diameters, although they thrive over periods of hundreds of years (You, 1983). However, host size still plays an important role for epiphytic lichens on some tree species in this area, e.g. *V. duclouxii*.

#### Vertical distribution of epiphytic lichen species

In the present study, lichen species number and cover tended to increase from the tree base to the tip in the PLF, while they first increased (up to different heights) and then decreased in the other forests. These results seem much more likely to reflect the general vertical patterns of epiphytes because

similar observations have been found for tracheophytes (Arévalo and Betancur, 2006; Cascante-Marín et al., 2006; ter Steege and Cornelissen, 1989), lichens (Normann et al., 2010) and bryophytes (Acebey et al., 2003) in the tropics. These differences among forest types are correlated with habitat conditions, e.g. canopy openness (de Souza Werneck and do Espírito-Santo, 2002). For example, the PLF represents the extreme of the closed canopies of the studied forests, resulting in very low light availability under the upper canopies, while other forests have more open canopies (Li et al., 2013a).

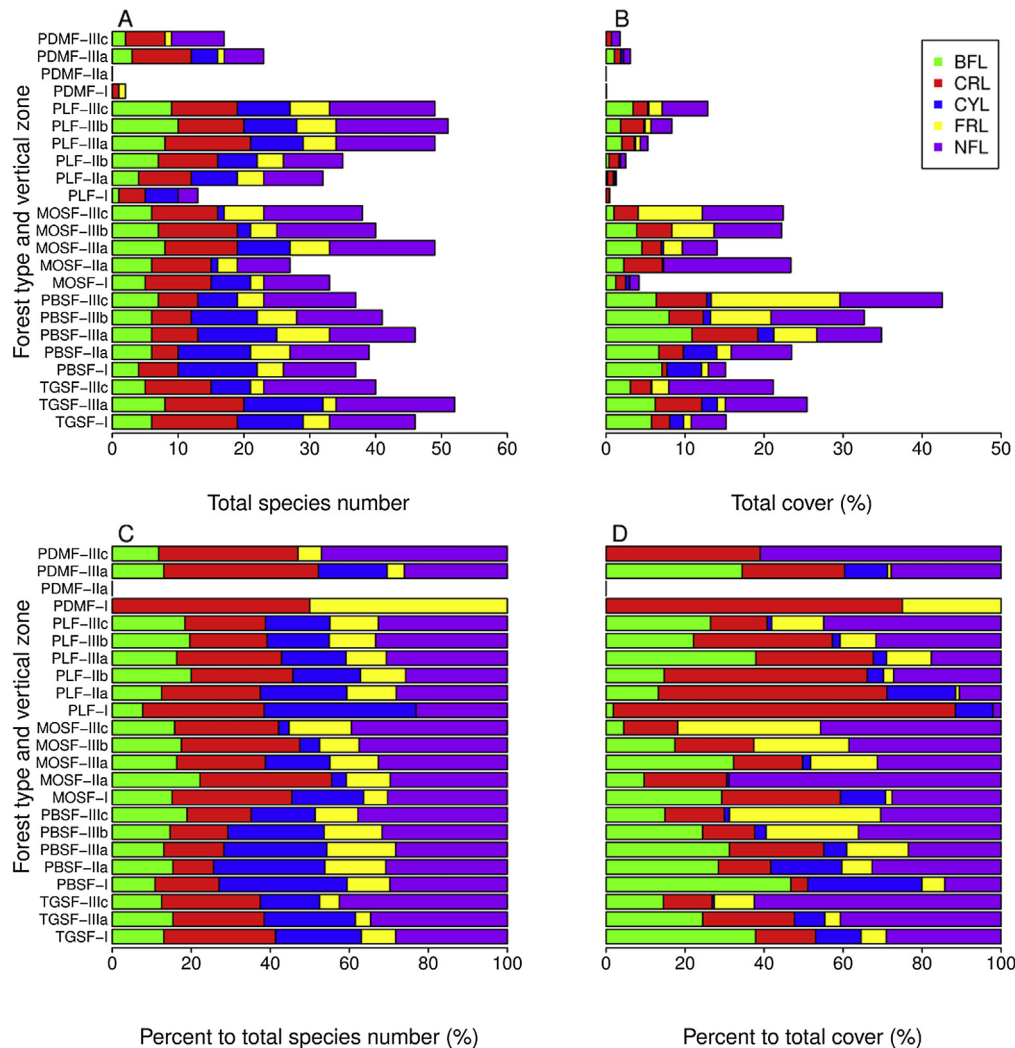
Epiphytic lichens showed specific vertical stratification both along the absolute and relative heights in subtropical forests. The vertical pattern in the PLF was similar to those on Sitka spruce (Coote et al., 2007; Ellyson and Sillett, 2003) and myrtle beech (Milne and Louwhoff, 1999). This pattern is likely to be strongly related to microclimatic gradients, with increasing light intensity, wind speed and temperature as well as decreasing humidity from the floor to the canopy (Barkman, 1958; Johansson, 1974; Krömer et al., 2007; Schneider and Schmitt, 2011). Considering that epiphytic lichens are well adapted to variable humidity conditions (Barkman, 1958; Li et al., 2013a; Richards, 1996), light availability appeared to be a more important driver than other factors in this region. The variations of bark quality and epiphyte flora associated with tree height may also cause changes in the distribution of epiphytic lichens (Kermit and Gauslaa, 2001; McCune, 1993). In the PDMF, the variations among height segments were not clear, presumably because this forest type had the lowest number of lichen species at tree level. When this was considered in combination with the vertical zone, however, a clear zonation was discovered.

In particular, epiphytic lichens exhibited a great preference for the intermediate vertical zones, e.g. the zone IIIb in the high-canopy PLF and IIIa in other low-canopy forests, reflecting the similar microenvironments in those zones. Other reports have corroborated this finding for vascular epiphytes (de Souza Werneck and do Espírito-Santo, 2002) and epiphytic bryophytes (Acebey et al., 2003). The intermediate zones were preferred partly because these zones have less direct and higher sunlight intensity, more variable humidity as well as higher temperature, and provide more appropriate microhabitats for the colonization of epiphytes (Coote et al., 2007).

By contrast, epiphytic lichens do poorly on tree bases in the PLF because of the limitations caused by low-light conditions (Barkman, 1958; Li et al., 2013a). Instead, the more open canopies allow more sunlight to penetrate the crowns and result in the relatively higher tree-base lichen richness in secondary forests (Li et al., 2013a,b). Similar results have been found in tropical forests by Cornelissen and ter Steege (1989) and Normann et al. (2010). In particular, lichen richness decreased noticeably in the utmost tip of trees in the PBSF and TGFSF, mainly as a direct consequence of the smallest number (only one) of sampling segments.

#### Vertical distribution of epiphytic lichen groups

In our study, five functional groups of epiphytic lichens showed distinct vertical stratification, which presumably



**Fig 5 – Species richness and cover and their percentages in total of five epiphytic lichen groups in vertical zones of five forest types in the Ailao Mountains, southwest China.**

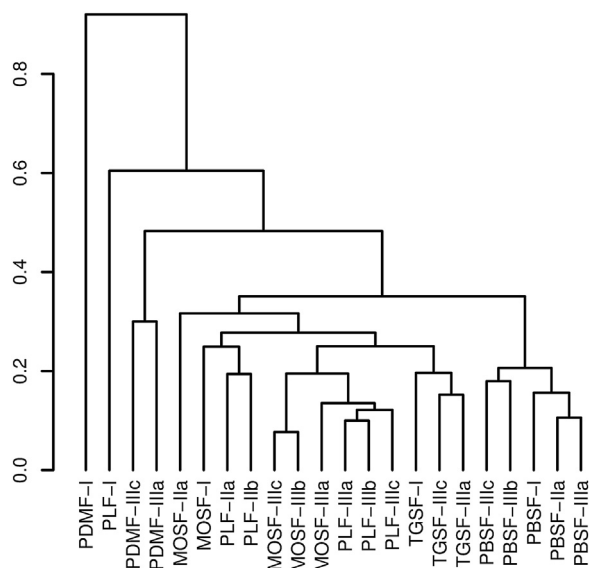
reflected the differing degrees of their adaptation to light and humidity conditions.

Narrowly-lobed foliose lichens showed a clear increase in species richness and cover with tree height; accordingly, this group is known to be restricted to the well-illuminated higher canopy zones and open forests (Barkman, 1958; Hale, 1967; Li et al., 2013a). Fruticose lichens, another well-known high-light tolerant group (Barkman, 1958), also tended to occur in the upper zones; however, they showed a wider-ranging vertical distribution in more open forests and were relatively evenly distributed throughout the trees. Broadly-lobed foliose lichens preferred the intermediate zones, probably because the majority of them are well adapted to moderate light intensity and higher humidity (Coote et al., 2007; Li et al., 2013a). The species richness of crustose lichens increased while their contribution decreased with increasing height in the PLF; this can be ascribed to the fact that many of them, such as the family Graphidaceae, usually occur on trunks and twigs of trees and bushes in sheltered habitats (Barkman, 1958; Hale,

1967; Li et al., 2013a). Other crustose species, such as *Amanidea punctata*, *Lecanora allophana* and *Pertusaria composita* (Appendix A–B), are better adapted to drought and excessive luminosity (Li et al., 2013a). The combination of their contrasting microhabitat requirements may, therefore, result in an inconspicuous vertical distribution, e.g. in the MOSF and PBSF. Similar patterns of the aforementioned lichen groups have also been found in other forest ecosystems (Cornelissen and ter Steege, 1989; Jarman and Kantvilas, 1995; Komposch and Hafellner, 2000; Sillett and Rambo, 2000; Williams and Sillett, 2007).

Cyanolichens often grow in the more humid lower zones of trees and occurred infrequently in the drier, more sun-exposed upper canopies in our area. Because cyanolichens require hydration by liquid water (Sillett and Antoine, 2004), their vertical pattern may reflect a water gradient, as previously reported in temperate and boreal hardwood forests, where their preference for tree bases is related to their successful adaptation to more shady and humid microhabitats





**Fig 6 – Similarity dendrogram (Cophenetic Coefficient of Correlation  $r_c = 0.96$ ) of epiphytic lichen communities among vertical zones in five forest types in the Ailao Mountains, southwest China.**

(Ellis and Coppins, 2006; Hedenäs and Ericson, 2000, 2004). In contrast, some studies suggest that cyanolichens are most abundant in the middle to even the upper vertical zones in old-growth coniferous forests (Ellyson and Sillett, 2003; Lyons et al., 2000; McCune, 1993; McCune et al., 1997; Sillett and Rambo, 2000); this can be attributed to the fact that the old forest age and high precipitation allow epiphytic lichens to advance to the position where functional groups typically found in low zones within a tree have successfully invaded the upper zones (McCune et al., 1997).

Finally, the six zone division, after Johansson (1974) and Cornelissen and ter Steege (1989), was a useful approach for analysis of vertical stratification of epiphytes in the subtropical forests. In those forests with low canopies, however, tree stratification was less well-defined and six zones were not necessary for lichen sampling. Moreover, a 2-m segment survey offered a complementary strategy for studying the vertical diversification of lichens, although it was time-consuming. More importantly, the combined use of the two schemes was a good way to increase basic knowledge of epiphytic lichens, since little research has been conducted on this subject in our region.

## Conclusions

In China, epiphytic lichens have received little attention and are largely ignored in forest protection and management, because the information on the lichen flora is extremely limited (Li et al., 2013b). In the present study, our results clearly suggest that strong vertical stratification of epiphytic lichens occurs in the subtropical forests in southwest China

and differs among forest types. The species composition of epiphytic lichens is also more determined by forest type than by vertical zone. Host species significantly affect the distribution of epiphytic lichens while host diameter and height have a modest influence. Epiphytic lichens favor the intermediate vertical zones, and lichen functional groups show great preference for specific zones, presumably reflecting their respective microhabitat requirements (Li et al., 2013a). Consequently, these findings can be used to predict the forest environment change and can offer useful information for forest conservation and management in subtropical montane forests. However, it is a pity that our data were only collected from the dominant tree species, as these cannot capture comprehensive information for the entire forest ecosystem. Further research is needed to better clarify the vertical stratification patterns of epiphytic lichens in these forests.

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## Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.funeco.2015.02.005>.

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