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Bole epiphytic lichens as potential indicators of environmental change in subtropical forest ecosystems in southwest China

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ABSTRACT

Lichen epiphytes are applied as excellent environmental indicators worldwide. However, very little is known about epiphytic lichen communities and their response to forest dynamics in subtropical China. This paper proposes the applications of the cover, diversity, and functional traits of epiphytic lichens to assess environmental changes associated with succession in subtropical forests of southwest China. Bole lichens were sampled from 120 plots of eight representative forest types in the Ailao Mountains. Total cover, species richness, diversity and community structure of bole lichens differed significantly among forest types, and the highest cover and diversity occurred in the *Populus bonatii* secondary forest (PBSF). Sixty-one indicator species were associated with particular forest types and more than 50% occurred in the PBSF. Both cover and diversity of most lichen functional groups varied regularly during forest succession. Lichen pioneer species were not displaced by competitively superior species as succession proceeds and cyanolichens were more prevalent in secondary forests. The results also highlight the importance of habitat variables such as canopy openness, host diversity, forest age, tree size, the size of the largest tree, tree density, and basal area on the lichen community. Consequently, our findings support the notion that epiphytic lichens, in terms of cover, diversity, species composition and functional traits can be used as effective indicators for large-scale and long-term forest monitoring. More importantly, the narrowly lobed foliose group was the best candidate indicator of environmental conditions in this region. The combined application of lichen indicator species and functional groups seemed to be a more reliable and more powerful method for monitoring forest dynamics in subtropical montane ecosystems.

1. Introduction

Lichen epiphytes are an important and diverse component in forest ecosystems (Sillett and Antoine, 2004). In recent decades, epiphytic lichens have been successfully employed as indicators of forest ecosystem health worldwide (Sillett and Antoine, 2004) due to their high sensitivity to human disturbance and environmental change resulting from their physiological characteristics (Nash, 2008). Epiphytic lichen diversity has been proved to be strongly affected by environmental changes, including climate (Ellis and Coppins, 2010; Hauck, 2009), air pollution (Ellis and Coppins, 2010; Giordani et al., 2002; Hauck, 2009; Käffer et al., 2011; Svoboda et al., 2010), land-use (Hauck, 2009), and forest composition, structure and dynamics (Ellis and Coppins, 2010; Hedenås and Ericson, 2004; McMullin et al., 2010; Rogers and Ryel, 2008; Svoboda et al., 2010). The approach of epiphytic lichen diversity can provide an economic way to perform large-scale environmental monitoring in forest ecosystems (McCune, 2000; Will-Wolf et al., 2002), although obtaining meaningful information from enormous datasets is often time-consuming.

A promising approach for monitoring environmental conditions is to examine the distribution of lichen indicator species. While some authors claim that lichen indicators could be effective in examining trends of aspen forest succession in the Rocky Mountains (Rogers and Ryel, 2008; Rogers et al., 2009), Holz and Gradstein (2005) suggest that certain lichens are indicative of forest regeneration in Costa Rica. In fact, lichen indicators are more often used as surrogates for total biodiversity (Ellis, 2012; Marmor et al., 2011; Nascimbene et al., 2010). Although the relationships between indicators and habitat variables have been studied in the USA (McCune, 2000; Rogers et al., 2009; Will-Wolf et al., 2002), it remains unclear whether the lichen indicators, as well as total diversity, are similarly related to certain habitat variables. Furthermore, the lichen indicator approach restricted to forest

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stands includes several pitfalls because epiphytic lichens are more likely to be microhabitat-limited and/or dispersal-limited (Dufrêne and Legendre, 1997; Ellis, 2012; Rolstad et al., 2002). Therefore, some studies have focused on the combination of indicator species analysis (ISA) and other methods, which provide a better predication of the response of indicators to environmental change (Doering and Coxson, 2010; Giordani, 2006; Li et al., 2011b; Rogers et al., 2009). In the subtropical Ailao Mountains, for example, a combination of canonical correspondence analysis (CCA) and ISA found that *Sulcaria sulcata* is strictly associated with the PBSF and responds positively to increasing light availability (Li et al., 2011b).

Likewise, recent research suggests lichen functional traits (e.g., growth form, photobiont type and reproductive strategy) are suitable candidates for detecting the environmental changes in forest ecosystems (Ellis and Coppins, 2006; Giordani et al., 2012; Marini et al., 2011; Pinho et al., 2012; Stofer et al., 2006). The members of a functional group generally share more ecological roles than members of different groups (McCune, 1993). Functional characteristics of epiphytic species, independent of species diversity and composition, are expected to be directly associated with environmental variables, allowing for the possibility of broader-scale analysis (Ellis and Coppins, 2006; Giordani et al., 2012). For example, cyanolichens are old-growth associated species, especially adapted to more shady and humid habitats in boreal forest ecosystems (Ellis and Coppins, 2006; Hedenås and Ericson, 2000, 2004). However, available data is limited, hindering their application in environment monitoring. Additionally, when considering the inherent complexity of different forests, an obvious question – is this approach useful in highly diverse subtropical forest ecosystems? – has not yet been answered.

Here we focus on epiphytic lichens on trunks in two primary and six secondary forests in the subtropical Ailao Mountains, which are a major feature of Yunnan Province in southwest China. In this region, the evergreen broad-leaved forests have been largely destroyed due to human disturbances and many of them are now degraded to secondary forests, shrublands, tree plantations and croplands (Wu, 1983). Epiphytes comprise a substantial portion of total species richness in these forests (Chen et al., 2010; Li et al., 2011b; You, 1983), however, information on lichen species diversity and distribution, particularly their response to environmental change, is still lacking.

In the present study, we sought to combine ISA, CCA and functional trait analysis to characterize the epiphytic lichen response to successional habitat conditions. Our main objective is to estimate the effectiveness of epiphytic lichens for environmental assessment in subtropical forests. Specifically, we address two questions: (1) how do bole lichens respond to forest characteristic changes associated with succession and (2) which lichen species/functional group is the most responsive indicator associated with habitat variables? We anticipate that these findings will allow deeper insight into the effects of environmental variables on lichen flora and ultimately on the use of lichens as indicators of forest change in subtropical zones.

2. Materials and methods

2.1. Study area

The study was conducted in the Xujiaba region (2000–2750 m a.s.l.; 23°35′–24°44′N, 100°54′–101°30′E), a core area of the Ailao National Nature Reserve, covering 5100 ha on the northern crest of the Ailao Mountains in southwest China (You, 1983). The mountain range is included in the Indo-Burma biodiversity hotspot and is a priority region for biodiversity conservation (Myers et al., 2000; Olson and Dinerstein, 1998). The mean annual rainfall is 1947 mm, with 85% falling in the rainy season (May–October). The mean annual relative air humidity is 85% and annual mean temperature is 11.3 °C (Li et al., 2011b).

Two primary and six secondary forest types were selected for the study (Table 1). The PLF is the most extensive forest from 2000 to 2600 m a.s.l. and is characterized by moist, shaded conditions, while the PDMF is restricted to elevation above 2600 m, exposed to constant and intense wind and mist events. Six secondary forests in this area have resulted from heavy human disturbance such as clear cutting, fire, and grazing in the last century (Qiu and Xie, 1998). The forest landscape is characterized by extensive, continuous primary forests, archipelagos of small secondary fragments and high forest connectivity (You, 1983). The six successional series in this area include (1) TGSF-MOSF-OOSF-PLF, (2) TGSF-PBSF-OOSF-PLF, (3) MOSF-OOSF-PLF, (4) PBSF-OOSF-PLF, (5) ANSF-OOSF-PLF and (6) PYSF-OOSF-PLF (Qiu and Xie, 1998; Wang, 1983; You, 1983).

2.2. Sampling method

2.2.1. Plot design and stand characteristics

Fieldwork was carried out from October 2008 to June 2011. A total of 120 plots were set up in Xujiaba. Because the secondary forest fragment size differed substantially (the patch size was generally <0.1 ha and it was even less than 0.01 ha in the youngest TGSF) and considering the species-accumulation curve (Appendix A), 25 plots of 20 m × 20 m were randomly located in the PLF, 10 in the PDMF, 10 in the OOSF, and 15 plots in each of other five secondary forest types (Table 1). The plot size was always large enough to collect lichen species in each forest type (Appendix B).

In each plot, all trees with a height > 2.0 m and diameter at breast height (DBH) > 3.5 cm were recorded. In the TGSF, trees with DBH > 2.0 cm were recorded because the mean DBH was very small (Table 1). The DBH, max DBH of the largest tree (MDBH), host density, basal area and host richness were surveyed. Canopy openness was estimated in 10% of classes. Stand age was determined from available documentation (Deng et al., 1993; He et al., 2003; Young et al., 1992), employees of Ailaoshan Station, and Management Authority.

2.2.2. Lichen sampling

In each plot, 20 large (DBH > 10.0 cm) and 10 small (DBH 3.5–10.0 cm) trees were randomly selected for lichen sampling. In some plots, however, the number of large and small trees selected for analysis varied according to how many could be located within the plot. In the TGSF, there were very few trees with DBH > 3.5 cm, and smaller trees (DBH 2.0–3.5 cm) were selected.

A total of 3600 trees (30 trees per plot) were inventoried in the eight forest types. On each tree, lichens were sampled at three height intervals: 0–0.5, 0.5–1.3 and 1.3–2.0 m. At each interval, two 20-cm × 20-cm or 10-cm × 40-cm quadrats (with 256 square-shaped, equal-area grid cells) were placed on the north and the south side for each large tree and one quadrat for each small tree. On smaller trunks of the TGSF, lichens were sampled using 5 cm × 40 cm quadrats (Appendix B). Both coverage and frequency of occurrence of each species in the plots were recorded, and the raw data transformed to percentage values to reduce the sampling errors associated with quadrat size in the statistical analyses. Voucher specimens were identified and retained in the laboratory of Kunming Division of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

Table 1
Environmental conditions (mean) of eight forest types in the Ailao Mountains, southwest China. *Sources*: Deng et al. (1993), He et al. (2003), Qiu and Xie (1998), Wang (1983), You (1983), and Young et al. (1992).

	Forest type							
	Primary dwarf mossy forest (PDMF)	Primary *Lithocarpus* forest (PLF)	Old-aged oak secondary forest (OOSF)	Middle-aged oak secondary forest (MOSF)	*Populus bonatii* secondary forest (PBSF)	*Alnus nepalensis* secondary forest (ANSF)	*Pinus yunnanensis* secondary forest (PYSF)	*Ternstroemia gymnanthera* secondary forest (TGSF)
Dominant canopy species	*Lithocarpus crassifolius*; *Rhododendron irroratum*; *Clethra delavayi*; *Ilex corallina*; *Gaultheria griffithiana*	*Lithocarpus xylocarpus*; *Lithocarpus hancei*; *Castanopsis wattii*; *Schima noronhae*; *Stewartia pteropetiolata*	*Lithocarpus hancei*; *Vaccinium duclouxii*	*Lithocarpus hancei*; *Vaccinium duclouxii*; *Ternstroemia gymnanthera*	*Populus bonatii*; *Lithocarpus hancei*; *Vaccinium duclouxii*	*Alnus nepalensis*	*Pinus yunnanensis*; *Ternstroemia gymnanthera*	*Ternstroemia gymnanthera*; *Vaccinium duclouxii*; *Gaultheria forrestii*
Stand age (year)	>300.00	>300.00	110.00	48.67	36.00	28.67	35.00	<20.00
Basal area (m^2/ha)	48.00	77.31	53.02	55.17	29.88	18.03	52.23	42.45
Canopy openness (%)	30.00	5.80	8.00	31.00	51.67	61.67	61.00	31.67
Mean DBH (cm)	7.91	19.23	16.94	9.84	8.50	11.53	10.35	4.31
Tree density (trees/ha)	8272.50	1656.00	1532.50	5903.33	4696.67	1576.67	5226.67	22,933.33
MDBH (cm)	23.31	80.57	64.99	36.62	22.62	26.66	24.19	9.91
Richness of trees	15.90	15.72	12.00	15.73	8.87	2.73	4.60	5.67
Shannon–Wiener index of trees	1.93	2.33	1.93	1.87	1.49	0.28	0.86	1.00
Simpson index of trees	0.77	0.86	0.79	0.77	0.67	0.13	0.44	0.48
Plot size (m^2)	400	400	400	400	100–400	400	100	25

2.3. Data analysis

The statistical analyses described below in detail were performed using the statistical package R 2.14.2 (R Development Core Team, 2012).

2.3.1. Host diversity

Host diversity was determined using Shannon–Wiener index and Simpson index.

2.3.2. Bole lichen cover and diversity

Bole lichen diversity was evaluated using (1) α-diversity, measured as species richness per plot, (2) γ-diversity, the species number in each forest type, (3) β-diversity, calculated as γ/α giving an estimate of heterogeneity within the community, (4) Shannon–Wiener index and (5) Simpson index. Additionally, non-metric multidimensional scaling (NMDS) was performed with the *metaMDS* function in the package *vegan* (Oksanen et al., 2012) to estimate lichen species similarities among plots. The NMDS was done with Wisconsin double standardizations, the Bray–Curtis distance index and a maximum number of 1000 iterations. Stress values lower than 20% generally lead to usable pictures and interpretations.

Modified from previous studies (McCune, 1993; Nimis and Martellos, 2008), lichen species were divided into five 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); and three reproductive strategies: mainly by isidia (ISL), by soredia (SOL) and by sexual reproduction (SEL). The cover and diversity of functional groups were considered in two ways: the absolute value and their percentage contribution to total.

Differences in cover and diversity of lichen species and functional group among forest types were tested using one-way ANOVA, and Tukey's HSD test for multiple pair-wise comparisons. All data were checked for normality using Shapiro–Wilk test and homogeneity of variances using Bartlett's test. When the assumptions could not be satisfied after transformation, comparisons of non-normal data were made using the non-parametric Kruskal–Wallis test and Wilcoxon rang sum test.

To test the differences in lichen community between forest types, a matrix of 120 plots × 107 species was subjected to multi-response permutation procedure (MRPP). MRPP is a non-parametric, multivariate method used to make statistical comparisons among two or more *a priori* groups (McCune and Grace, 2002). The agreement statistic (A) represents the degree of within group homogeneity compared with the random expectation, P evaluates the likelihood of getting, by chance, a within-group distance as extreme or more extreme than that observed. In community ecology, A values are generally below 0.1 and $A > 0.3$ is considered high (McCune and Grace, 2002). We performed the MRPP with the *mrpp* function of the *vegan* package using Bray–Curtis index and 5000 permutations (Oksanen et al., 2012).

The *indval* function in the *labdsv* package (Roberts, 2012) was used for indicator species analysis (ISA; Dufrêne and Legendre, 1997) to determine individual species that are mainly associated with one forest type. The indicator value ranges from 0 (one species was absent from one forest type) to 1 (one species occurred in all plots of one forest type and was absent from other plots). The significance was tested using a Monte Carlo permutation with 1000 replicates.

Patterns of bole lichen species distribution in relation to environmental variables were determined using canonical correspondence analysis (CCA). CCA is one of the most popular constrained ordination techniques for direct gradient analysis in

Table 2
Total cover and diversity of bole lichens in the eight forest types in the Ailao Mountains, southwest China. Values marked with different letters represent significant differences ($P<0.05$).

	Forest type								χ^2	P
	PDMF	PLF	OOSF	MOSF	PBSF	ANSF	PYSF	TGSF		
Total cover (%)	0.82 ± 0.13a	0.60 ± 0.08a	0.23 ± 0.03d	2.81 ± 0.66b	13.69 ± 2.59e	4.20 ± 0.36c	2.01 ± 0.30b	4.89 ± 0.83c	87.92	<0.001
α-Diversity	13.60 ± 1.24d	7.12 ± 0.44b	6.80 ± 0.79b	25.00 ± 2.63ac	37.00 ± 1.92e	26.00 ± 1.20a	18.87 ± 1.33c	27.80 ± 2.34a	91.97	<0.001
β-Diversity	2.43	5.90	3.38	2.72	1.84	1.73	2.07	2.01		
γ-Diversity	33	42	23	68	68	45	39	56		
Shannon–Wiener index	2.16 ± 0.13b	1.60 ± 0.06c	1.57 ± 0.11c	2.66 ± 0.08a	2.92 ± 0.04d	2.54 ± 0.06a	2.12 ± 0.09b	2.65 ± 0.09a	87.35	<0.001
Simpson index	0.83 ± 0.03bc	0.74 ± 0.02d	0.73 ± 0.03de	0.90 ± 0.01a	0.92 ± 0.00f	0.88 ± 0.01ab	0.81 ± 0.02ce	0.89 ± 0.01a	80.84	<0.001

community ecology for describing community–environment relationships (McCune and Grace, 2002; Økland, 1996). After the species with an occurrence in fewer than five plots were excluded, a matrix of 120 plots × 65 species was subjected to CCA. Prior to the analysis, count data were $\log_{10}(x+1)$ transformed. To avoid multi-collinearity, the environmental data were assessed using the Akaike information criterion (AIC) and then a stepwise procedure was used to select a subset (Appendix C). When the variance inflation factor (VIF) of selected variables had a value less than 10, there was no redundancy in variables (Oksanen, 2011). Finally, a Monte Carlo permutation test was performed as an estimate of significance. These analyses were conducted using the *cca* function in the *vegan* package (Oksanen et al., 2012).

Finally, linear regression models were used to test the effect of single environmental variable on cover and diversity of lichen species and functional group.

3. Results

3.1. Cover and diversity

One hundred and seven lichen species were found on 3600 trunks in the 120 plots. Fifty-three percent (57) of species occurred in primary forests whereas 86% (92) were found in secondary forests. Significant differences in diversity and cover were detected among the eight forest types, despite, in some cases, there being no significant variations between forest types (Table 2). The total cover, α-diversity, γ-diversity, Shannon–Wiener index and Simpson index were significantly higher in the PBSF, and lowest in the OOSF.

The β-diversity was highest in the PLF and lowest in the ANSF. This analysis was consistent with those obtained from NMDS (Fig. 1). Moreover, the PLF, the PDMF and the OOSF were clearly separated from the other five forest types in the NMDS ordination, while the separations were less distinct among the remaining types.

3.2. Species composition

The MRPP analysis indicated significant differences in lichen assemblage structure among forest types ($A=0.271$, $P<0.001$). Subsequent pairwise comparisons indicated significant differences between all forest types, although all A values were relatively low (Table 3). Furthermore, 9% (10) of lichen species occurred across all forest types, while 32% (34) were unique to certain forest types. The number of unique species was highest in the PLF (12), followed by the MOSF (11), the PBSF (7), the PDMF (3) and the TGSF (1), and with no unique species observed in the other three forest types.

The ISA suggested that 61 epiphytic lichen species were significantly associated with particular forest types (Table 4). More than 50% (32) of indicator species occurred in the PBSF. Seven indicator species occurred in the ANSF and the TGSF, six in the MOSF, and four in the PDMF and the PYSF. Only *Graphis tenella* was an indicator for the PLF, but no species was significantly associated with the OOSF.

Table 3
Effect size A with P (<0.01**; <0.001***) values for MRPP pairwise comparisons of bole lichen community composition between forest types in the Ailao Mountains, southwest China.

	Forest type						
	PDMF	PLF	OOSF	MOSF	PBSF	ANSF	PYSF
PLF	0.083***						
OOSF	0.081**	0.034**					
MOSF	0.066***	0.097***	0.134***				
PBSF	0.171***	0.213***	0.226***	0.135***			
ANSF	0.197***	0.212***	0.242***	0.179***	0.201***		
PYSF	0.201***	0.261***	0.282***	0.188***	0.255***	0.265***	
TGSF	0.151***	0.200***	0.209***	0.072***	0.109***	0.176***	0.148***

The CCA ordination was significant ($P=0.005$), revealing that bole lichen species composition was related to the measured environmental variables (Fig. 2). The first axis explained 15.5% of the total variation and was strongly associated with forest age ($r=0.842$), canopy openness ($r=-0.811$), MDBH ($r=0.771$), host richness ($r=0.691$) and basal area ($r=0.667$). The second axis, representing 6.8% of the variation, was closely correlated with mean DBH ($r=-0.651$) and tree density ($r=0.589$). The third axis (not shown) accounted for 3.4% of total variation but was slightly related to these variables. Also, axis 1 and 2 separated the PLF, the PDMF and the ANSF from the other five forests clearly (Fig. 2b). Furthermore, species with a preference for older and sheltered plots

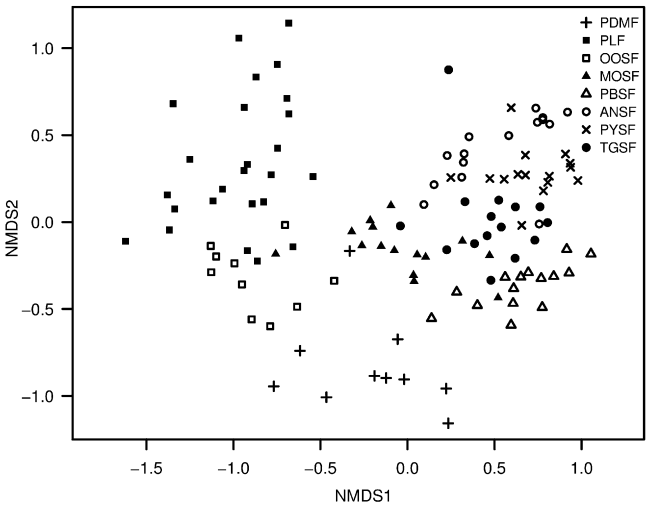

Fig. 1. Similarity of bole lichen species in 120 plots of eight forest types in the Ailao Mountains, southwest China. Two-dimensional scatterplot of NMDS based on Bray–Curtis distance index (stress = 17.7%; $r^2=0.97$ for nonmetric fit and $r^2=0.86$ for linear fit of ordination distances with observed dissimilarities).

Table 4
Indicator species analysis of bole lichens of eight forest types in the Ailao Mountains, southwest China. Indicator values and *P* values for significant indicator species are shown in bold type. BFL: broadly lobed foliose lichens; CRL: crustose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

Species	Abbr.	Functional group	Indicator value								*P*
			PDMF	PLF	OOSF	MOSF	PBSF	ANSF	PYSF	TGSF	
Amandinea punctata	AMPU	CRL/SEL	0.000	0.021	< 0.001	0.013	0.064	**0.833**	0.006	0.015	**0.001**
Anzia hypoleucoides	ANHY	NFL/SEL	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.160
Anzia leucobatoides f. *hypomelaena*	ANLE	NFL/SEL	0.000	0.000	0.000	0.119	0.115	0.000	0.000	0.114	0.210
Anzia physoidea	ANPH	NFL/SEL	0.030	0.000	0.000	0.023	0.006	0.000	0.000	0.053	0.529
Anzia cf. *semiteres*	ANSE	NFL/SEL	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.133	0.084
Arthonia cinnabarina	ARCI	CRL/SEL	0.000	0.080	0.000	0.000	0.000	0.000	0.000	0.000	0.173
Bryoria confusa	BRCO	FRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.789
Caloplaca flavorubescens	CAFL	CRL/SEL	0.000	0.000	0.000	0.000	0.193	**0.306**	< 0.001	0.000	**0.007**
Cetrelia braunsiana	CEBR	BFL/ISL	0.000	0.000	0.000	**0.200**	0.000	0.000	0.000	0.000	**0.014**
Cetrelia olivetorum	CEOL	BFL/SOL	0.008	< 0.001	< 0.001	0.133	**0.562**	0.014	0.042	0.216	**0.001**
Cladonia coniocraea	CLCO	FRL/SOL	0.149	< 0.001	0.002	0.124	0.025	0.005	**0.626**	0.024	**0.001**
Cladonia furcata	CLFU	FRL/SEL	**0.900**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.001**
Coccocarpia erythroxyli	COER	CYL/SEL	0.008	0.001	0.000	0.051	**0.631**	0.000	0.000	< 0.001	**0.001**
Coenogonium luteum	COLU	CRL/SEL	0.000	0.006	0.000	0.066	0.024	0.000	0.000	0.000	0.337
Diorygma hieroglyphicum	DIHI	CRL/SEL	0.000	0.031	0.012	**0.161**	0.000	0.000	0.000	0.005	**0.019**
Diorygma junghuhnii	DIJU	CRL/SEL	0.109	0.000	0.000	0.060	0.000	0.000	0.000	0.000	0.095
Diorygma macgregorii	DIMA	CRL/SEL	0.000	0.014	0.018	0.020	0.000	0.000	0.000	0.024	0.924
Diorygma soozana	DISO	CRL/SEL	0.007	0.012	0.003	0.265	**0.309**	0.033	0.019	0.286	**0.008**
Dirinaria applanata	DIAP	NFL/SOL	0.000	0.000	0.000	0.007	0.084	0.000	0.000	0.036	0.256
Erioderma meiocarpum	ERME	CYL/SEL	0.000	0.000	0.000	0.000	0.133	0.000	0.000	0.000	0.091
Everniastrum cirrhatum	EVCI	NFL/SEL	0.006	0.000	0.001	0.005	**0.632**	0.014	0.000	0.004	**0.001**
Everniastrum nepalense	EVNE	NFL/SEL	< 0.001	0.000	< 0.001	0.093	0.231	**0.280**	0.081	0.264	**0.012**
Everniastrum rhizodendroideum	EVRH	NFL/SEL	0.000	0.004	0.000	0.011	0.000	0.000	0.000	0.049	0.554
Fissurina dumastii	FIDU	CRL/SEL	0.021	0.002	0.014	0.040	0.000	0.000	0.000	0.000	0.916
Graphina fissofurcata	GRFI	CRL/SEL	0.032	0.163	0.018	**0.240**	0.129	0.116	0.013	0.102	**0.032**
Graphis alpestris	GRAL	CRL/SEL	0.165	0.247	0.160	**0.265**	0.000	0.033	0.002	0.012	**0.001**
Graphis hossei	GRHO	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Graphis longiramea	GRLO	CRL/SEL	0.027	0.125	0.000	0.000	0.005	0.000	0.000	0.000	0.117
Graphis proserpens	GRPR	CRL/SEL	0.007	0.031	0.000	0.154	0.068	0.002	0.003	**0.219**	**0.014**
Graphis tenella	GRTE	CRL/SEL	0.003	**0.330**	0.018	0.294	< 0.001	0.086	0.000	0.001	**0.001**
Haematomma africanum	HAAF	CRL/SEL	0.000	0.000	0.000	0.010	**0.465**	0.013	0.000	0.000	**0.001**
Haematomma persoonii	HAPE	CRL/SEL	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.181
Haematomma puniceum subsp. *pacificum*	HAPU	CRL/SEL	0.000	0.000	0.000	0.000	0.077	0.234	**0.291**	0.119	**0.015**
Hemithecium chapadanum	HECH	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Heterodermia boryi var. *boryi*	HEBB	NFL/SEL	0.004	0.000	0.000	0.014	**0.525**	0.263	0.003	0.056	**0.001**
Heterodermia comosa	HECO	NFL/SEL	0.000	0.000	0.000	0.000	0.004	**0.940**	0.001	0.015	**0.001**
Heterodermia dendritica	HEDE	NFL/SEL	< 0.001	< 0.001	0.000	0.018	0.123	**0.634**	0.039	0.137	**0.001**
Heterodermia hypoleuca	HEHY	NFL/SEL	0.000	0.000	0.000	0.004	**0.962**	< 0.001	0.001	0.005	**0.001**
Hypogymnia yunnanensis	HYYU	NFL/SEL	0.000	0.000	0.000	0.025	0.020	< 0.001	**0.536**	0.267	**0.001**
Hypotrachyna adducta	HYAD	NFL/SEL	0.000	0.000	0.000	0.000	0.005	**0.745**	0.006	0.075	**0.001**
Hypotrachyna pseudosinuosa	HYPS	NFL/SOL	0.019	< 0.001	0.001	0.101	0.152	0.050	0.290	**0.372**	**0.001**
Hypotrachyna sinuosa	HYSI	NFL/SOL	0.000	0.000	0.000	0.000	**0.317**	0.006	0.000	0.000	**0.002**
Laurera megasperma	LAME	CRL/SEL	0.000	0.080	0.000	0.000	0.000	0.000	0.000	0.000	0.247
Lecanora allophana	LEAO	CRL/SEL	0.001	0.019	0.011	0.151	0.176	0.151	**0.210**	0.160	**0.044**
Lecanora argentata	LEAR	CRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.797
Lecidella euphorea	LEEU	CRL/SEL	0.000	0.000	0.000	**0.267**	0.000	0.000	0.000	0.000	**0.002**
Leioderma sorediatum	LESO	CYL/SOL	0.033	0.000	0.000	0.092	0.091	0.001	0.001	**0.519**	**0.001**
Lepraria incana	LEIN	CRL/SOL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Lepraria lobificans	LELO	CRL/SOL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Leprocaulon arbuscula	LEARB	FRL/ISL	0.000	0.042	0.013	0.070	0.000	0.000	0.000	0.000	0.438
Leptogium azureum	LEAZ	CYL/SEL	0.020	0.001	0.010	0.119	**0.614**	0.111	< 0.001	0.052	**0.001**
Leptogium burgessii	LEBU	CYL/SEL	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.775
Leptogium menziesii	LEME	CYL/SEL	0.000	0.000	0.000	0.009	**0.742**	0.026	0.007	< 0.001	**0.001**
Leptogium saturninum	LESA	CYL/ISL	0.000	0.000	0.000	0.000	**0.243**	0.126	0.000	0.000	**0.011**
Lobaria isidiophora	LOIS	BFL/ISL	0.000	0.000	0.000	0.000	**0.333**	0.000	0.000	0.000	**0.001**
Lobaria isidiosa	LOID	CYL/ISL	0.000	0.000	0.000	< 0.001	**0.514**	0.061	0.000	0.008	**0.001**
Lobaria kurokawae	LOKU	CYL/SEL	0.000	0.000	0.000	< 0.001	**0.265**	0.000	0.000	0.000	**0.004**
Lobaria retigera	LORE	CYL/ISL	0.104	< 0.001	< 0.001	0.090	**0.503**	0.009	< 0.001	0.046	**0.001**
Menegazzia terebrata	METE	NFL/SOL	0.005	0.000	0.000	0.043	**0.542**	< 0.001	0.056	0.139	**0.002**
Micarea misella	MIMI	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Mycoblastus sanguinarius	MYSA	CRL/SEL	0.000	0.000	0.000	0.133	0.000	0.000	0.000	0.000	0.088
Myelochroa irrugans	MYIR	NFL/SEL	0.000	0.000	0.000	0.001	0.073	**0.821**	0.003	0.013	**0.001**
Nephroma helveticum	NEHE	CYL/ISL	0.001	0.000	0.000	0.001	**0.503**	0.004	0.003	0.030	**0.001**
Nephromopsis ornata	NEOR	BFL/SEL	0.016	0.000	0.000	0.130	0.049	0.000	0.024	0.131	0.198
Nephromopsis pallescens	NEPA	BFL/SEL	0.000	0.000	0.000	0.047	0.207	0.000	0.020	**0.444**	**0.001**
Nephromopsis stracheyi	NEST	BFL/SEL	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.819
Ochrolechia trochophora	OCTR	CRL/SEL	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.797
Oropogon asiaticus	ORAS	FRL/SEL	0.000	0.000	0.000	0.000	0.133	0.000	0.000	0.000	0.075
Pannaria rubiginosa	PARU	CYL/SEL	0.000	0.000	0.000	< 0.001	**0.817**	< 0.001	0.000	0.021	**0.001**
Parmelia adaugescens	PAAD	NFL/SEL	0.000	0.000	0.000	0.055	0.043	0.000	< 0.001	**0.494**	**0.001**
Parmelina quercina	PAQU	NFL/SEL	0.000	0.000	0.000	0.030	0.055	0.004	0.000	**0.188**	**0.023**

Table 4 (*Continued*)

Species	Abbr.	Functional group	Indicator value								*P*
			PDMF	PLF	OOSF	MOSF	PBSF	ANSF	PYSF	TGSF	
Parmotrema eciliatum	PAEC	BFL/SEL	0.000	0.000	0.000	<0.001	**0.841**	0.013	<0.001	0.001	**0.001**
Parmotrema reticulatum	PARE	BFL/SOL	0.000	0.000	0.000	<0.001	**0.602**	0.048	0.028	0.039	**0.001**
Parmotrema tinctorum	PATI	BFL/ISL	<0.001	<0.001	0.000	0.059	0.248	0.083	0.154	**0.410**	**0.001**
Peltigera rufescens	PERU	CYL/SEL	**0.819**	0.000	0.000	0.000	0.013	0.000	0.000	0.002	**0.001**
Pertusaria composita	PECM	CRL/SOL	0.011	<0.001	0.002	0.075	**0.764**	0.017	0.006	0.099	**0.001**
Pertusaria hemisphaerica	PEHE	CRL/SOL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.821
Pertusaria multipuncta	PEMU	CRL/SOL	0.000	0.066	0.000	0.000	0.011	0.000	0.000	0.000	0.283
Pertusaria pertusa	PEPE	CRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.802
Pertusaria tetrathalamia	PETE	CRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.779
Pertusaria trachythallina	PETR	CRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.790
Phaeophyscia ciliata	PHCI	NFL/SEL	0.000	0.000	0.000	0.000	**0.366**	0.027	0.000	0.001	**0.002**
Phyllopsora cf. *furfuracea*	PHFU	CRL/ISL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Platygramme discurrens	PLDI	CRL/SEL	0.000	0.005	0.000	0.117	0.000	0.000	0.000	0.000	0.067
Porina nucula	PONU	CRL/SEL	0.000	0.106	0.012	0.000	0.000	0.000	0.000	0.000	0.083
Pyrenula concatervans	PYCO	CRL/SEL	0.000	0.092	0.012	0.021	0.000	0.000	0.000	0.000	0.168
Pyrenula dermatodes	PYDE	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Pyrenula leucostoma	PYLE	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Pyrenula subferruginea	PYSU	CRL/SEL	0.000	0.080	0.000	0.000	0.000	0.000	0.000	0.000	0.151
Ramalina conduplicans	RACO	FRL/SEL	0.000	0.000	0.000	0.004	**0.597**	0.265	0.022	0.027	**0.001**
Ramalina peruviana	RAPE	FRL/SOL	0.000	0.000	0.000	0.000	**0.185**	0.000	0.000	0.005	**0.019**
Ramalina sinensis	RASI	FRL/SEL	0.000	0.000	0.000	0.000	**0.262**	0.003	0.000	0.000	**0.004**
Rimelia cetrata	RICE	BFL/SEL	0.000	<0.001	0.000	0.006	**0.764**	0.071	0.016	0.067	**0.001**
Sticta duplolimbata	STDU	CYL/ISL	**0.347**	0.002	0.034	0.201	0.205	<0.001	0.001	0.068	**0.002**
Sticta fuliginosa	STFU	CYL/ISL	0.000	0.000	0.000	0.000	**0.611**	0.000	0.000	0.044	**0.001**
Sticta gracilis	STGR	CYL/SEL	0.201	0.000	<0.001	**0.255**	0.175	0.076	<0.001	0.135	**0.014**
Sticta nylanderiana	STNY	BFL/SEL	**0.155**	0.000	0.000	0.006	0.059	0.000	0.000	0.000	**0.026**
Sticta weigelii	STWE	CYL/ISL	0.000	0.000	0.000	0.004	**0.398**	0.013	0.000	0.000	**0.001**
Sulcaria sulcata var. *sulcata*	SUSS	FRL/SEL	0.000	0.000	0.000	0.004	**0.611**	0.000	<0.001	0.025	**0.001**
Thalloloma anguinum	THAN	CRL/SEL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.784
Thecaria quassiicola	THQU	CRL/SEL	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Trypethelium variolosum	TRVA	CRL/SEL	0.000	0.018	0.056	0.000	0.000	0.000	0.000	0.000	0.308
Usnea florida	USFL	FRL/SEL	0.000	0.000	0.000	0.015	**0.427**	0.136	0.103	0.113	**0.001**
Usnea glabrescens	USGL	FRL/SOL	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.793
Usnea nidifica	USNI	FRL/SOL	0.000	0.000	0.000	0.000	**0.267**	0.000	0.000	0.000	**0.004**
Usnea rubicunda	USRU	FRL/SOL	0.000	0.000	0.000	0.000	**0.226**	0.000	0.000	0.010	**0.007**
Usnea sp.	USSP	FRL/SEL	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.033	1.000

(e.g., *Diorygma hieroglyphicum*, *Diorygma macgregorii*, *Graphina fissofurcata*, *Graphis alpestris, Graphis longiramea, Graphis tenella*, *Leprocaulon arbuscula* and *Pyrenula concatervans*) were positively correlated with axis 1. Species associated with younger and exposed plots (e.g., *Haematomma puniceum* subsp. *pacificum* and *Hypotrachyna adducta*) were negatively correlated with axis 1. Along the second axis, *Cladonia furcata*, *Peltigera rufescens* and *Sticta nylanderiana* were mainly associated with the plots with higher density and smaller DBH, while *Leptogium saturninum*, *Caloplaca flavorubescens* and *Heterodermia comosa* preferentially occurred in the plots with the opposite characteristics.

3.3. Impact of environmental variables

The diversity and cover of epiphytic lichens were significantly related to habitat variables (Table 5). Species richness, Shannon–Wiener index and Simpson index were significantly and positively related to canopy openness and tree density, and negatively related to other variables. The relationships between cover and variables showed similar results, although, tree density was not a significant factor. The $r^2_{adj.}$ values for all regressions varied from 0.024 to 0.454. Canopy openness was the most important variable to explain the variations in lichen diversity and cover ($r^2_{adj.} = 0.237–0.446$), followed by stand age ($r^2_{adj.} = 0.146–0.454$) and MDBH ($r^2_{adj.} = 0.109–0.368$).

3.4. Functional traits

Both cover and species richness differed significantly for the eight lichen functional groups across all forest types ($\chi^2 = 48.56–99.66$, $P < 0.001$). Moreover, the analysis of cover and richness, based on their percent contribution, showed different patterns during secondary forest successions (Fig. 3). The relative coverages of crustose and sexual functional groups generally declined from the PLF to the earlier stages of successions, while those of broadly lobed foliose, fruticose, narrowly lobed foliose groups increased (Fig. 3a–h). The coverages of cyanolichen, isidiate and sorediate groups also increased in some, but not all, succession series. The species number of functional group showed similar patterns (Fig. 3a′–h′). Additionally, crustose, cyanolichen and sexual groups presented higher values in the PDMF.

The cover and species richness of functional groups, as well as their percent contribution to the total, were significantly associated with habitat variables (Table 5). These were positively related to canopy openness and tree density, and negatively related to other factors, with the exceptions that the percent values of crustose and sexual groups showed the opposite gradient. Overall, the effects of canopy openness ($r^2_{adj.} = 0.050–0.639$) were stronger than those of other variables, whereas tree density had very low effects on lichen functional groups ($r^2_{adj.} = 0.033–0.209$).

In terms of functional group, narrowly lobed foliose lichens were the most responsive group and significantly associated with most variables, and the $r^2_{adj.}$ values varied from 0.053 to 0.632.

Table 5
Linear regression ($r^2_{adj.}$) on the influence of environmental variables on bole lichen species and functional group in the eight forest types in the Ailao Mountains, southwest China.

	Variables								
	Stand age	Basal area	Canopy openness	Mean DBH	Tree density	Max DBH	Richness of trees	Shannon–Wiener index of trees	Simpson index of trees
Lichen species									
Total cover	0.146*** (−)	0.245*** (−)	0.237*** (+)	0.108*** (−)	ns	0.109*** (−)	0.081*** (−)	0.050** (−)	0.024* (−)
Richness	0.454*** (−)	0.364*** (−)	0.446*** (+)	0.357*** (−)	0.072** (+)	0.365*** (−)	0.164*** (−)	0.155*** (−)	0.083*** (−)
Shannon–Wiener index	0.391*** (−)	0.276*** (−)	0.351*** (+)	0.382*** (−)	0.104*** (+)	0.368*** (−)	0.077** (−)	0.107*** (−)	0.054** (−)
Simpson index	0.275*** (−)	0.173*** (−)	0.249*** (+)	0.278*** (−)	0.087*** (+)	0.265*** (−)	0.038* (−)	0.075** (−)	0.042* (−)
Lichen functional group									
Cover per group									
BFL	0.092*** (−)	0.149*** (−)	0.138*** (+)	0.079** (−)	ns	0.069** (−)	0.034** (−)	ns	ns
CRL	0.089*** (−)	0.202*** (−)	0.165*** (+)	0.059** (−)	ns	0.051** (−)	0.025* (−)	ns	ns
CYL	0.067** (−)	0.131*** (−)	0.105*** (+)	0.062** (−)	ns	0.074** (−)	ns	ns	ns
FRL	0.092*** (−)	0.179*** (−)	0.256*** (+)	0.048** (−)	ns	0.070** (−)	0.083*** (−)	0.063** (−)	0.039* (−)
NFL	0.240*** (−)	0.341*** (−)	0.361*** (+)	0.156*** (−)	ns	0.179*** (−)	0.237*** (−)	0.197*** (−)	0.148*** (−)
ISL	0.158*** (−)	0.206*** (−)	0.187*** (+)	0.189*** (−)	0.058** (+)	0.162*** (−)	0.063** (−)	ns	ns
SEL	0.131*** (−)	0.287*** (−)	0.253*** (+)	0.068** (−)	ns	0.084*** (−)	0.103*** (−)	0.083*** (−)	0.064** (−)
SOL	0.121*** (−)	0.142*** (−)	0.165*** (+)	0.117*** (−)	ns	0.101*** (−)	0.038* (−)	ns	ns
Percent to total cover									
BFL	0.378*** (−)	0.117*** (−)	0.227*** (+)	0.348*** (−)	0.209*** (+)	0.318*** (−)	0.108*** (−)	0.106*** (−)	0.048** (−)
CRL	0.480*** (+)	0.277*** (+)	0.639*** (−)	0.462*** (+)	0.136*** (−)	0.564*** (+)	0.340*** (+)	0.387*** (+)	0.260*** (+)
CYL	ns	ns	ns	0.042* (−)	ns	0.040* (−)	0.030* (+)	ns	0.028* (+)
FRL	0.056** (−)	ns	0.302*** (+)	0.036* (−)	ns	0.085*** (−)	0.110*** (−)	0.142*** (−)	0.109*** (−)
NFL	0.443*** (−)	0.257*** (−)	0.632*** (+)	0.231*** (−)	0.053** (+)	0.355*** (−)	0.574*** (−)	0.607*** (−)	0.505*** (−)
ISL	ns	ns	0.051** (+)	0.133*** (−)	0.062** (+)	0.111*** (−)	ns	ns	ns
SEL	0.229*** (+)	0.025* (+)	0.232*** (−)	0.344*** (+)	0.192*** (−)	0.329*** (+)	0.065** (+)	0.081*** (+)	0.024* (+)
SOL	0.252*** (−)	ns	0.222*** (+)	0.297*** (−)	0.170*** (+)	0.292*** (−)	0.074** (−)	0.087*** (−)	0.030* (−)
Species number per group									
BFL	0.565*** (−)	0.319*** (−)	0.571*** (+)	0.391*** (−)	0.099*** (+)	0.436*** (−)	0.370*** (−)	0.331*** (−)	0.211*** (−)
CRL	0.093*** (−)	0.032* (−)	0.050** (+)	ns	ns	ns	ns	ns	ns
CYL	0.138*** (−)	0.180*** (−)	0.093*** (+)	0.200*** (−)	0.033* (+)	0.179*** (−)	ns	ns	ns
FRL	0.334*** (−)	0.344*** (−)	0.512*** (+)	0.319*** (−)	0.033* (+)	0.330*** (−)	0.180*** (−)	0.164*** (−)	0.086*** (−)
NFL	0.541*** (−)	0.441*** (−)	0.577*** (+)	0.414*** (−)	0.107*** (+)	0.442*** (−)	0.336*** (−)	0.312*** (−)	0.207*** (−)
ISL	0.253*** (−)	0.190*** (−)	0.188*** (+)	0.163*** (−)	ns	0.172*** (−)	ns	ns	ns
SEL	0.416*** (−)	0.355*** (−)	0.409*** (+)	0.306*** (−)	0.065** (+)	0.319*** (−)	0.178*** (−)	0.155*** (−)	0.088*** (−)
SOL	0.476*** (−)	0.326*** (−)	0.530*** (+)	0.486*** (−)	0.116*** (+)	0.466*** (−)	0.174*** (−)	0.208*** (−)	0.120*** (−)
Percent to total species number									
BFL	0.435*** (−)	0.148*** (−)	0.534*** (+)	0.319*** (−)	0.082*** (+)	0.396*** (−)	0.380*** (−)	0.421*** (−)	0.317*** (−)
CRL	0.494*** (+)	0.331*** (+)	0.524*** (−)	0.559*** (+)	0.135*** (−)	0.598*** (+)	0.228*** (+)	0.328*** (+)	0.218*** (+)
CYL	ns	ns	ns	0.051** (−)	ns	0.031* (−)	0.064** (+)	0.025* (+)	0.039* (+)
FRL	0.103*** (−)	0.108*** (−)	0.309*** (+)	0.186*** (−)	ns	0.208*** (−)	0.076** (−)	0.112*** (−)	0.066** (−)
NFL	0.533*** (−)	0.309*** (−)	0.608*** (+)	0.389*** (−)	0.103*** (+)	0.445*** (−)	0.432*** (−)	0.498*** (−)	0.393*** (−)
ISL	0.054** (−)	ns	ns	ns	ns	ns	ns	ns	ns
SEL	0.202*** (+)	0.052** (+)	0.172*** (−)	0.221*** (+)	0.051** (−)	0.225*** (+)	ns	0.068** (+)	0.037* (+)
SOL	0.150*** (−)	0.060** (−)	0.234*** (+)	0.270*** (−)	0.088*** (+)	0.267*** (−)	0.044* (−)	0.125*** (−)	0.095*** (−)

Not significant: ns. (+): positive trend; (−): negative trend. BFL: broadly lobed foliose lichens, CRL: crustose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

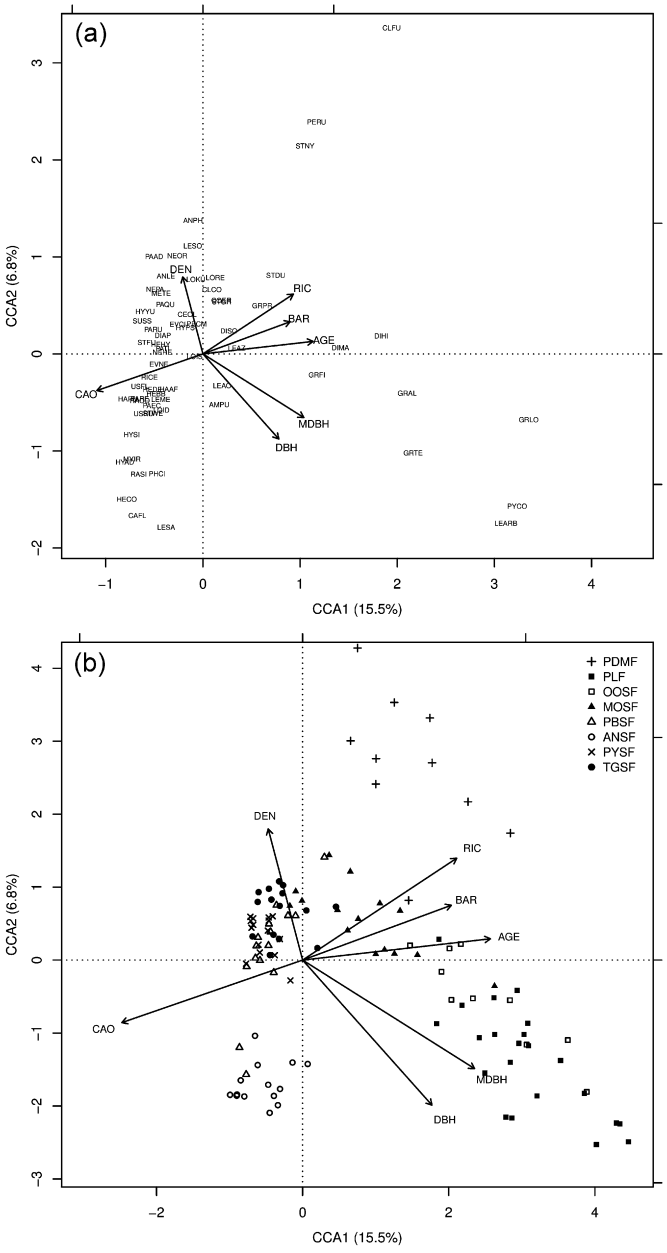

Fig. 2. Bole lichen species and environmental variables on the biplot of CCA of axis 1 and axis 2: (a) ordination of lichen species; (b) ordination of sampling plots. The inertia is 2.103 and the contributions of axes to total variance in species composition are labeled in parentheses. Abbreviations of species are given in Table 4. Stand age: AGE; basal area: BAR; canopy openness: CAO; mean DBH: DBH; tree density: DEN; max DBH of the largest tree: MDBH; host richness: RIC.

Conversely, both cyanolichen ($r^2_{adj.} = 0.025–0.200$) and isidiate ($r^2_{adj.} = 0.051–0.253$) groups were significantly affected by the fewest variables, and of those DBH was the most important variable.

4. Discussion

4.1. Bole lichen cover and diversity potential response to environmental change

Significant response of bole lichens to forest type was detected in this study. Primary forests had lower γ-diversity and α-diversity than secondary forests. This certainly does not imply that primary forests are not suitable for the establishment of lichens because most species tended to occur in the canopy due to too low light availability in the understory (Li L.H. et al., 2011a, Li S. et al., 2011b; Li et al., 2007). This pattern is in accordance with earlier studies showing that some lichens persist higher up in the canopy in old forests compared to young forests where they dwell further down the trunks (Hedenås and Ericson, 2000; McCune, 1993). Accordingly, the higher diversity in secondary forests can mainly be attributed to extensive primary forests and high forest connectivity, since primary forests can serve as a persistent source of lichen propagules (Dettki et al., 2000; Li et al., 2011b).

Furthermore, the analysis of β-diversity indicated that more heterogeneous lichen communities occurred in primary than in secondary forests, in general agreement with results on macrolichen litter (Li et al., 2011b) and forest structure heterogeneity (You, 1983) in the same area.

Our study also provided useful information about the complexity of the response of epiphytic lichens to environmental variables. An earlier study highlighted the importance of canopy openness, MDBH and host diversity on the macrolichen community in this region (Li et al., 2011b). For example, canopy openness, a proxy for the combination of light, humidity and temperature, proved to be the most important factor affecting epiphytic lichen distribution. Similarly, a number of studies suggest that these variables can drive changes in bole lichen flora in boreal and temperate regions (McCune, 1993; McMullin et al., 2010; Peck and McCune, 1997; Rogers and Ryel, 2008; Sillett and Goslin, 1999). However, the response of lichens to certain factors can vary widely with forest type. Lichen diversity, for example, increases with stand age in aspen forests (Hedenås and Ericson, 2004; Rogers and Ryel, 2008), decreases in subtropical forests (this study), but does not change significantly in the Italian forest landscape (Giordani et al., 2012).

4.2. Bole lichen individual species potential response to environmental change

Lichen species composition differed significantly among forest types and most indicators were found in the PBSF, and these findings were corroborated by the CCA ordinations. According to an earlier study based on litterfall data (Li et al., 2011b), 11 macrolichen indicators are significantly associated with the canopies of the MOSF in this area. Interestingly, most of them became indicators associated with the trunks of the PBSF. A possible explanation is that lichen indicators show similar response patterns to similar microhabitats offered by different forest types. For example, both the trunks of the PBSF and the canopies of the MOSF offered humid but exposed niches for *Lobaria isidiophora* (Table 6). This supports the view that lichen indicators are niche specialists, dependent on forest structural attribute rather than forest type (Ellis, 2012). In addition, 57 indicators and another eight species were subjected to CCA. The first axis is interpreted as succession gradients, which were accompanied by increasing stand age, DBH, host richness and basal area, and decreasing canopy openness. The second axis is a gradient of trunk traits from sparse, large to dense, small trees within stand, which resulted from altitude (from the PLF to the PDMF) and succession (from secondary forests to the PLF) (You, 1983). As trunk density increases, the number of humid, shaded microhabitats may increase, leading to the increased colonization of certain lichens in more open forests (McMullin et al., 2010; Sillett and Antoine, 2004). Moreover, the concentrated distribution of lichens around the centroid showed that high lichen diversity would occur in early-secondary forests with intermediate environmental conditions (Li et al., 2011b, 2007).

In accordance with other results (Fabiszewski and Szczepańska, 2010; Hale, 1967; Li et al., 2011b; Wirth, 2010), indicators and some non-indicator species have important ecological implications in the Ailao Mountains. Four lichen species, including *Leptogium*

Table 6
Bole lichen indicator species (including some non-indicator species) and associated environmental conditions in the Ailao Mountains, southwest China. Indicator species are shown in bold type. *Sources*: Barkman (1958), Fabiszewski and Szczepańska (2010), Hale (1967), Käffer et al. (2011), Li et al. (2011b), Wirth (2010), and You (1983).

Environmental condition	Indicator species (including some non-indicator species)
Humid habitat (without consideration of light level)	*Arthonia cinnabarina*; ***Coccocarpia erythroxyli***; *Erioderma meiocarpum*; ***Haematomma africanum***; ***Leptogium azureum***; *Leptogium burgessii*; ***Menegazzia terebrata***; *Mycoblastus sanguinarius*; ***Nephroma helveticum***; ***Parmotrema reticulatum***; *Phyllopsora* cf. *furfuracea*; *Trypethelium variolosum*
Exposed habitat (without consideration of humidity level)	***Amandinea punctata***; ***Cladonia furcata***; ***Everniastrum cirrhatum***; ***Everniastrum nepalense***; *Everniastrum rhizodendroideum*; ***Heterodermia boryi* var. *boryi***; ***Heterodermia comosa***; ***Heterodermia dendritica***; ***Heterodermia hypoleuca***; ***Hypotrachyna adducta***; ***Hypotrachyna pseudosinuosa***; ***Hypotrachyna sinuosa***; ***Lecanora allophana***; ***Myelochroa irrugans***; ***Parmelia adaugescens***; ***Parmelina quercina***; ***Parmotrema tinctorum***; ***Peltigera rufescens***; ***Pertusaria composita***; ***Phaeophyscia ciliata***; ***Rimelia cetrata***; ***Ramalina conduplicans***; ***Ramalina peruviana***; ***Ramalina sinensis***; ***Usnea nidifica***; ***Usnea rubicunda***; *Usnea* sp.
Humid and shaded habitat	*Coenogonium luteum*; ***Diorygma hieroglyphicum***; *Diorygma junghuhnii*; *Diorygma macgregorii*; ***Diorygma soozana***; *Fissurina dumastii*; ***Graphina fissofurcata***; ***Graphis alpestris***; *Graphis hossei*; *Graphis longiramea*; ***Graphis proserpens***; ***Graphis tenella***; *Hemithecium chapadanum*; *Lepraria incana*; *Lepraria lobificans*; *Leprocaulon arbuscula*; ***Lobaria isidiosa***; ***Lobaria kurokawae***; ***Lobaria retigera***; *Porina nucula*; *Pyrenula dermatodes*; *Pyrenula leucostoma*; *Pyrenula subferruginea*; *Pyrenula concatervans*; ***Sticta duplolimbata***; ***Sticta fuliginosa***; ***Sticta gracilis***; ***Sticta weigelii***
Humid but exposed habitat	*Bryoria confusa*; ***Cetrelia braunsiana***; ***Cetrelia olivetorum***; ***Cladonia coniocraea***; ***Haematomma puniceum* subsp. *pacificum***; ***Hypogymnia yunnanensis***; ***Lecidella euphoria***; ***Leioderma sorediatum***; ***Leptogium menziesii***; ***Leptogium saturninum***; ***Lobaria isidiophora***; *Nephromopsis ornata*; ***Nephromopsis pallescens***; *Nephromopsis stracheyi*; ***Parmotrema eciliatum***; ***Sticta nylanderiana***; ***Sulcaria sulcata* var. *sulcata***; ***Usnea florida***

menziesii, *Parmotrema eciliatum*, *Sticta gracilis* and *S. sulcata* var. *sulcata*, are strictly associated with certain forest types and can be considered good indicators of microclimatic conditions (Li et al., 2011b). The presence of *S. gracilis* in the MOSF indicates moist conditions while the other three indicators imply humid but exposed conditions in the PBSF. *Amandinea punctata*, *C. flavorubescens*, *Pannaria rubiginosa* and *Ramalina sinensis* are specialists on deciduous substrate (Giordani, 2006; Hedenås and Ericson, 2000; Jørgensen, 2000), demonstrating that the presence of a deciduous component increases lichen diversity in subtropical forest ecosystems. *Lepraria* species usually occurred on rough bark while *Diorygma* and *Graphis* species occurred on smooth bark (Hale, 1967; Käffer et al., 2011), emphasizing the importance of host species or bark texture for lichen growth. *C. furcata* and *P. rufescens*, which are typical terrestrial species, were characteristic of the PDMF, indicating that the trunks have a thick humus layer and can provide soil-forming and acidic niches (Chen et al., 2010; Hale, 1967; Liu et al., 2010). *Cladonia coniocraea*, which was especially abundant in the PYSF, is known as an acid-loving species characteristic of the tree-bases (Hale, 1967). The distribution of indicators also successfully captured the microclimatic features of associated habitats (Table 6).

4.3. Bole lichen functional group potential response to environmental change

Our study clearly suggests that both cover and diversity of most lichen functional groups undergo regular variation as succession proceeds, in agreement with other studies that have focused on the importance of successional stages in explaining lichen community changes (Ellis and Coppins, 2006; Hedenås and Ericson, 2000; Rogers et al., 2009). The patterns point to predictable successional trends and give better insight on the response of lichen community to habitat dynamics. However, our data do not support a replacement pattern that pioneer species are displaced by competitively superior ones (Ellis and Coppins, 2006), possibly because of the poor coverage of epiphytes on trunks in all forests. Light availability can be invoked to explain the decreases in lichen cover and diversity during successions (Li L.H. et al., 2011a, Li S. et al., 2011b; Li et al., 2007). If moisture is adequate for lichen growth, functional groups may become limited by understory light levels, e.g., fruticose and foliose lichens with green algae (Barkman, 1958; Hale, 1967).

Nevertheless, in contrast to epiphytic cyanolichens are old-growth associated species (Hedenås and Ericson, 2004; Kuusinen, 1996; McCune, 1993), this group was more prevalent in early-secondary forests in the Ailao Mountains. Due to the high humidity, these results can be attributed to constant input of propagules, presence of pioneer deciduous trees and modest increasing canopy openness (Goward and Arsenault, 2000; Hedenås and Ericson, 2003; Li et al., 2011b, 2007). These results are somewhat analogous to other studies demonstrating that cyanolichens may occur earlier in the epiphyte community succession in moist habitats (Barkman, 1958; Ellis and Coppins, 2006).

Although inefficient dispersal of propagules is important in limiting lichen colonization in young forests (Dettki et al., 2000; Hilmo and Såstad, 2001), we found that asexual species were more frequently encountered in secondary than in primary forests. In addition to landscape characteristics such as extensive primary forests and high forest connectivity (Dettki et al., 2000; Li et al., 2011b), this result can be attributed to the fact that some asexual species (e.g., *Hypotrachyna pseudosinuosa*, *L. isidiophora* and *Nephroma helveticum*) are able to produce both asexual and sexual propagules, promoting their establishment in secondary forests.

In the subtropical Ailao Mountains, bole lichen groups have great potential as environmental indicators, because most of them respond similarly to habitat variables. Narrowly lobed foliose lichens were the best candidate group due to their highly significant association with all variables. Crustose and sexual groups were also valuable as indicators because both absolute and percentage values were significantly related to habitat variables but in opposing direction. These findings are partially in accord with those of Giordani et al. (2012), who found crustose, narrowly lobed and broadly lobed foliose groups are ideal indicators for rainfall, acidic deposition and forest structure, respectively. On the other hand, canopy openness was the best predictor of the distribution of functional groups, especially for narrowly lobed foliose and fruticose lichens, while other factors were less informative in this region.

4.4. The application of bole lichens as indicators of environmental change

An important application of our results is the possibility to use lichens as environmental indicators in subtropical forest ecosystems. Total cover, richness and diversity of bole lichens are proposed for monitoring the changes associated with forest succession, as those in other ecosystems (Giordani et al., 2012; Hedenås and Ericson, 2000; Nascimbene et al., 2010; Rogers and Ryel, 2008).

Based on ISA, many lichen species can be used as indicators of habitat quality and will add to the insights gained from forest

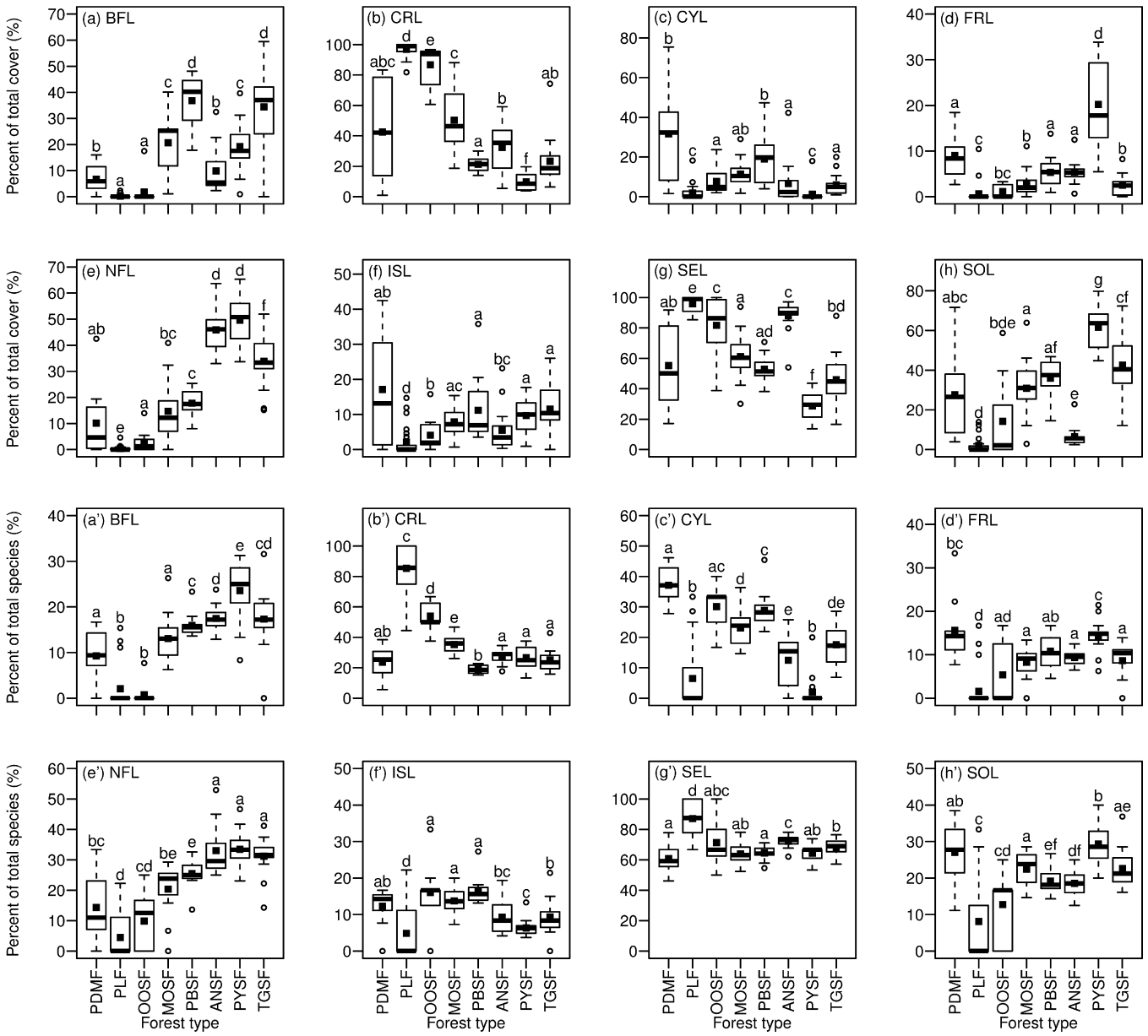

Fig. 3. Box-plots of the percentages of cover (a–h) and species richness (a′–h′) of bole lichens for eight functional groups in the eight forest types in the Ailao Mountains, southwest China. Different letters with bars represent significant differences ($P < 0.05$). BFL: broadly lobed foliose lichens; CRL: crustose lichens; CYL: cyanolichens; FRL: fruticose lichens; NFL: narrowly lobed foliose lichens; ISL: isidiate lichens; SEL: sexual lichens; SOL: sorediate lichens.

monitoring. Nevertheless, it should be noted that several authors claim that the application of lichen indicators restricted to forest stands may be problematic because lichens are niche specialists and/or dispersal-limited species (Ellis, 2012; Rolstad et al., 2002). The comparison of different sample methods for determining indicators provides support for this view (Li et al., 2011b). Moreover, according to Marmor et al. (2011), the use of common indicators in forest monitoring is much better than using rare species. Obviously, ISA can be well coupled with CCA, to make it even more powerful in the detection of the level of the heterogeneity of forest structure or microhabitats within forest ecosystems. In addition, although both the present method and the litterfall method can provide important ecological information on the Ailao Mountains (Li et al., 2011b), the former is a far more convenient method than the latter for large-scale lichen sampling.

Recent studies have moved towards the use of lichen functional groups as indicators of air quality (Rogers et al., 2009), land-use (Pinho et al., 2012; Stofer et al., 2006), climate and forest dynamics (Ellis and Coppins, 2006; Giordani et al., 2012; Marini et al., 2011; Rogers et al., 2009), and this approach seems very well suited to capture comprehensive information. In our study, this approach has been extended to subtropical forests with more diverse communities and more undulating topography (Wu, 1983), where it also provided additional information on forest dynamics. The application of lichen functional groups as indicators is a feasible and promising alternative for evaluating environmental changes in subtropical forest landscape.

Consequently, we recommend that the combined use of lichen species diversity, indicator species and functional group may be the best way to obtain detailed information, which is crucial for large-scale and long-term forest monitoring and biodiversity conservation. Certainly, the combined use of indicator species and functional groups tend to be more convenient.

5. Conclusions

The cover, richness, diversity, community structure of bole lichens differed greatly among forest types and responded significantly to habitat variables. The narrowly lobed foliose group was the best environmental indicator in subtropical forests. Our results support the notion that epiphytic lichens are ideal indicators of forest structure and dynamics. The use of lichen indicators and functional groups can capture distinct changes in environmental variables. The indicator approach can lead to deeper understanding of habitat heterogeneity, while the functional group approach can greatly reduce the errors associated with uneven taxonomic knowledge (Giordani et al., 2012; Will-Wolf et al., 2002). When accuracy, validity and feasibility are considered, we suggest that the combined use of lichen indicators and functional groups is a reliable and sensitive protocol to monitor forest dynamics in subtropical China.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2012.12.012.

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