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Forest Type and Tree Characteristics Determine the Vertical Distribution of Epiphytic Lichen Biomass in Subtropical Forests

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Abstract: Epiphytic lichens are an important component in subtropical forests and contribute greatly to forest biodiversity and biomass. However, information on epiphytic lichens still remains scarce in forest conservation owing to the difficulty of accessing all canopy layers for direct observation. Here, epiphytic lichens were quantified on 73 whole trees in five forest types in Southwest China to clarify the vertical stratification of their biomass in subtropical forests. Lichen biomass was significantly influenced by forest type and host attributes, varying from 187.11 to 8.55 $g \cdot tree^{-1}$ among forest types and from 289.81 to <0.01 $g \cdot tree^{-1}$ among tree species. The vertical stratification of lichen biomass was also determined by forest type, which peaked at the top in primary *Lithocarpus* forest and middle-aged oak secondary forest and in the middle upper heights in other forests. Overall, the proportion of lichen biomass accounted for 73.17–100.00% of total lichen biomass on branches and 0.00–26.83% on trunks in five forests, and 64.53–100.00% and 0.00–35.47% on eight host species. Seven functional groups showed marked and various responses to tree height between and among forest types. This information improves our understanding of the distribution of epiphytic lichens in forest ecosystems and the promotion of forest management in subtropical China.

Keywords: epiphyte; forest type; functional group; host species; subtropical forest; vertical stratification

1. Introduction

Epiphytic lichens grow on branches and trunks of trees, sometimes with heavy cover, in many forest ecosystems. They can contribute greatly to biodiversity and may constitute a large proportion of epiphyte biomass [1,2]. Epiphytic lichens have been documented to be indicative of forest community health, conservation and management, environmental changes, human disturbance, and air pollution [1,2]. Lichens also provide food resources and refuges for vertebrates (e.g., birds, reindeer/caribou, monkeys, and rodents) and invertebrates (e.g., arthropods, gastropods, rotifers, and tardigrades), and influence forest hydrology and nutrient cycling [1,3–5]. Despite the remarkable contribution of epiphytic lichens to forest ecosystem, their biomass is difficult to assess directly because canopy surveys require difficult means of access, and the removal of lichens from bark is a very time-consuming task [3]. The indirect method of measuring litterfall is practicable for assessing epiphytic lichen biomass, but it is not without problems due to the fact that litterfall varies with wind, precipitation, decomposition, and herbivores [6–8]. Therefore, information on the biomass of epiphytic lichens is still deficient for many regions, e.g., the subtropics and the tropics.

The majority of studies involving lichen biomass at tree- and stand-level have been conducted in North American temperate/boreal hardwoods [9–12] and coniferous forests [3,13–17]. Epiphytic lichens constitute a small proportion of the total forest biomass in these forests, and the biomass distribution is controlled by forest (e.g., stand age and community structure) and host (e.g., species, diameter, and height) characteristics [11,15,18,19]. In general, old-growth forests and large trees support high lichen biomass [14,17,20,21]. In boreal and temperate forests, epiphytic lichen biomass ranged from 47 to 31,300 $\text{g}\cdot\text{tree}^{-1}$ among coniferous tree species [13,14,22,23].

Likewise, the data on the vertical distribution of epiphytic lichen biomass have been largely restricted to boreal and temperate coniferous forests [15,17,18,21,24,25]. The vertical stratification is related to a gradient with tree height, which is determined by the interactions among microclimate, microhabitat, and tree architecture [26–29]. Lichen biomass is more plentiful on branches than on trunks [13,16,18,30]. Different lichen functional groups often have contrasting vertical diversification due to their different sensitivities to light and humidity [14,21,31,32]. Forest type also alters the stratification pattern of lichen groups; for example, cyanolichens that occurred typically in low zones can invade the upper zones in old-growth forests compared to young forests [16,21,31]. However, there was no evidence that this vertical pattern, which is found in coniferous forests, is appropriate for epiphytic lichens in other floristically-distinct forest ecosystems, e.g., subtropical and tropical forests with highly diverse communities and tree species. It is, therefore, necessary to verify the vertical stratification pattern of epiphytic lichens across multiple scales.

The subtropical forests in the Ailao Mountains in Yunnan Province, Southwest China, which differed from boreal forests in terms of forest structure and lichen assemblages [33–35], were chosen to examine the vertical stratification pattern of epiphytic lichens associated coniferous forests. Abundant lichens occur in these forests [35], and newly wind-fallen trees offer an opportunity to study epiphytic lichens along the entire tree [29,36]. Here, we present the first quantitative information on the vertical distribution of epiphytic lichen biomass in two primary and three secondary forests, on the basis of combined surveying of recent treefalls and standing trees. The aims of the present paper are to: (1) estimate epiphytic lichen biomass; (2) verify the vertical pattern of lichen biomass for total and functional groups; and (3) determine the influences of forest type and host characteristics on lichen biomass.

2. Materials and Methods

2.1. Study Area

The study was conducted at an altitude of 2000–2750 m in the Xujiaba region, a core area of the Ailao National Nature Reserve (23°35′–24°44′ N, 100°54′–101°30′ E) in central-southern Yunnan, China (Figure 1). The forest landscape is characterized by an extensive area of continuous primary forests, small secondary fragments, and high connectivity [35].

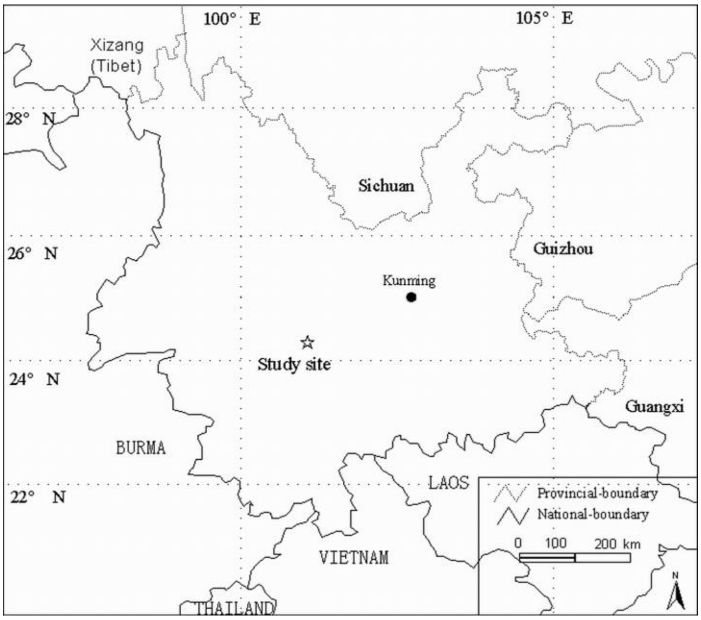

Figure 1. The location of the study site in the Ailao Mountains, Yunnan, Southwest China.

In order to capture the biomass and vertical distribution of epiphytic lichens, we examined two primary and three secondary forest types in this study (Table 1): primary *Lithocarpus* forest (PLF), primary dwarf mossy forest (PDMF), middle-aged oak secondary forest (MOSF), *Populus bonatii* secondary forest (PBSF), and *Ternstroemia gymnanthera* secondary forest (TGSF). Details of their meteorology and forest structure can be found in Li et al. [35,37].

Table 1. Environmental conditions of five forest types in the Ailao Mountains, Southwest China.

Forest Type	Primary Dwarf Mossy Forest (PDMF)	Primary *Lithocarpus* Forest (PLF)	Middle-Aged Oak Secondary Forest (MOSF)	*Populus bonatii* Secondary Forest (PBSF)	*Ternstroemia gymnanthera* Secondary Forest (TGSF)
Dominant canopy species	*Lithocarpus crassifolius* A. Camus; *Rhododendron irroratum* Franch.	*Lithocarpus xylocarpus* (Kurz) Markgr.; *Lithocarpus hancei* (Benth.) Rehder; *Castanopsis wattii* (King ex Hook. f.) A. Camus	*Lithocarpus hancei*; *Vaccinium duclouxii* (H. Lév.) Hand.-Mazz.	*Populus bonatii* Levl.	*Ternstroemia gymnanthera* (Wigrt et Arn.) Bedd
Stand age (year)	>300	>300	49	36	<20
Basal area (m^2/ha)	48.00	77.31	55.17	29.88	42.45
Canopy openness (%)	30.00	5.80	31.00	51.67	31.67
Mean diameter at breast height (dbh, cm)	7.91	19.23	9.84	8.50	4.31
Tree density (trees/ha)	8273	1656	5903	4697	22,933
Tree species richness	15.90	15.72	15.73	8.87	5.67

2.2. Sampling Method

Fieldwork was conducted between April 2009 and December 2010. Two sampling methods were used to examine the biomass of epiphytic lichens, and only dominant trees with typical and/or abundant lichen species assemblages within each forest type were selected for sampling [38]. In the PLF and the PBSF, treefalls occurred in the wet–dry season transition (April–May and October–November). They were easy to access and offered the opportunity to study epiphytes along the entire tree [29,36]. The treefalls of *Lithocarpus hancei* (Benth.) Rehder (nine trees), *Ilex corallina* Franch. (five trees), *Vaccinium duclouxii* (H. Lév.) Hand.-Mazz. (five trees), and other mixed species (nine trees) were sampled in the PLF, and *Populus bonatii* Levl. (10 trees) was sampled in the PBSF. In other three forests, few treefalls were found; however, the canopies were low (3–8 m) and standing trees could be accessed using an extendable ladder or a free-climbing. Dominant *Lithocarpus crassifolius* A. Camus (seven trees) and *Rhododendron irroratum* Franch. (seven trees) were sampled in the PDMF, *L. hancei* (seven trees) and *V. duclouxii* (seven trees) in the MOSF, and *Ternstroemia gymnanthera* (Wigrt et Arn.) Bedd (seven trees) in the TGSF.

Since tree height changed significantly among host species and forest types, and tree stratification was less well-defined in those forests with low canopies [38], either sampling method, based only on zone division or tree height, cannot provide an overall comparable description of lichen vertical distribution among forest type and host species. In this study, each tree was, thus, divided into 2-m segments, and the basal trunk (0–2 m) was further divided into 0–0.5, 0.5–1.3, and 1.3–2 m intervals [37], and then schematically divided into six zones: (I) basal trunk, (IIa) lower trunk, (IIb) upper trunk, (IIIa) lower canopy, (IIIb) middle canopy, and (IIIc) upper canopy (modified from Johansson [39] and Cornelissen and ter Steege [40]). For a more detailed description of tree sampling and height division, see Li et al. [38].

At each 2-m segment, all macrolichens were gathered from one 1-m-long segment at the trunk midpoint and one third branches to assess the total lichen biomass. Only fruticose and foliose lichens were collected. Crustose lichens were excluded because of their negligible biomass and due to time constraints. In some cases, lichen biomass was very poor at 2-m segment and/or the segment was less than 2 m; macrolichens were sampled from the whole segment. The samples were cleaned of adhering debris, placed in bags, and then air dried for storage.

In the laboratory, epiphytic lichens were sorted by taxa and then weighed to 0.0001 g after drying by ventilation at 60 °C for 24 h. They were divided into four groups according to growth form and photobiont: cyanolichens (with cyanobacterial photobionts), fruticose chlorolichens (with green algal photobionts), broadly-lobed foliose chlorolichens, and narrowly-lobed foliose chlorolichens; and three reproductive strategies: isidiate (mainly by isidia or isidia-like structures), sorediate (mainly by soredia or soredia-like structures), and sexual reproduction [21,37]. Lichen species taxonomy followed Li et al. ([35], see Appendix 2).

2.3. Data Analysis

All statistical analyses were implemented in R 3.1.1 [41].

The epiphytic lichen biomass per tree/segment for total species and each functional group was calculated within the forest type and on the host species. The absolute and percent contributions of lichen groups to the total were considered in each vertical zone.

After checking for normality using the Shapiro–Wilk test and the homogeneity of variances using Bartlett's test, the assumptions of one-way Analysis of Variance for our data could not be satisfied even after transformation. A nonparametric Kruskal–Wallis rank-sum test, followed by the Wilcoxon rank-sum test, was carried out to test for differences in lichen biomass among forest types and among host species.

The lme4 package [42] was used to perform generalized linear mixed models (GLMMs) with a Gaussian distribution and a log-link function, and a Gamma distribution and a log-link function, to explore the correlations between tree attributes and the biomass of the total and functional groups of epiphytic lichens. All analyses included "forest type" and "host species" as random effects. The effect of tree attributes was estimated from marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) coefficients of determination. The $R^2_{GLMM(m)}$ describes the variance in the fixed effects only, while the $R^2_{GLMM(c)}$ describes the variance in both the fixed and random effects [43,44]. $R_{\Sigma}{}^2$, which also shows the proportion of generalized variance explained by the fixed predictors, and the partial correlation values were calculated using the r2glmm package [45].

3. Results

3.1. Biomass among Forest Types

The per-tree epiphytic lichen biomass differed significantly among the five forest types (Kruskal–Wallis $\chi^2 = 27.950$, $p < 0.001$; Figure 2), as well as lichens on branches ($\chi^2 = 24.652$, $p < 0.001$) and on trunks ($\chi^2 = 51.720$, $p < 0.001$). Lichen biomass averaged 187.11 g·tree^{-1} in the MOSF, 183.61 g·tree^{-1} in the PBSF, 90.51 g·tree^{-1} in the PLF, 51.46 g·tree^{-1} in the TGSF, and 8.55 g·tree^{-1} in the PDMF, and its proportion on branches and trunks accounted for 89.23% and 10.77% of the total lichen biomass, 73.17% and 26.83%, 94.67% and 5.33%, 77.96% and 22.04%, and 100.00% and 0.00%, respectively.

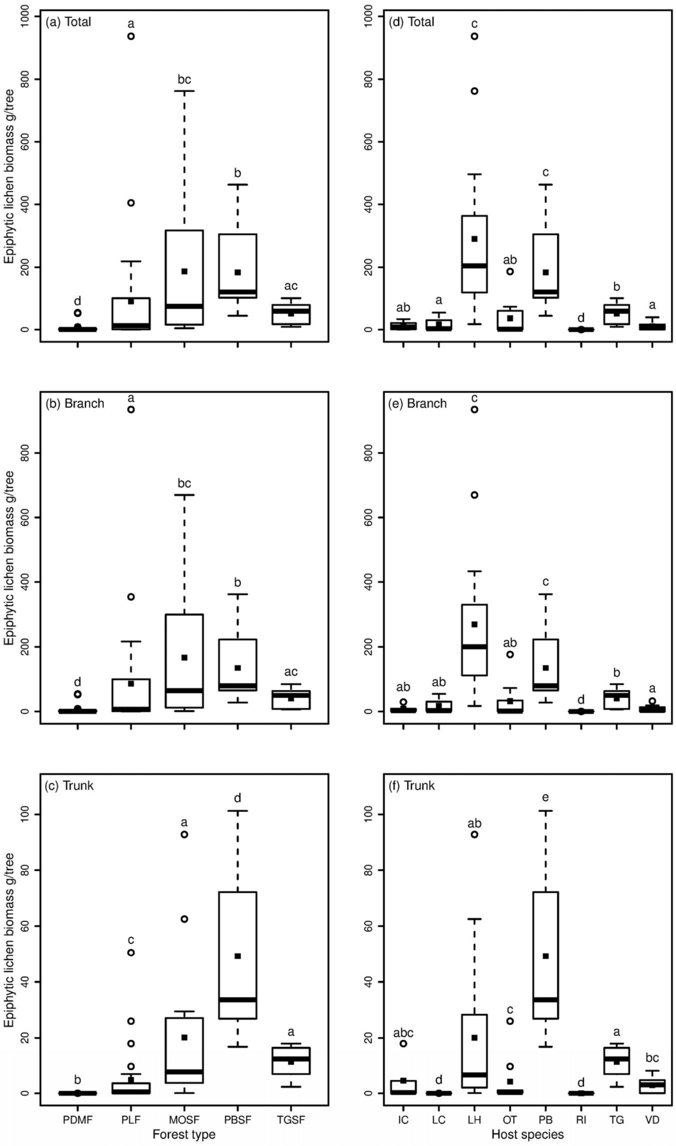

Figure 2. Epiphytic lichen biomass in five forest types (**a**–**c**) and on eight host species (**d**–**f**) in the Ailao Mountains, Southwest China. Different letters with bars represent significant differences. Solid squares symbolize the mean value. PDMF: primary dwarf mossy forest; PLF: primary *Lithocarpus* forest; MOSF: middle-aged oak secondary forest; PBSF: *Populus bonatii* secondary forest; TGSF: *Ternstroemia gymnanthera* secondary forest. IC: *Ilex corallina*; LC: *Lithocarpus crassifolius*; LH: *Lithocarpus hancei*; OT: other mixed species; PB: *Populus bonatii*; RI: *Rhododendron irroratum*; TG: *Ternstroemia gymnanthera*; VD: *Vaccinium duclouxii*.

All lichen groups were distributed very unevenly among forest types (χ^2 = 13.190–38.253, all $p < 0.001$; Figure 3). In the PDMF, broadly-lobed foliose (74.67% of the total) and sorediate (54.77%) lichens dominated the lichen biomass. In the PBSF, fruticose and sexual lichens represented 44.29% and 78.18%, respectively. In other three forests, narrowly-lobed foliose and sexual lichens accounted for 41.12–72.25% and 63.18–88.08%, respectively. The contribution of cyanolichens toward lichen biomass was lowest, with the highest percentage (7.37%) in the PBSF and the lowest (0.42%) in the MOSF.

Among 60 macrolichens, the dominant lichen species were significantly different among the five forest types (Table 2).

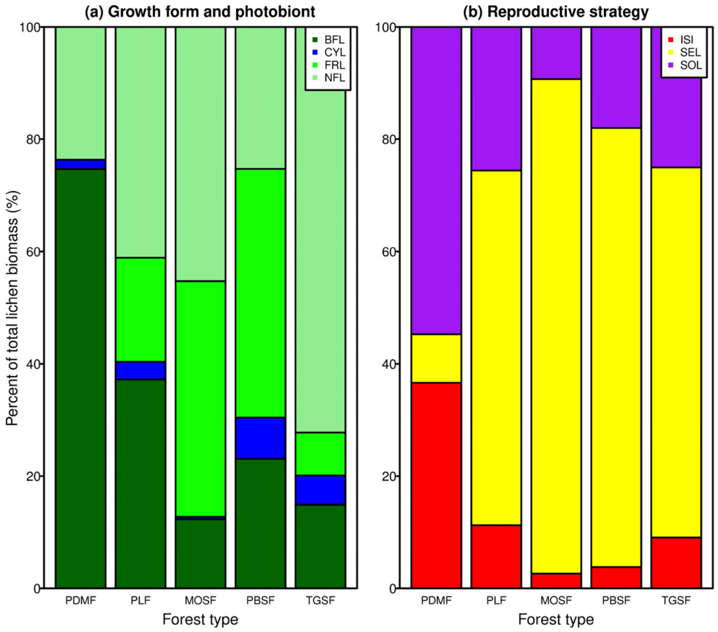

Figure 3. The biomass composition of functional groups divided by (**a**) growth form and photobiont and (**b**) reproductive strategy of epiphytic lichens in five forest types in the Ailao Mountains, Southwest China. PDMF: primary dwarf mossy forest; PLF: primary *Lithocarpus* forest; MOSF: middle-aged oak secondary forest; PBSF: *Populus bonatii* secondary forest; TGSF: *Ternstroemia gymnanthera* secondary forest. BFL: broadly-lobed foliose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly-lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

Table 2. The biomass (g·tree^{-1}) of epiphytic lichen species in five forest types in the Ailao Mountains, southwest China. PDMF: primary dwarf mossy forest; PLF: primary *Lithocarpus* forest; MOSF: middle-aged oak secondary forest; PBSF: *Populus bonatii* secondary forest; TGSF: *Ternstroemia gymnanthera* secondary forest. BFL: broadly-lobed foliose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly-lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

Species	Functional Group	Forest Type				
		PDMF	PLF	MOSF	PBSF	TGSF
Anzia leucobatoides f. *hypomelaena* A. Zahlbruckner	NFL/SEL	0.000	3.906	3.026	0.161	0.000
Anzia physoidea A. L. Sm	NFL/SEL	0.000	0.220	0.063	0.000	0.000
Bryoria confusa (D. D. Awasthi) Brodo & D. Hawksw.	FRL/SEL	0.000	0.351	2.280	0.000	0.000
Cetrelia olivetorum (Nyl.) W. L. Culb. & C. F. Culb.	BFL/SOL	3.393	7.563	7.172	16.521	2.713
Cladonia coniocraea (Flök.) Spreng.	FRL/SOL	0.001	0.221	0.005	0.017	0.015
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	CYL/SEL	<0.001	0.000	0.002	0.038	0.008
Collema fasciculare (L.) Weber ex F. H. Wigg.	CYL/SEL	0.000	0.000	0.000	0.000	0.008
Erioderma meiocarpum Nyl.	CYL/SEL	0.000	0.000	0.000	0.017	0.000
Everniastrum cirrhatum (Fr.) Hale ex Sipman	NFL/SEL	<0.001	1.586	15.308	20.403	3.601

Table 2. *Cont.*

Species	Functional Group	Forest Type				
		PDMF	PLF	MOSF	PBSF	TGSF
Everniastrum nepalense (Taylor) Hale ex Sipman	NFL/SEL	0.000	8.265	22.522	2.871	14.532
Everniastrum rhizodendroideum (J. C. Wei & Y. M. Jiang) Sipman	NFL/SEL	0.000	0.017	0.753	0.060	0.641
Heterodermia boryi (Fée) Hale	NFL/SEL	0.000	1.660	0.481	1.409	0.048
Heterodermia comosa (Eschw.) Follmann & Redón	NFL/SEL	0.164	0.424	1.979	1.238	0.240
Heterodermia dendritica (Pers.) Poelt	NFL/SEL	0.163	3.475	10.195	2.673	1.787
Heterodermia hypoleuca (Mühlbr.) Trevis.	NFL/SEL	0.116	0.437	0.003	14.434	0.000
Heterodermia obscurata (Nyl.) Trevis.	NFL/SOL	0.000	0.000	0.000	0.000	0.218
Hypogymnia yunnanensis Y. M. Jiang & J. C. Wei	NFL/SEL	0.219	3.230	9.999	<0.001	2.154
Hypotrachyna adducta (Nyl.) Hale	NFL/SEL	0.074	1.676	7.476	0.353	2.135
Hypotrachyna pseudosinuosa (Asahina) Hale	NFL/SOL	1.290	8.685	7.394	0.437	4.388
Hypotrachyna revoluta (Flörke) Hale	NFL/SOL	0.000	0.000	0.000	0.000	0.015
Hypotrachyna sinuosa (Sm.) Hale	NFL/SOL	<0.001	0.002	0.000	0.051	0.000
Leioderma sorediatum D. J. Galloway & P. M. Jørg.	CYL/SOL	<0.001	0.165	0.099	0.018	0.237
Leptogium azureum (Sw. ex Ach.) Mont.	CYL/SEL	0.000	0.140	0.301	1.103	0.140
Leptogium menziesii (Sm.) Mont.	CYL/SEL	0.000	0.154	0.103	3.013	0.000
Leptogium saturninum (Dicks.) Nyl.	CYL/ISL	0.000	0.000	0.020	0.134	0.000
Lobaria isidiophora Yoshim.	BFL/ISL	0.000	2.231	0.000	1.179	0.000
Lobaria isidiosa (Müll. Arg.) Vain.	CYL/ISL	0.000	0.000	0.000	1.143	0.137
Lobaria kurokawae Yoshim.	CYL/SEL	0.000	0.010	0.000	0.000	0.000
Lobaria retigera (Bory) Trevis.	CYL/ISL	0.138	1.371	0.252	2.704	1.097
Menegazzia terebrata (Hoffm.) A. Massal.	NFL/SOL	<0.001	1.371	1.320	1.072	0.292
Myelochroa aurulenta (Tuck.) Elix & Hale	NFL/SOL	0.000	0.000	0.000	0.000	3.650
Myelochroa irrugans (Nyl.) Elix & Hale	NFL/SEL	0.000	0.215	0.137	0.373	0.757
Myelochroa subaurulenta (Ny1) Elix & Hale	NFL/SEL	0.000	0.000	0.000	0.000	1.383
Nephroma helveticum Ach.	CYL/ISL	0.001	0.242	0.000	0.103	0.748
Nephromopsis ornata (Müll. Arg.) Hue	BFL/SEL	0.000	8.850	6.994	0.102	0.004
Nephromopsis pallescens (Schaer.) Y. S. Park	BFL/SEL	0.000	1.969	2.742	0.693	0.796
Nephromopsis stracheyi (Bab.) Müll. Arg.	BFL/SEL	0.000	0.535	0.000	0.000	0.000
Oropogon asiaticus Asahina	FRL/SEL	0.000	0.000	0.000	0.519	0.000
Pannaria rubiginosa (Thunb.) Delise	CYL/SEL	0.000	0.000	0.000	4.215	0.000
Parmelia adaugescens Nyl.	NFL/SEL	0.000	0.789	0.773	0.041	0.653
Parmelina quercina (Willd.) Hale	NFL/SEL	0.000	1.259	3.348	0.059	0.682
Parmotrema eciliatum (Nyl.) Hale	BFL/SEL	0.000	0.589	0.065	8.074	0.000
Parmotrema mellissii (C. W. Dodge) Hale	BFL/ISL	0.000	0.000	0.000	0.000	0.146
Parmotrema reticulatum (Taylor) M. Choisy	BFL/SOL	<0.001	4.645	1.387	14.888	1.326
Parmotrema tinctorum (Desper. ex Nyl.) Hale	BFL/ISL	2.994	5.589	4.647	0.863	2.527
Peltigera rufescens (Weiss) Humb.	CYL/SEL	0.000	0.000	0.000	0.000	0.132
Phaeophyscia ciliate (Hoffm.) Moberg	NFL/SEL	0.000	0.000	0.000	0.796	0.000
Ramalina conduplicans Vain.	FRL/SEL	0.000	3.421	16.915	57.671	0.297
Ramalina sinensis Jatta	FRL/SEL	0.000	0.000	0.000	0.191	0.000
Rimelia cetrata (Ach.) Hale & A. Fletcher.	BFL/SEL	0.000	0.000	0.000	0.000	0.122
Sticta duplolimbata (Hue) Vain.	CYL/ISL	0.000	0.380	0.004	0.237	0.000
Sticta fuliginosa (Dicks.) Ach.	CYL/ISL	0.000	0.361	0.000	0.609	0.007
Sticta gracilis (Müll. Arg.) A. Zahlbruckner	CYL/SEL	0.000	0.026	0.009	0.200	0.205
Sticta nylanderiana A. Zahlbruckner	BFL/SEL	0.000	1.712	0.000	0.000	0.000
Sulcaria sulcata (Lév.) Bystrek ex Brodo & D. Hawksw.	FRL/SEL	0.000	0.027	0.706	3.920	0.000
Usnea baileyi (Stirt.) A. Zahlbruckner	FRL/SOL	0.000	<0.001	0.000	0.000	0.028
Usnea florida (L.) Weber ex F. H. Wigg.	FRL/SEL	0.000	12.237	56.740	18.906	3.588
Usnea nidifica Taylor	FRL/SOL	0.000	0.497	0.000	0.001	0.000
Usnea rubicunda Stirt.	FRL/SOL	0.000	0.000	0.000	0.082	0.000
Usnea sp.	FRL/SEL	0.000	0.007	1.889	0.014	0.000

3.2. Biomass among Host Species

Epiphytic lichen biomass showed significant host-tree specificity (χ^2 = 51.559, p < 0.001; Figure 2). Lichens had the highest biomass on *Lithocarpus hancei* (289.81 g·tree^{-1}) and the least on *Rhododendron irroratum* (<0.01 g·tree^{-1}). Lichens on branches (χ^2 = 50.243, p < 0.001) and trunks (χ^2 = 50.404, p < 0.001) showed similar patterns.

Lichen biomass was more prolific on branches than on trunks, in which it accounted for 100.00% and 0.00% of the total on both *Lithocarpus crassifolius* and *Rhododendron irroratum*, 93.07% and 6.93% on *Lithocarpus hancei*, 88.38% and 11.62% on other mixed trees, 72.56% and 27.44% on *Vaccinium duclouxii*, and 64.53% and 35.47% on *Ilex corallina*. Moreover, on *Ilex corallina*, the dominant lichens were *Parmotrema tinctorum* (Desper. ex Nyl.) Hale (49.02%), *Nephromopsis stracheyi* (Bab.) Müll. Arg. (20.44%), and *Nephroma helveticum* Ach. (10.37%); on *Lithocarpus crassifolius*, *Cetrelia olivetorum* (Nyl.) W. L. Culb. & C. F. Culb. (39.68%), *P. tinctorum* (35.02%), and *Hypotrachyna pseudosinuosa* (Asahina)

Hale (15.04%) were dominant; on *Lithocarpus hancei*, *Usnea florida* (L.) Weber ex F. H. Wigg. (23.98%) and *Everniastrum nepalense* (Taylor) Hale ex Sipman (11.01%) were dominant; on *Rhododendron irroratum*, *H. pseudosinuosa* (100.00%) was dominant; on other mixed trees, *Lobaria isidiophora* Yoshim. (15.51%), *P. tinctorum* (15.26%), and *Parmotrema reticulatum* (Taylor) M. Choisy (10.51%) were dominant; and on *Vaccinium duclouxii*, *H. pseudosinuosa* (23.22%), *C. olivetorum* (18.40%), *P. tinctorum* (15.46%), and *Everniastrum cirrhatum* (Fr.) Hale ex Sipman (10.13%) were dominant.

3.3. The Effect of Tree Attributes

GLMMs showed that tree dbh and height were positively correlated with total lichen biomass as well as those of lichen functional groups (Table 3), while their interactions showed negative correlations. For total biomass, the model explained 76.7% of the total variation ($R^2_{GLMM(c)} = 0.767$), of which 19.5% was explained by the fixed factors and their interaction ($R^2_{GLMM(m)} = 0.195$), while $R_{\Sigma}{}^2$ yielded a significantly higher explained variance ($R_{\Sigma}{}^2 = 0.418$) than $R^2_{GLMM(c)}$. The estimates for partial R^2 showed that tree height was significantly influenced the biomass of all groups except fruticose lichens, while tree dbh and its interaction was significantly influenced that of broadly-lobed foliose, cyano-, isidiate, and sorediate lichens. Moreover, tree height and dbh showed much stronger correlations with lichen biomass on branches than on trunks for the total and lichen groups.

Table 3. The results of generalized linear mixed models testing the influence of tree dbh and height on epiphytic lichen biomass per tree in five forest types in the Ailao Mountains, Southwest China. $R^2_{GLMM(m)}$: marginal coefficient, describes the variance in the fixed effects; $R^2_{GLMM(c)}$: conditional coefficient, describes the variance in both the fixed and random effects; $R_{\Sigma}{}^2$: the proportion of generalized variance explained by the fixed predictors; Partial R^2_{height}: the proportion of generalized variance explained by the tree height; Partial $R^2{}_{dbh}$: the proportion of generalized variance explained by the tree dbh; Partial $R^2{}_{height:dbh}$: the proportion of generalized variance explained by the interaction between tree height and dbh. $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***.

Lichen Biomass		$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$	$R_{\Sigma}{}^2$	Partial R^2_{height}	Partial R^2_{dbh}	Partial $R^2_{height:dbh}$
Total	All	0.195	0.767	0.418	0.122 *	0.073	0.047
	Branch	0.183	0.745	0.389	0.096 *	0.076 *	0.048
	Trunk	0.104	0.659	0.251	0.126 *	0.048	0.049 *
Broadly-lobed foliose lichens	All	0.283	0.663	0.446	0.095 *	0.121 **	0.077 *
	Branch	0.294	0.609	0.437	0.081	0.142 *	0.093 *
	Trunk	0.158	0.500	0.220	0.096	0.083 *	0.082 **
Cyanolichens	All	0.170	0.360	0.345	0.164 ***	0.097 ***	0.093 ***
	Branch	0.370	0.560	0.558	0.332 ***	0.269 ***	0.272 ***
	Trunk	0.150	0.329	0.265	0.111 ***	0.019 *	0.016 *
Fruticose lichens	All	0.081	0.727	0.197	0.080	0.025	0.022
	Branch	0.091	0.725	0.213	0.089	0.024	0.022
	Trunk	0.004	0.269	0.008	0.000	0.008	0.008
Narrowly-lobed foliose lichens	All	0.186	0.734	0.375	0.088 *	0.017	0.005
	Branch	0.190	0.722	0.375	0.084 *	0.021	0.007
	Trunk	0.010	0.639	0.041	0.019	0.022	0.025
Isidiate lichens	All	0.018	0.912	0.013	0.005 ***	0.003 ***	0.003 ***
	Branch	0.231	0.456	0.301	0.071 *	0.049	0.031
	Trunk	0.167	0.310	0.297	0.138 ***	0.013	0.012
Sexual lichens	All	0.200	0.788	0.437	0.146 *	0.032	0.017
	Branch	0.198	0.789	0.432	0.123 *	0.026	0.010
	Trunk	0.017	0.345	0.048	0.010	0.018	0.015
Sorediate lichens	All	0.162	0.579	0.276	0.020	0.076 *	0.042
	Branch	0.153	0.521	0.252	0.009 ***	0.076 **	0.040 ***
	Trunk	0.007	0.664	0.122	0.003	0.118 ***	0.105 ***

3.4. Vertical Distribution among Height Segments

Epiphytic lichen biomass showed a marked response to tree height in five forest types (Figure 4). In the PDMF, total lichen and all groups initially increased with tree height up to 2–4 m, followed by a decline toward the top. In the PLF, total biomass increased with increasing height, while cyanolichens peaked at 18–20 m and other groups peaked at 22–24 m. In the MOSF, lichen biomass exhibited a continuous increase with height. Cyano-, sorediate, and broadly-lobed foliose lichens peaked at different heights, and other groups showed similar patterns to the total. In the PBSF, lichen biomass peaked at 10–12 m (155.88 g·tree^{-1}), subsequently decreased to 44.99 g·tree^{-1} at 12–14 m and finally increased to 68.88 g·tree^{-1} at 14–16 m. All lichen groups showed similar tendencies but with variable processes. In the TGSF, lichens had a similar pattern to those in the PDMF; however, different lichen groups peaked at different heights.

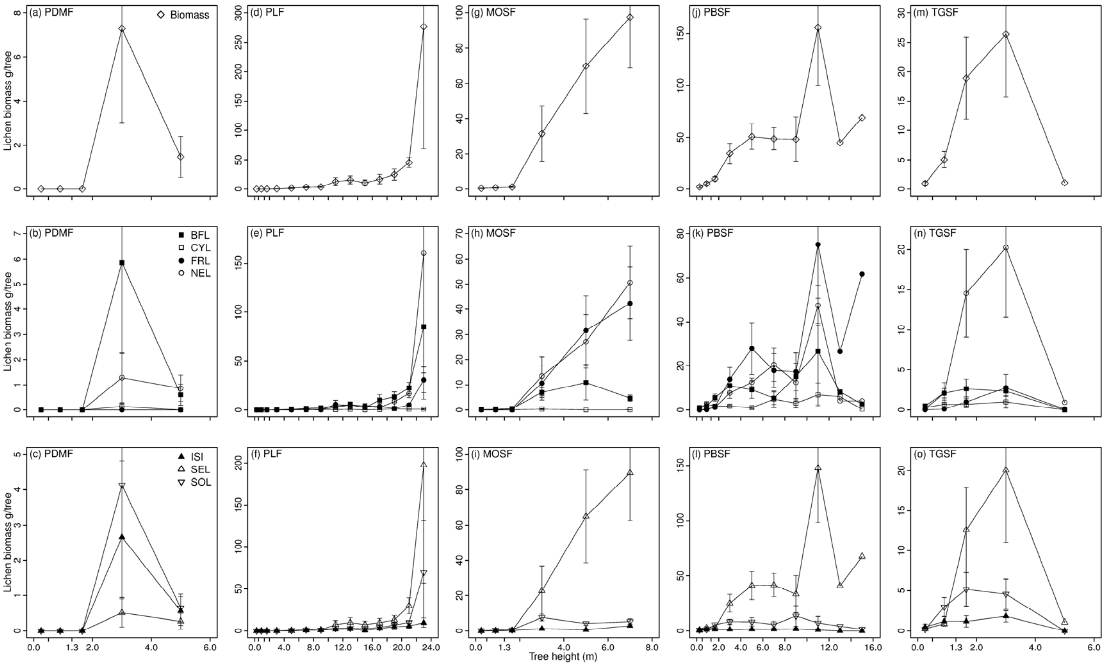

Figure 4. The biomass of epiphytic lichens at each height segment in five forest types ((**a**–**c**): the PDMF; (**d**–**f**): the PLF; (**g**–**i**): the MOSF; (**j**–**l**): the PBSF; (**m**–**o**): the TGSF) in the Ailao Mountains, Southwest China. PDMF: primary dwarf mossy forest; PLF: primary *Lithocarpus* forest; MOSF: middle-aged oak secondary forest; PBSF: *Populus bonatii* secondary forest; TGSF: *Ternstroemia gymnanthera* secondary forest. BFL: broadly-lobed foliose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly-lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

3.5. Vertical Distribution among Vertical Zones

The biomass of epiphytic lichens and its percentage to the total were significantly stratified among vertical zones for total lichens and functional groups (χ^2 = 4.525–186.850, all $p < 0.033$). It also exhibited different patterns among five forests (Figure 5). Overall, the highest total biomass occurred in zones IIIa–IIIc and the lowest in I; most groups had similar patterns to the total within forests.

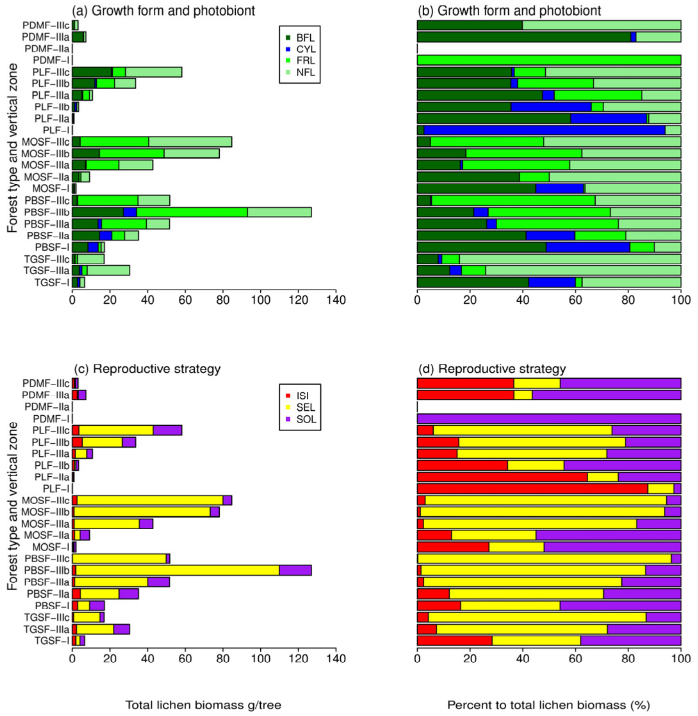

Figure 5. The biomass and percentages of epiphytic lichen groups in the vertical zones of five forest types in the Ailao Mountains, Southwest China. (**a**) biomass of lichen groups divided by growth form and photobiont; (**b**) biomass of lichen groups divided by reproductive strategy; (**c**) the percentage to total biomass of lichen groups divided by growth form and photobiont; (**d**) the percentage to total biomass of lichen groups divided by reproductive strategy. PDMF: primary dwarf mossy forest; PLF: primary *Lithocarpus* forest; MOSF: middle-aged oak secondary forest; PBSF: *Populus bonatii* secondary forest; TGSF: *Ternstroemia gymnanthera* secondary forest. I: basal trunk; IIa: lower trunk; IIb: upper trunk; IIIa: lower canopy; IIIb: middle canopy; IIIc: upper canopy. BFL: broadly-lobed foliose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly-lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

The biomass of broadly-lobed foliose lichens peaked in zone IIIc in the PLF (20.76 g$\cdot$tree^{-1}), IIIb in the MOSF (14.36 g$\cdot$tree^{-1}) and PBSF (27.14 g$\cdot$tree^{-1}), and IIIa in the PDMF (5.87 g$\cdot$tree^{-1}) and TGSF (3.74 g$\cdot$tree^{-1}). Its percentage was higher in all zones (35.43–58.15%) except I in the PLF, and decreased from I (42.19–48.85%) to IIIc (4.90–7.90%) in three secondary forests and from IIIa (80.97%) to IIIc (39.79%) in the PDMF.

Cyanolichens were most abundant in zone IIb of the PLF (1.03 g$\cdot$tree^{-1}), MOSF (0.38 g$\cdot$tree^{-1}) and TGSF (1.36 g$\cdot$tree^{-1}), and IIIb of the PBSF (6.93 g$\cdot$tree^{-1}); however, their percentage was the highest in zone I (17.76–91.50%) within these forests. In the PDMF, cyanolichens only occurred in IIIa (0.14 g$\cdot$tree^{-1} and 1.94%).

The biomass of fruticose lichens was higher in zones IIIa–IIIc in all forests, and peaked in IIIa in the TGSF (2.79 g$\cdot$tree^{-1}), IIIb in the PLF (9.68 g$\cdot$tree^{-1}) and PBSF (58.90 g$\cdot$tree^{-1}), and IIIc in the MOSF (36.39 g$\cdot$tree^{-1}). Accordingly, its percentage was highest in IIIa (9.17%), IIIa (33.20%), IIIc (62.01%), and IIIb (43.99%). In the PDMF, only very few fruticose lichens occurred in IIIa–IIIb (<0.01 g$\cdot$tree^{-1}).

Narrowly-lobed foliose lichens showed similar, more pronounced patterns to those of fruticose lichens. They were most abundant in zone IIIa in the TGSF (22.54 g$\cdot$tree^{-1}), IIIb in the PBSF (33.97 g$\cdot$tree^{-1}), and IIIc in the other forests (1.84–44.09 g$\cdot$tree^{-1}); however, the highest percentage occurred in IIIc (32.57–84.05%) in all forests.

For three groups with different reproductive strategies, the percentages of asexual and sexual lichens showed contrasting patterns. Isidiate and sorediate lichens had the highest percentages in Zone I (16.45–87.43% and 38.03–100.00%) and the lowest in IIIc (0.18–36.60% and 3.64–45.80%), whereas sexual lichens showed the opposite gradient (9.85–37.67% in I and 17.60–96.19% in IIIc), with the exceptions that isidiate lichens were absent in I–IIa of the PDMF and sorediate lichens were the highest in IIb (44.36%) of the PLF.

4. Discussion

4.1. Influences of Forest Type and Host Attribute

Our study showed that epiphytic lichen biomass ranged from 8.55 to 187.11 $\text{g}\cdot\text{tree}^{-1}$ in the subtropical Ailao Mountains. These data are low compared with the data from temperate/boreal oak woodland (545 $\text{g}\cdot\text{tree}^{-1}$ [12]) and coniferous forests (47–31,300 $\text{g}\cdot\text{tree}^{-1}$ [13–16,18,22–25,30]). However, when these data are considered in combination with the host density [37], a crude approximation for lichen stand-level biomass was 71 $\text{kg}\cdot\text{ha}^{-1}$ in the PDMF, 150 $\text{kg}\cdot\text{ha}^{-1}$ in the PLF, 1105 $\text{kg}\cdot\text{ha}^{-1}$ in the MOSF, 862 $\text{kg}\cdot\text{ha}^{-1}$ in the PBSF, and 1180 $\text{kg}\cdot\text{ha}^{-1}$ in the TGSF, falling within the high range of those reported in hardwoods (100-1800 $\text{kg}\cdot\text{ha}^{-1}$ [10,12]), tropical rain forest (7 $\text{kg}\cdot\text{ha}^{-1}$ [46]), and coniferous forests (120-4700 $\text{kg}\cdot\text{ha}^{-1}$ [10,13,14,17,18,20–22,24,25,47]). Moreover, the lichen biomass in the PLF was close to that reported in this forest previously (130 $\text{kg}\cdot\text{ha}^{-1}$ [8]), while it was underestimated by Chen et al. (1 $\text{kg}\cdot\text{ha}^{-1}$ [48]) in the PDMF.

The contribution of lichen groups to their total biomass differs significantly among forest ecosystems. As in the study by Li et al. [8], conducted in the same area, and one study conducted in the inner Himalayas [49], we found that epiphytic lichen biomass was dominated by foliose and fruticose species. These results differ from those found in tropical, temperate, and boreal forests, where epiphytic lichen communities were found to be dominated by cyanolichens and/or alectorioid lichens [17,18,21,23,46].

Our results confirmed the importance of forest type in its effect on lichen communities [11,15,21,35]. In our study, lichen biomass in secondary forests may benefit from increased light and substrate availability compared to primary forests, as well as from the landscape mosaic, with which primary forests maintained a persistent source of propagules and promoted the fast dispersal of lichens to secondary forests [8,37]. In contrast, the extreme closed canopy in the PLF resulted in light intensity insufficient to limit lichen growth [8,37]. The low lichen biomass in the PDMF could be attributed to its high altitude, which would lead to a decrease in foliose lichens and an increase in fruticose lichens [3,50]. However, the rarity of fruticose species, especially alectorioid lichens, accelerates the decrease in total lichen biomass caused by altitude in the studied area [35].

Tree species also had an important effect on epiphytic lichen biomass. However, not all studied host species can provide suitable substrates for lichen growth [14,23,35]. For example, *Lithocarpus hancei* and *Populus bonatii* supported high lichen biomass, while *Rhododendron irroratum* only hosted one lichen species with negligible biomass. The host-tree characteristics affecting lichen cover were possibly related to bark attributes such as chemistry, texture, and stability [1,26].

Lichen biomass, in contrast to species richness [38], was strongly and positively affected by tree diameter and height in these subtropical forests. Large trees offer a larger substrate area and more favorable and diverse microhabitat conditions for lichen colonization [15,17,19,51]. However, the GLMMs results indicated that tree diameter and height were less important than forest type and tree species for epiphytic lichens in this area.

4.2. Vertical Distribution

Epiphytic lichen biomass was stratified vertically in the studied forests. Earlier studies document that the vertical gradient is intrinsically tied to epiphyte succession, such that pioneer foliose lichens are displaced by alectorioid species and finally succeed to cyanolichens and bryophytes [21,51–53]. However, our data do not support this displacement pattern, possibly because the epiphyte community we studied is unsaturated [2,37] and alectorioid lichens are absent in this moist area [35].

Alternatively, humidity tends to have strong effects on the vertical stratification of lichen biomass among forest ecosystems on large spatial scale [13,21,31].

Observed epiphytic lichen biomass was highest in the uppermost canopy in the PLF and the MOSF, and in the upper-middle position in other forests. The latter result is similar to that reported from coniferous forests [15,17,18,20,21]. The stand-level differences can be related to forest structure heterogeneity [21], e.g., canopy openness [37].

Epiphytic lichen biomass was more plentiful on branches than on trunks. Their vertical stratification was largely due to the observed, greatly-increasing biomass of foliose and fruticose lichens with increasing tree height. This involved a response to microclimatic gradients compressed into the length of an individual tree, with increasing light intensity, wind speed, and temperature, and decreasing humidity from the base to the apex [20,21,26]. In the Ailao Mountains, light is a more important driver of epiphytic lichens; the benefits of increased light intensity may exceed the costs of accompanying heat and/or desiccation stress [8,37]. The higher lichen biomass observed in the middle and upper zones concurred with those observed in boreal to temperate forests [13,16,18,20,21,30]. This probably related to the combination of less direct but higher insolation, variable humidity, higher temperature, and larger substrate area, which, together, promote lichen colonization [17–19,21,54].

More importantly, epiphytic lichen groups showed variable vertical patterns, reflecting the different degrees of adaptation to light and humidity [15,18,21,26]. Broadly-lobed foliose lichen biomass peaked at the intermediate and upper zones, possibly because of its adaption to the relatively equilibrated conditions of intermediate light level and higher air humidity [26,37,54]. This decreasing proportion of total biomass from low to upper zones substantiated the view that the penetration of light and humidity was a major driver determining lichen distribution. Together, fruticose and narrowly-lobed foliose lichens were mostly restricted to the canopy zones and constituted the bulk of lichen biomass, a result consistent with the idea that they are highly light-tolerant species and can reactivate by absorbing atmospheric water, allowing them to grow prolifically in higher zones and open forests [26,37,55]. Cyanolichens contributed the least to total biomass and were restricted to lower zones than chlorolichens were. This result, coupled with the distribution of their species richness [38], indicated that cyanolichens were strongly limited by liquid water, rather than atmospheric water in subtropical forests [1,53,56]. Photoinhibition caused by high amounts of light also hinders their occurrence in higher zones [57]. In old-growth forests, however, increasing forest age and high precipitation can accelerate cyanolichen establishment into the upper zones [16,21,31].

Reproduction strategy also influenced the vertical distribution of epiphytic lichen biomass. The contrasting vertical stratification of asexual and sexual groups is probably due to the greater dispersibility of sexual, as opposed to asexual, propagules from the tree bases to the canopy top [17,58,59]. Alternatively, larger propagules, e.g., isidia, tend to be more competitive and more readily establish and grow, and smaller ones, e.g., spores, tend to be stress-tolerant [56,60,61]. The bark of the lower parts of trees is generally rougher and provides a more static environment; thus, it is can facilitate the attachment and establishment of large lichen propagules [26,55].

5. Conclusions

The importance of epiphytes for subtropical forest ecosystems has been recognized in the few studies conducted thus far in China [8,35,37,62–64]. In the Ailao Mountains, epiphytic lichens contribute greatly to biodiversity and so merit conservation efforts [35] and environmental monitoring [8,37]. They also play critical roles in nutrient cycling [48,65] and the food web [4]. These studies provide new insights into the ecology and function of epiphytes in subtropical forests.

Biomass estimates are important for understanding lichen function in forest ecosystems. Despite the significant limitations of this study, our results elucidate the vertical stratification patterns of epiphytic lichens and confirm the importance of forest type and host attributes in the distribution of lichen biomass in this area [38]. Although the primary forests conserve abundant lichen species, however, they have a lower biomass than secondary forests, which also have high lichen diversity [35].

Considering that epiphyte conservation should aim to maintain epiphyte species and biomass, the studied secondary forests are thus most likely to contribute positively to forest conservation and should also be preserved in this region. In addition, average N and P contents of chlorolichens are 0.96% and 0.09% in this area [65], and the estimates of lichen N and P totaled 0.68–11.33 kg ha^{-1} and 0.06–1.06 kg ha^{-1} in the studied forests. These results, coupled with the fast decay of epiphytic lichens [65], indicated that epiphytic lichens, particularly cyanolichens, may provide important N-inputs for epiphyte succession in oligotrophic arboreal habitats, especially in secondary forests [1,2].

We also found that tree species were unequally important as habitats for lichen colonization, and increasing tree diameter and height were associated with increased epiphyte biomass [1,2,21], indicating that the importance of tree attributes for lichen conservation is particularly noteworthy in forest practices.

The different patterns observed among functional groups indicate that the distribution of epiphytic lichens was related to the environmental variations within, and among, forest types. Epiphytic lichens were non-uniformly distributed across forest type and tree species. Moreover, their variable vertical distribution patterns appear to depend more on forest type and reflecting the different degrees of adaptation to light and humidity [15,18,21,26]. Therefore, the change in canopy structure resulting from natural disturbance and unlawful cutting will alter the penetration of light and humidity, and accordingly influence the vertical distribution patterns of epiphytic lichens.

Currently, forest conservation and management practices are largely based on the conservation needs of vascular plants in China. Epiphytic lichens are often overlooked in forest ecological studies and conservations [35]. Here, we emphasize the importance of epiphytes in subtropical forests, as well as sustainable forest management that integrates the conservation needs of lichens and their required ecological settings.

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