Biomass, diversity and composition of epiphytic macrolichens in primary and secondary forests in the subtropical Ailao Mountains, SW China

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ABSTRACT

Epiphytic macrolichen litterfall was collected over 3 years from primary evergreen broad-leaved forests (PF), *Populus bonatii* secondary forests (PBSF), middle-aged oak secondary forests (MOSF) and old-aged oak secondary forests (OOSF) of the Ailao Mountains in SW China. To assess changes in the epiphyte communities of the subtropical forests, we compared the differences in biomass, species diversity and community structure of epiphytic lichens from the four forest types. A total of 51 species were recorded in this study. Species richness was highest in the PF, while α-diversity was highest in the MOSF. Lichen biomass differed markedly across the four forest types and was highest in the MOSF. The contribution of each dominant species to total biomass, except *Nephromopsis ornata*, was significantly different among forest types. Moreover, the percent contribution of foliose chlorolichens to litterfall tended to be higher in later-succession forest types, whereas the contributions of cyanolichens and fruticose chlorolichens were lower in these forest types. Compared to the PF, the lichen community structure in secondary forests differed significantly, implying that at least a few hundred years were needed for the restoration of these lichen communities. In particular, nineteen lichens were suggested as indicators, and eleven of them were present in the MOSF. Canonical correspondence analysis (CCA) indicated that the observed differences were mainly attributed to canopy openness and the size of the largest tree, which represented an environmental gradient from exposed to sheltered habitats. The diversity of host tree species was also important in determining the composition and distribution of macrolichens. Our findings support the idea that the maintenance of the forest landscape mosaic of heterogeneous forest types may be an important management practice to maintain or promote the epiphytic lichen community of the subtropical Ailao Mountains.

1. Introduction

Evergreen broad-leaved forests, endemic to eastern Asia, are an important global vegetation type in subtropical China (Qiu et al., 1998; Wang et al., 2007). In the canopies of undisturbed montane evergreen broad-leaved forests, abundant epiphytes comprise a substantial amount of the biomass and species diversity (You, 1983; Xu and Liu, 2005; Wang et al., 2008; Hsu and Wolf, 2009). Lichens are a nearly ubiquitous group of epiphytes in subtropical forests. In general, they are considered to significantly contribute to the total biomass, species diversity and nutrient cycling in forest ecosystems and appear particularly sensitive to anthropogenic disturbances and climate change (Galloway, 1992). Detailed studies of canopy lichens in Asian forests are relatively limited but are

"urgently needed" to gain a deeper understanding of epiphytes (Rhoades, 1995; Sillett and Antoine, 2004).

Most previous studies that deal with the dynamics of epiphytic lichen communities during secondary forest succession have mainly focused on boreal forests in Europe and northern America (Lang et al., 1980; McCune, 1993; Hedenås and Ericson, 2000; Sillett and Antoine, 2004; Rogers and Ryel, 2008), with studies providing data from tropical Costa Rica and northern Thailand (Wolseley and Aguirre-Hudson, 1997; Holz and Gradstein, 2005). Old forests are generally considered to have greater lichen biomass and diversity than young forests because of more open canopies and diverse structures, which allow adequate penetration of light and humidity (Lang et al., 1980; McCune, 1993; Lehmkuhl, 2004). On the contrary, excessively closed or open canopies may restrict lichen growth in relatively species-poor, homogeneous areas (Neitlich and McCune, 1997; Boudreault et al., 2009). In western Oregon and Washington, for example, the biomass of the cyanolichen group is 1.14 Mg ha^{-1} in old-growth forests, but the group is scarce in

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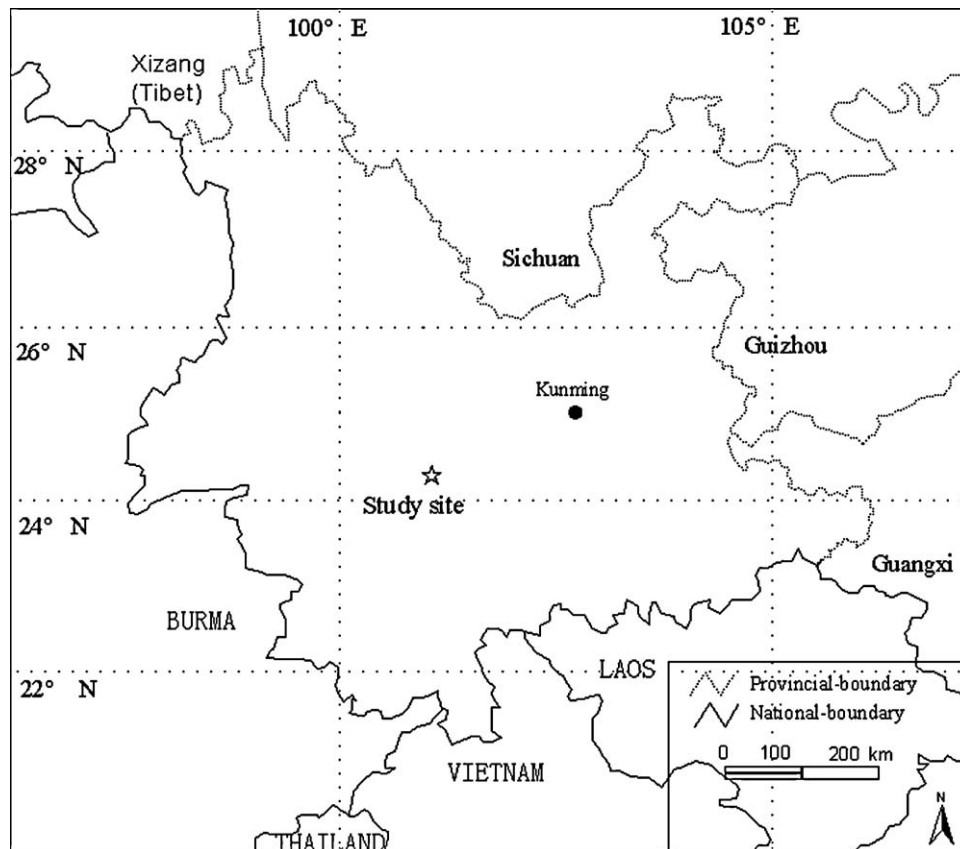*E-mail address:* liuwy@xtbg.ac.cn (W. Liu).

Fig. 1. Location of the study site in the Ailao Mountains, Yunnan, SW China (from Yang et al., 2008).

younger forests (McCune, 1993). Variations between young and old forests in the distribution of certain lichens along tree height can also be explained by environmental variables such as moisture, light and structural heterogeneity (Hale, 1965; Lang et al., 1980; McCune, 1993). Similarly, indicator species change markedly in abundance across successional states (Hedenås and Ericson, 2000; Lehmkuhl, 2004; Rogers and Ryel, 2008). In tropical Costa Rica, however, the high species richness of secondary forests has been ascribed to closed canopies, which result in constant high humidity in these forests (Holz and Gradstein, 2005). Additionally, a preliminary survey in subtropical Ailao Mountains has shown that the species richness of epiphytic lichen is similar between primary and secondary forests; however, many species present on trunks and in the canopies of secondary forests were only found in the canopies of the primary, closed forest (Li et al., 2007). Nevertheless, the available documentation of epiphytic lichens is rather scarce, although the importance of epiphytes is well recognized in this region (Liu et al., 2002b; Xu and Liu, 2005; Ma et al., 2009).

Information on canopy lichen assemblages is still insufficient, largely because of difficulties in access and sampling (Rhoades, 1995). An effective method for estimating lichen biomass is to sample lichen litterfall because of a strong relationship between total biomass and late-summer litterfall for three functional groups (in a ratio of 100:1) in boreal forests (McCune, 1994). Interestingly, this method can also be used to compare lichen abundance, diversity and community structure among forest types (Sillett and Goslin, 1999; Lehmkuhl, 2004). Caldiz and Brunet (2006) further assumed that a similarly consistent relationship between lichen litterfall and crop biomass may exist in *Nothofagus* forests. Consequently, the method is a viable alternative to study canopy lichens without directly sampling, and it may be applied to tropical and subtropical forests where the ecology of lichens is poorly understood. Further-

more, although the late-summer collection is sufficient to detect the diversity and biomass of epiphytic lichens in boreal forests, long-term collection is probably more suitable for surveying in subtropical forests with more diverse communities and more distinct seasonal dynamics of litterfall (Deng et al., 1993; Liu et al., 2002a).

Ailao Mountains National Nature Reserve (NNR), with an area of 50400 ha, is one of the largest tracts of natural evergreen broad-leaved forest in China (Young and Herwitz, 1995; Qiu et al., 1998; Liu et al., 2002a). The landscape is characterized by a mosaic of primary montane forest and some secondary forests at different stages of succession (Qiu et al., 1998; Yang et al., 2008). Thus, the NNR provides an ideal site to examine variation in the epiphytic lichen communities of primary and secondary forests. We compared diversity and biomass of epiphytic lichens using a detailed litterfall collection over 3 years in three secondary forests (*Populus bonatii* secondary forests, middle-aged oak secondary forests and old-aged oak secondary forests) and one primary forest type. The objectives were to (1) quantify the biomass, diversity and community structure of epiphytic macrolichens in the four forest types, (2) assess the key drivers that influence lichen assemblages within secondary forest succession, and (3) determine indicator species associated with different forest types.

2. Materials and methods

2.1. Study area

This study was conducted in the Xujiaba region, a core area of the Ailao Mountains NNR, covering 5100 ha on the northern crest of the Ailao Mountains in central-southern Yunnan (23°35′–24°44′ N, 100°54′–101°30′ E, Fig. 1). The altitude range is 2000–2650 m. Meteorological observations at the Ailaoshan Station for Sub-

tropical Forest Ecosystem Studies (24°32′ N, 101°01′ E) during 1996–2005 show a mean annual precipitation of 1947 mm, with 85% falling in the rainy season from May to October. The average annual evaporation is 1192 mm, and the relative humidity is 85%. The annual mean temperature is 11.3 °C. The coldest month is January (5.6 °C), and the hottest month is July (15.7 °C). The frost-free period is approximately 200 days. The active accumulated temperature above 10 °C is approximately 3420 °C, making this region similar to the warm temperate zone. Natural disturbances include frequent, strong winds and occasional cold spells, which may be accompanied by snowfall. The soil is typically yellow-brown earth developed over schist, gneiss, and diorite. The soil texture is loam, with an acidic pH (4.2–4.9) (Qiu et al., 1998; Yang et al., 2008).

The predominant vegetation of the NNR is the montane moist evergreen broad-leaved primary forest (henceforth PF), which accounts for nearly 80% of the total area (Qiu et al., 1998). The PF has two tree layers, both of which are occupied by abundant epiphytes. The upper canopy is almost closed, and the dominant tree species are *Lithocarpus xylocarpus* (Kurz) Markgr., *L. hancei* (Benth.) Rehder, *Castanopsis rufescens* (Hook. f. et Th.) Huang et Y.T. Chang, *Schima noronhae* Reinw. ex Blume and *Stewartia pteropetiolata* Cheng (Qiu et al., 1998). Based on the facts such as the presence of numerous large, old trees, and the lack of widespread anthropogenic disturbances, this forest is sometimes called over-mature or old-growth forest (You, 1983; Yang et al., 2008).

A reservoir was initially constructed approximately 100 years ago on Xujiaba and some surrounding forests were logged. Today, most of the cleared area has been converted to secondary forests after severe anthropogenic disturbances. The old-aged oak secondary forest (henceforth OOSF) represents advanced succession after a clear-cutting that occurred approximately 100 years ago (Young et al., 1992), with over 95% canopy cover. The middle-aged oak secondary forest (henceforth MOSF) developed after deforestation during the rebuilding of the reservoir in the late 1950s (He et al., 2003); now, the canopy cover is 60–70%. Both secondary forests share most of their tree species with the nearby PF, but the same species differ significantly in floristics and structure across habitat types (Young et al., 1992; He et al., 2003). The *P. bonatii* secondary forest (henceforth PBSF), with 60–70% canopy cover, also resulted from cutting, fire, and grazing in the last century (Yang et al., 2008). It is mainly dominated by pioneer *P. bonatii* Levl. and is associated with *L. hancei*, *Vaccinium duclouxii* (H. Lév.) Hand.-Mazz. and *L. xylocarpus*. The PBSF is widely believed to naturally succeed first to old-aged oak secondary forest and finally to the evergreen broad-leaved forest (Qiu et al., 1998).

2.2. Field and laboratory methods

Epiphytic macrolichens were studied using litterfall sampling (McCune, 1994; Lehmkuhl, 2004).

We randomly established 14 plots of 20 m × 20 m, of which five were in PF and three in each of the secondary forest types in Xujiaba of the Ailao Mountains NNR. The distance between the plots ranged between 500 and 3000 m in PF and 100 and 3000 m in secondary forest types. Epiphytic lichen litter was collected on the forest floor from five 4-m × 4-m areas in the corners and in the middle of each plot. Samples were collected at 1-month intervals for 3 years, from January 2006 to December 2008.

Fragments larger than 1 cm were collected. Lichens attached to fallen branches with a base diameter less than 10 cm or hung up at a height less than 2 m above the ground were picked up (McCune, 1994). The litterfall collected in each plot was carefully cleaned of adhering soil and other debris, placed in a single bag, and then air dried for storage.

In the laboratory, lichens were dried at 60 °C for 24 h and then sorted by species. Samples within a plot were weighed

to the nearest 10^{-3} g. Litter was also divided into three functional groups, modified from McCune (1994): cyanolichens (CYL, macrolichens with cyanobacteria), foliose chlorolichens (FOL, foliose macrolichens with green algae) and fruticose chlorolichens (FRL, fruticose macrolichens with green algae). Voucher specimens were identified and retained in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences.

2.3. Data analysis

2.3.1. Diversity and biomass

Based on litter collection over 3 years, alpha diversity (α) was measured as the average species richness per plot, gamma diversity (γ) was the total number of lichen species in each forest type, and beta diversity (β) was calculated as γ/α, which gave an estimate of heterogeneity within community. Litterfall biomass was estimated at total, functional group and individual species levels.

Differences in biomass and diversity at the plot-level among forest types were tested using one-way ANOVA, and multiple pair-wise comparisons of forest types were detected with Tukey's HSD test. To ensure the assumptions of ANOVA, all data sets were submitted to Shapiro–Wilk normality test and Bartlett test for homogeneity of variances. When data did not meet the assumption even after transformation, nonparametric Kruskal–Wallis rank sum test and pair-wise Wilcoxon rang sum test were used for comparisons.

2.3.2. Community structure

Multivariate statistics were performed in R 2.11.1 statistics system (R Development Core Team, 2010). The forest type × species abundance matrix was 14 plots × 51 species. A multi-response permutation procedure (MRPP) with the *mrpp* function of the *vegan* package (Oksanen et al., 2010) was used to test the hypothesis of no differences in species composition between forest types based on species frequency and biomass (Zimmerman et al., 1985). MRPP is a non-parametric procedure used to test multivariate differences between two or more a priori groups. The test statistics describe the significant separation between groups (P) and effect size (A). When $A = 1$, all samples are identical within groups, and when $A = 0$, the within-group heterogeneity equals the expectation by chance. In community ecological statistics, 0.3 is regarded as fairly high for A, indicating that groups are significantly different from each other.

The association between the lichen assemblages and plot variables was examined using a canonical correspondence analysis (CCA). CCA is a non-linear ordination technique that provides an ordination for a matrix of species by plots (ter Braak, 1986). To reduce noise, lichen species with biomass less than 0.5% relative to the total litter were removed from the data, and a matrix of 14 plots × 22 species was subjected to CCA. Environmental variables were recorded for each plot, but some of them were correlated with one another. After the examination of ordination plots and the calculation of the Akaike information criterion (AIC), a stepwise procedure was used to select a subset of variables. When the variance inflation factor (VIF) of selected variables had a value less than 10, a low AIC was given, and there was no redundancy in variables (Oksanen, 2010). As a result, only three variables (canopy openness, size of the largest tree, and species diversity of host trees) were used in the analysis. In each plot, the maximum diameter of the largest tree (MDBH) was measured at breast height (1.3 m). The canopy openness (CAO) was estimated in 10% of classes. All trees with a DBH > 3.5 cm and a height > 2 m were recorded. The species diversity of trees (SDT) was determined using the Shannon–Wiener diversity index. Prior to the analysis, count data were operated using logarithm transformation for a Monte Carlo significance test. All computations were performed using the function *cca* of the

Table 1
Diversity (mean ± standard error) of epiphytic macrolichens in the four forest types in the Ailao Mountains, SW China. Values marked with different letters represent significant differences ($P < 0.05$).

	Forest type				F	P
	PBSF	MOSF	OOSF	PF		
α-Diversity	33.33 ± 2.33 ab	40.33 ± 1.86 a	26.33 ± 1.67 b	33.60 ± 2.25 ab	5.73	0.015
β-Diversity	1.18 ± 0.09 a	1.10 ± 0.05 a	1.19 ± 0.08 a	1.39 ± 0.09 a	2.39	0.130
γ-Diversity	39	44	31	46		

vegan package (Oksanen et al., 2010) in R statistics system (R Development Core Team, 2010).

The representative lichens for each forest type were determined by indicator species analysis (ISA) based on the species' relative abundance and frequency (Dufrêne and Legendre, 1997). The maximum indicator value (ISA = 1) indicates one species was collected in only one forest type and the species occurred in all plots of this forest type, while an ISA value of 0 indicates that one species was absent from this forest type. The species was an indicator for the forest type in which it had the highest indicator value. These values were tested for statistical significance against the random expectation using a Monte Carlo permutation with 1000 replicates. $P < 0.05$ was used as the significance level for indicator species. The ISA was calculated with the function *indval* of *labdsv* package (Roberts, 2010) in the R statistics system (R Development Core Team, 2010).

3. Results

3.1. Diversity

Over 3 years, 51 epiphytic macrolichens belonging to 22 genera and 11 families were recorded in the four forest types. More than 90% of the lichen species were present in primary forests, and 94% were present in secondary forests. Species richness differed between the OOSF and the other three forest types. The highest richness occurred in the PF and lowest occurred in the OOSF (Table 1). In terms of numbers of genera, the MOSF (21) was the most diverse forest, followed by the PF (20), the PBSF (20) and the OOSF (17).

α-Diversity differed greatly among the four forest types (ANOVA, $F = 5.73$, $P = 0.015$), while the difference was not significant for β-diversity (ANOVA, $F = 2.39$, $P = 0.130$) (Table 1). For multiple comparisons, no significant differences in α-diversity were found between forest types, except for the MOSF and the OOSF ($P_{adj.} = 0.009$), while no significant variations were observed for β-diversity ($P_{adj.} = 0.130–1.000$).

3.2. Biomass

The litterfall biomass (mean ± standard error) was $21.60 ± 4.05$ kg ha^{-1} year^{-1} in the PBSF, $31.02 ± 4.57$ kg ha^{-1} year^{-1} in the MOSF, $11.18 ± 1.18$ kg ha^{-1} year^{-1} in the OOSF and $17.87 ± 2.82$ kg ha^{-1} year^{-1} in the PF. These differences were significant (ANOVA, $F = 6.03$, $P = 0.002$). Annual litterfall was significantly higher in the MOSF than in the OOSF ($P_{adj.} = 0.001$) and in the PF ($P_{adj.} = 0.029$), while no significant differences were found for any other comparisons ($P_{adj.} = 0.078–0.689$).

The dominant macrolichens were *Cetrelia olivetorum*, *Everniastrum cirrhatum*, *E. nepalense*, *Nephromopsis ornata*, *Ramalina conduplicans* and *Usnea florida* (Table 2). With the exception of *N. ornata*, their litterfalls were significantly different among the four forest types (Fig. 2). *C. olivetorum* was common in most of plots, with its contribution to total litterfall varying from 2.97% to 6.68%. The biomass of *E. cirrhatum* was significantly higher in the MOSF and showed a marked decrease from the MOSF to the PF, while *U. florida* showed similar patterns within successions. *E. nepalense* accounted

for 27.81% of the total biomass in the PF, while few were collected in the other forest types. *N. ornata* accounted for 2.86–9.43% of the total biomass. Litterfall of *R. conduplicans* was higher in the PBSF and the MOSF than in the OOSF and the PF. Additionally, other common species were *Parmotrema cetratum* (3.99%), *P. eciliatum* (4.46%) and *Sulcaria sulcata* (4.05%) in the PBSF; *Heterodermia dendritica* (3.31%), *Hypogymnia yunnanensis* (2.58%) and *P. cetratum* (2.62%) in the MOSF.

3.3. Functional groups

Significant differences in biomass and species richness among three functional groups were detected (except the species richness of the FRL) (Table 3; Fig. 3). For the CYL, biomass and species richness, as well as their percentage contribution to the total, were higher in the PBSF and in the MOSF, declining towards the PF. The FRL contributed more to the total litterfall and showed similar patterns during succession. However, the FOL contributed most to total biomass and was significantly higher at later successional stages.

3.4. Community structure

MRPP revealed significant differences in species composition among the forest types ($A = 0.334$, $P < 0.001$). Pair-wise comparisons indicated that differences were significant between the PF and the OOSF ($P = 0.019$), the PF and the MOSF ($P = 0.021$), and the PF and the PBSF ($P = 0.031$). Furthermore, the macrolichen community in the PF differed much more from that of the MOSF ($A = 0.346$) than from that of the OOSF ($A = 0.290$) and the PBSF ($A = 0.201$). However, the smaller A values indicated broad overlap in the lichen communities of the PF and the OOSF, as well as in those of the PF and the PBSF. In contrast, no significant differences were detected between the OOSF and the MOSF ($A = 0.349$, $P = 0.098$), the OOSF and the PBSF ($A = 0.128$, $P = 0.099$), or the MOSF and the PBSF ($A = 0.158$, $P = 0.195$). Broad overlaps were also observed for the latter two comparisons.

The CCA ordination revealed that the composition of lichen species was closely associated with the measured variables ($P = 0.005$) (Fig. 4). The first axis explained 36.69% of total variance in species composition and was closely related to canopy openness ($r = -0.887$) and MDBH ($r = 0.854$). The second axis accounted for 11.25% of total variation and showed a strong correlation with SDT ($r = -0.946$). The third axis (not shown) represented 3.97% of variation but was only weakly associated with three variables. The PF was clearly separated from the secondary forests along axis 1 and 2, while less obvious separation was found among the three secondary forest types. These results are consistent with the results obtained by MRPP.

The CCA biplot also showed changes in lichen composition along the first two axes. Lichens predominantly occurred in larger MDBH and sheltered plots showed higher positive correlation with axis 1 (e.g., *E. nepalense*, *E. rhizodendroideum* and *Hypotrachyna adducta*), while lichens associated with smaller MDBH and exposed plots showed higher negative correlation with axis 1 (e.g., *S. sulcata* and *H. boryi*). Along the second axis, *E. cirrhatum* and *Hypotrachyna* sp. preferentially occurred in lower SDT plots and showed higher positive correlation with axis 2, while *E. nepalense* was predominantly

Table 2
Litterfall biomass (mean ± standard error, g ha^{-1} year^{-1}) of epiphytic macrolichen species in the four forest types in the Ailao Mountains, SW China.

Species	Functional group	Forest type			
		PBSF	MOSF	OOSF	PF
Anzia hypoleucoides	FOL	20 ± 11	0	0	39 ± 17
Anzia leucobatoides f. *hypomelaena*	FOL	468 ± 267	333 ± 110	125 ± 59	335 ± 148
Anzia physoidea	FOL	42 ± 41	29 ± 29	1 ± 1	51 ± 25
Bryoria confusa	FRL	89 ± 65	137 ± 75	0	13 ± 10
Cetrelia olivetorum	FOL	1442 ± 327	1438 ± 252	332 ± 45	847 ± 214
Coccocarpia erythroxyli	CYL	2 ± 2	1 ± 1	0	0
Erioderma meiocarpum	CYL	5 ± 5	3 ± 3	0	0
Everniastrum cirrhatum	FOL	5273 ± 1413	9052 ± 1066	4627 ± 464	979 ± 203
Everniastrum nepalense	FOL	173 ± 72	811 ± 202	64 ± 32	4970 ± 611
Everniastrum rhizodendroideum	FOL	172 ± 99	261 ± 136	68 ± 26	353 ± 79
Heterodermia boryi	FOL	401 ± 116	492 ± 92	76 ± 27	186 ± 49
Heterodermia comosa	FOL	139 ± 37	367 ± 78	115 ± 17	215 ± 38
Heterodermia dendritica	FOL	429 ± 47	1028 ± 244	517 ± 106	539 ± 84
Heterodermia hypoleuca	FOL	94 ± 49	26 ± 15	4 ± 2	80 ± 25
Hypogymnia yunnanensis	FOL	253 ± 125	801 ± 164	148 ± 30	384 ± 72
Hypotrachyna adducta	FOL	67 ± 20	154 ± 50	88 ± 17	470 ± 118
Hypotrachyna pseudosinuosa	FOL	205 ± 51	502 ± 116	175 ± 28	589 ± 174
Hypotrachyna sp.	FOL	200 ± 73	269 ± 77	315 ± 63	175 ± 56
Leioderma sorediatum	CYL	0	61 ± 33	0	<1
Leptogium azureum	CYL	0	29 ± 21	1 ± 1	4 ± 3
Leptogium menziesii	CYL	15 ± 4	0	0 ± 0	8 ± 5
Leptogium saturninum	CYL	0	10 ± 7	31 ± 20	0
Lobaria isidiophora	FOL	0	24 ± 11	0	<1
Lobaria isidiosa	CYL	0	32 ± 17	0	<1
Lobaria kurokawae	CYL	3 ± 1	8 ± 4	0	4 ± 3
Lobaria retigera	CYL	32 ± 16	336 ± 111	<1	<1
Menegazzia terebrata	FOL	171 ± 50	233 ± 69	129 ± 25	162 ± 45
Nephroma helveticum	CYL	0	8 ± 5	5 ± 5	4 ± 4
Nephromopsis laii	FOL	0	0	0	50 ± 32
Nephromopsis ornata	FOL	1353 ± 502	886 ± 178	681 ± 162	1685 ± 309
Nephromopsis pallescens	FOL	762 ± 215	339 ± 96	80 ± 30	463 ± 122
Nephromopsis stracheyi	FOL	149 ± 110	<1	0	16 ± 14
Oropogon asiaticus	FRL	6 ± 5	0 ± 0	0	<1
Parmelia adaugescens	FOL	75 ± 24	146 ± 52	92 ± 27	268 ± 64
Parmotrema cetratum	FOL	861 ± 201	813 ± 196	347 ± 107	754 ± 169
Parmotrema eciliatum	FOL	964 ± 266	126 ± 43	27 ± 13	208 ± 62
Parmotrema tinctorum	FOL	370 ± 74	390 ± 47	201 ± 44	673 ± 136
Ramalina conduplicans	FRL	2357 ± 236	1753 ± 212	608 ± 107	1098 ± 238
Ramalina peruviana	FRL	0	0	0	10 ± 5
Ramalina sinensis	FRL	5 ± 4	0	0	<1
Sticta duplolimbata	CYL	2 ± 2	1 ± 1	0	<1
Sticta fuliginosa	CYL	0	23 ± 19	0	0
Sticta gracilis	CYL	0	19 ± 12	0	0
Sticta nylanderiana	FOL	70 ± 30	12 ± 9	0	34 ± 16
Sticta platyphylloides	FOL	0	0	0	<1
Sulcaria sulcata	FRL	874 ± 352	80 ± 32	5 ± 5	91 ± 50
Usnea florida	FRL	3968 ± 888	9638 ± 1788	2237 ± 591	1953 ± 384
Usnea nidifica	FRL	35 ± 20	112 ± 49	18 ± 18	55 ± 25
Usnea orientalis	FRL	1 ± 1	52 ± 34	0	15 ± 9
Usnea rubicunda	FRL	0	120 ± 89	5 ± 3	71 ± 40
Usnea sp.	FRL	52 ± 30	62 ± 16	59 ± 24	19 ± 8

found in higher SDT plots and showed higher negative correlation with axis 2.

The ISA revealed that 19 macrolichens were significantly associated with particular forest types (Table 4). Of these, 11 indicator species occurred in the MOSF; however, most of them were rare in the canopies. Four indicators, such as *E. nepalense*, *H. adducta*, *N. laii* and *R. peruviana* occurred in the PF; the latter two species were also rare and only occurred in this forest type. Three indicators were found in the PBSF, and only one was found in the OOSF. In addition, 6 other species were

Table 3
Diversity and biomass (mean ± standard error) of epiphytic macrolichen litterfall for three functional groups in the four forest types in the Ailao Mountains, SW China.

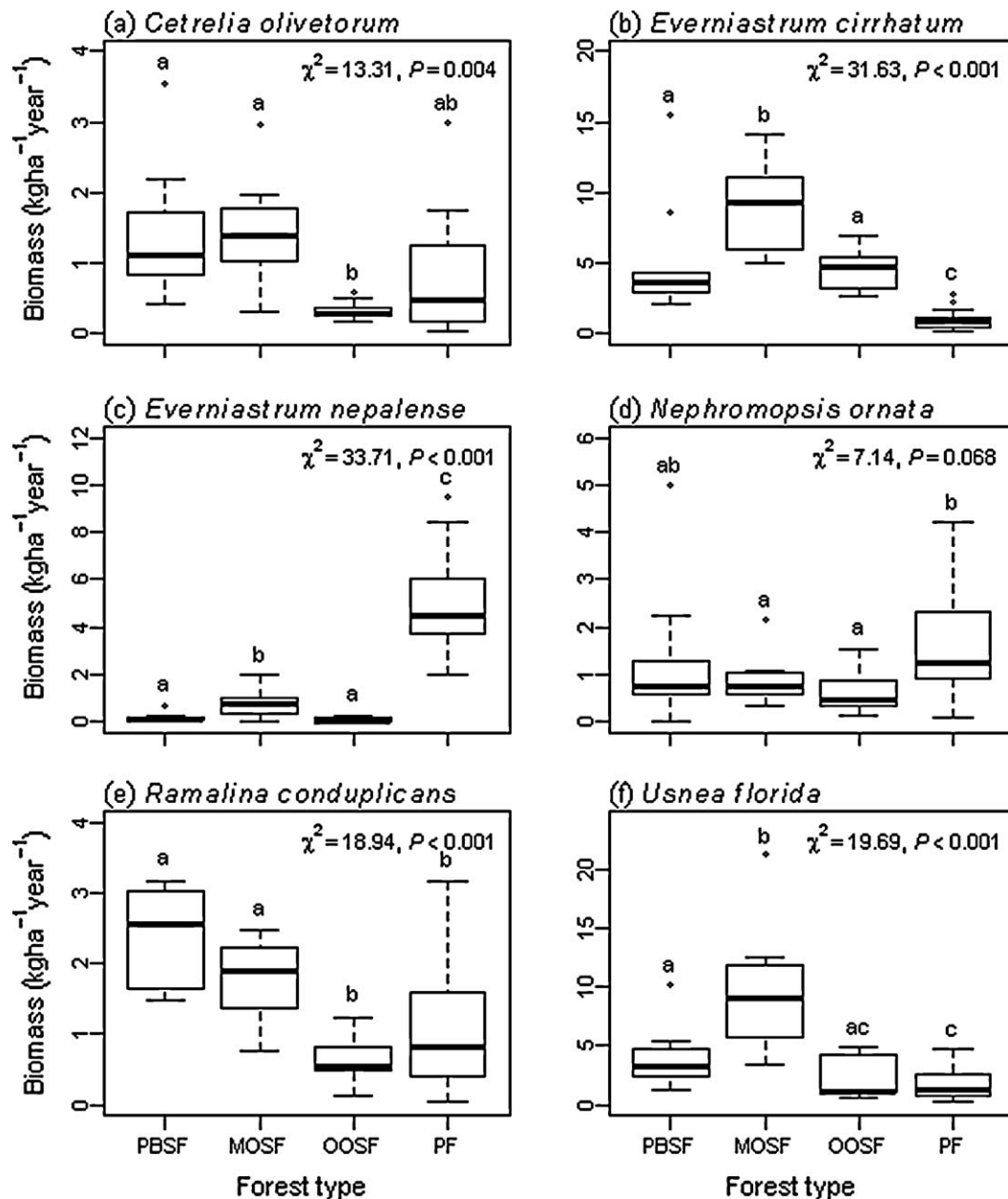|	Forest type				F (or χ^2)	P
	PBSF	MOSF	OOSF	PF		
Diversity						
No. of CYL species	4.00 ± 1.15 a	9.67 ± 1.20 b	2.67 ± 0.33 a	2.40 ± 0.87 a	11.55	0.001
No. of FOL species	22.33 ± 0.33 ab	22.33 ± 0.33 ab	20.00 ± 0.58 a	24.00 ± 0.71 b	7.52	0.006
No. of FRL species	7.00 ± 1.00 a	8.00 ± 0.00 a	3.67 ± 0.88 a	7.20 ± 1.16 a	5.42	0.143
Biomass (kg ha^{-1} year^{-1})						
Biomass of CYL	0.06 ± 0.02 a	0.53 ± 0.15 c	0.04 ± 0.02 ab	0.02 ± 0.01 b	22.73	<0.001
Biomass of FOL	14.15 ± 2.78 ab	18.53 ± 2.40 a	8.21 ± 0.68 b	14.53 ± 2.05 a	10.40	0.015
Biomass of FRL	7.39 ± 1.42 a	11.95 ± 2.10 a	2.93 ± 0.64 b	3.33 ± 0.65 b	19.39	<0.001

Fig. 2. Box-plots of litterfall biomass of six dominant epiphytic macrolichens in the four forest types in the Ailao Mountains, SW China. Kruskal–Wallis χ^2 and P values are shown in the graphs, and different letters with bars represent significant differences ($P < 0.05$) according to pair-wise Wilcoxon rank sum tests.

marginally significant ($P < 0.100$) as indicators for particular forest types.

4. Discussion

4.1. Litterfall sampling for canopy lichens

The litterfall method, developed by McCune (1994), is generally used in late summer (August) to avoid litterfall pulses in boreal forests. Although originally intended for comparison of epiphytic lichen biomass among forests, this method has been expanded to estimate of lichen abundance, diversity and community structure (Sillett and Goslin, 1999; Lehmkuhl, 2004). However, some studies have demonstrated that the litterfall method is not without problems because litterfall varies with wind, precipitation, decomposition and herbivores (McCune, 1994; Peck and McCune, 1997; Price and Hochachka, 2001; Caldiz and Brunet, 2006). Furthermore,

the late-summer sampling may not always be warranted in other regions (Stevenson and Coxson, 2003). In the Ailao Mountains, lichen litterfall showed distinct fluctuations among the four forest types over the 3 years of the study (Fig. 5). Our results suggest that a long-term litterfall sampling is necessary to understand the ecology of canopy lichens in the subtropical forests.

Additionally, McCune (1994) found a strong relationship between total biomass and late-summer litterfall (in a ratio of 100:1) in the boreal forests of Washington and Oregon. However, no similar studies have been performed in other regions, probably due to the lack of detailed information about canopy lichen biomass (Price and Hochachka, 2001; Caldiz and Brunet, 2006). Based on felled trees in the Ailao Mountains, a preliminary survey showed that the canopy lichen biomass was approximately 130 kg ha^{-1} in the PF (unpublished data). In our study, the average monthly litterfall was 1.49 kg ha^{-1}, and the average in the late wet season (October), corresponding to late summer in the boreal forest was
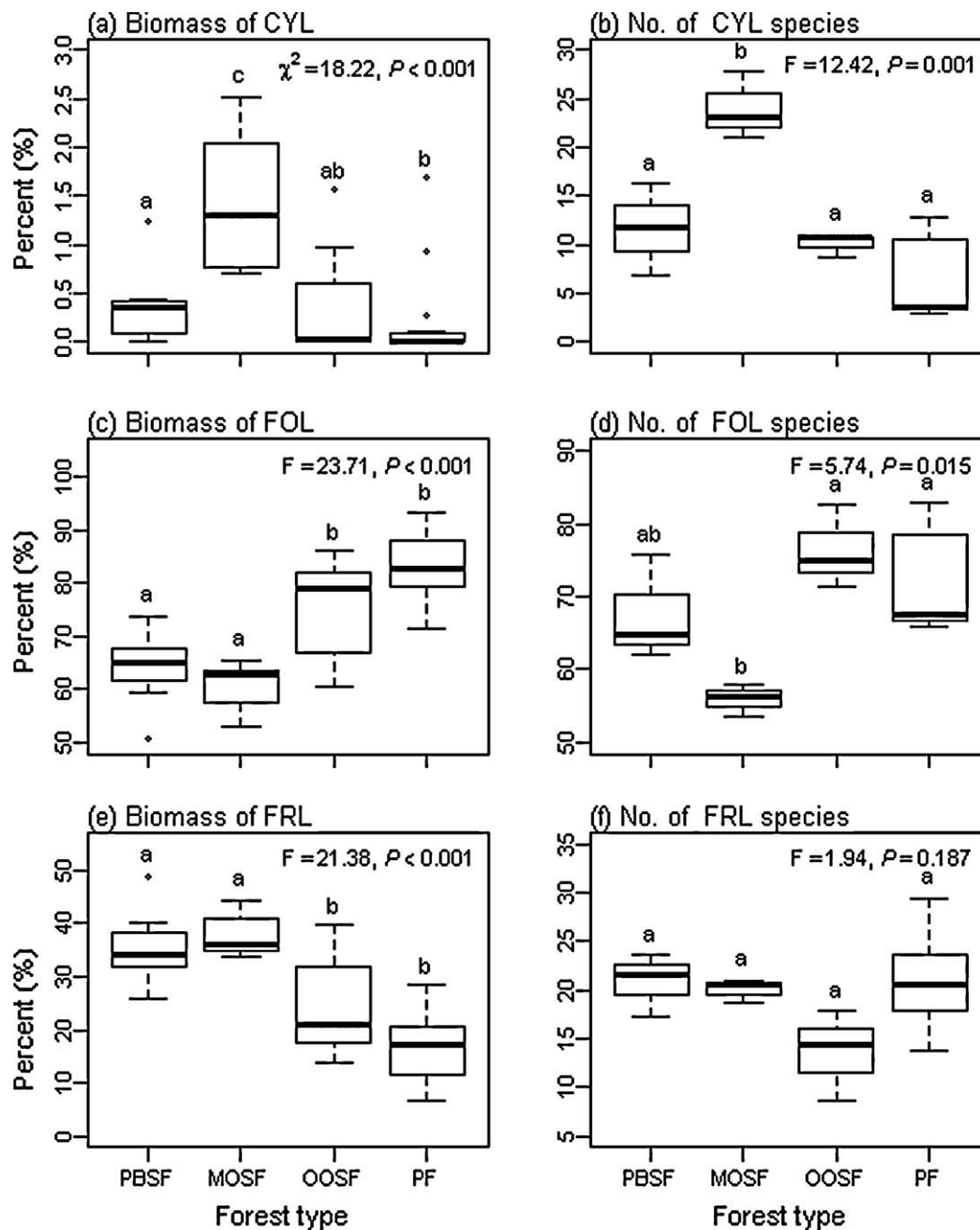
Fig. 3. Box-plots of the percentages of litterfall biomass and species richness of macrolichens for three functional groups in the four forest types in the Ailao Mountains, SW China. ANOVA F, Kruskal–Wallis χ^2 and P values are shown in the graphs, and different letters with bars represent significant differences ($P < 0.05$) according to Tukey's HSD tests and pair-wise Wilcoxon rank sum tests.

1.36 kg ha^{-1} in the PF (Fig. 5). These data indicate that the relationship between canopy lichen biomass and monthly litterfall in the PF was approximately 100:1. Consequently, we propose that the ratio is a constant in subtropical forests in this region.

4.2. Diversity in primary and secondary forests

Previous studies have shown that lichen species richness is considerably reduced in young forests compared to primary or old-growth forests (Lang et al., 1980; Jüriado et al., 2003). However, we found that the lichen diversity in the PBSF and in the MOSF were similar to that of the PF, and no significant loss was observed. The results are not only in agreement with the findings obtained by Holz and Gradstein (2005) but are also consistent with those reported

for bole lichens and bryophytes from the same area (Li et al., 2007; Ma et al., 2009). In contrast to numerous studies (Kuusinen, 1996a; Hedenås and Ericson, 2000; Sillett and Antoine, 2004), the MOSF hosted more cyanolichens (all but one) than the PF (Table 2). Several alternative explanations for the results are discussed here.

First, inefficient dispersal of lichens may have failed to delay or prevent their recolonization in young forests. Macrolichens generally disperse a short distance from the propagule source (old-growth stands or remnant trees), which results in their slow colonization of young stands (Dettki et al., 2000; Caldiz and Brunet, 2006). However, our study area was a mosaic of different-aged forests and showed no obvious spatial isolation between fragments. Therefore, the PF maintained a persistent source of propagules and promoted the fast dispersal of lichens to secondary forests. In addi-

Table 4
Indicator values of epiphytic macrolichens in the four forest types in the Ailao Mountains, SW China. Indicator values and *P* values of indicator species are given in bold type.

Species	Forest type				P
	PBSF	MOSF	OOSF	PF	
Anzia hypoleucoides	0.343	0.000	0.000	0.525	0.184
Anzia leucobatoides f. *hypomelaena*	0.371	0.265	0.099	0.266	0.488
Anzia physoidea	0.115	0.078	0.003	0.246	0.696
Bryoria confusa	0.249	0.573	0.000	0.032	0.122
Cetrelia olivetorum	0.355	0.354	0.082	0.209	0.474
Coccocarpia erythroxyli	0.427	0.120	0.000	0.000	0.264
Erioderma meiocarpum	0.218	0.115	0.000	0.000	0.764
Everniastrum cirrhatum	0.265	0.454	0.232	0.049	0.065
Everniastrum nepalense	0.029	0.135	0.011	**0.826**	**0.002**
Everniastrum rhizodendroideum	0.134	0.305	0.080	0.413	0.263
Heterodermia boryi	0.347	0.426	0.066	0.161	0.274
Heterodermia comosa	0.166	**0.439**	0.137	0.257	**0.011**
Heterodermia dendritica	0.171	**0.409**	0.206	0.214	**0.016**
Heterodermia hypoleuca	0.461	0.126	0.013	0.393	0.181
Hypogymnia yunnanensis	0.160	**0.505**	0.094	0.242	**0.003**
Hypotrachyna adducta	0.086	0.198	0.113	**0.603**	**0.002**
Hypotrachyna pseudosinuosa	0.139	0.341	0.119	0.401	0.653
Hypotrachyna sp.	0.209	0.280	0.328	0.183	0.538
Leioderma sorediatum	0.000	**0.993**	0.000	0.001	**0.005**
Leptogium azureum	0.000	**0.857**	0.031	0.045	**0.044**
Leptogium menziesii	**0.639**	0.000	0.000	0.144	**0.048**
Leptogium saturninum	0.000	0.236	**0.764**	0.000	**0.039**
Lobaria isidiophora	0.000	**0.971**	0.000	0.011	**0.007**
Lobaria isidiosa	0.000	**0.971**	0.000	0.012	**0.006**
Lobaria kurokawae	0.122	0.558	0.000	0.104	0.103
Lobaria retigera	0.085	**0.910**	0.001	0.001	**0.010**
Menegazzia terebrata	0.246	0.335	0.186	0.233	0.596
Nephroma helveticum	0.000	0.307	0.106	0.045	0.548
Nephromopsis laii	0.000	0.000	0.000	**1.000**	**0.001**
Nephromopsis ornata	0.294	0.193	0.148	0.366	0.304
Nephromopsis pallescens	0.464	0.206	0.048	0.282	0.075
Nephromopsis stracheyi	0.299	0.002	0.000	0.039	0.599
Oropogon asiaticus	0.328	0.000	0.000	0.003	0.444
Parmelia adaugescens	0.129	0.251	0.158	0.461	0.190
Parmotrema cetratum	0.310	0.293	0.125	0.272	0.809
Parmotrema eciliatum	**0.727**	0.095	0.020	0.157	**0.048**
Parmotrema tinctorum	0.226	0.239	0.123	0.412	0.094
Ramalina conduplicans	0.405	0.301	0.105	0.189	0.080
Ramalina peruviana	0.000	0.000	0.000	**1.000**	**0.001**
Ramalina sinensis	0.654	0.000	0.000	0.004	0.059
Sticta duplolimbata	0.183	0.167	0.000	0.040	0.756
Sticta fuliginosa	0.000	0.667	0.000	0.000	0.121
Sticta gracilis	0.000	**1.000**	0.000	0.000	**0.015**
Sticta nylanderiana	0.606	0.070	0.000	0.174	0.062
Sticta platyphylloides	0.000	0.000	0.000	0.200	1.000
Sulcaria sulcata	**0.833**	0.076	0.002	0.035	**0.014**
Usnea florida	0.270	0.325	0.205	0.039	0.644
Usnea nidifica	0.223	**0.542**	0.126	0.110	**0.024**
Usnea orientalis	0.160	0.509	0.027	0.251	0.164
Usnea rubicunda	0.006	**0.759**	0.000	0.133	**0.026**
Usnea sp.	0.000	0.612	0.017	0.290	0.146

tion, a time span of more than 50 years was probably long enough to allow the establishment of most species in the secondary forests.

Second, because of the importance of the host species (Kuusinen, 1996b; Li et al., 2007; Jüriado et al., 2009), a similar diversity of phorophytes (Fig. 4) may result in a similar diversity of substrates for epiphytic lichens in the three forest types.

In addition, available light was likely a major limiting factor in determining lichen microhabitats. As constant high air humidity (Liu et al., 2002b; Ma et al., 2009) and low canopy openness were observed in most of the forests, it is possible that the light level was too low but the moisture was adequate for lichen growth. Substrate availability was modified by the light gradient. In the closed-canopy PF, only a small proportion of the total surface area was available for lichens (mostly occupied the canopies). In contrast, in the more open PBSF and MOSF, a higher proportion of substrates (both canopies and trunks) was available for lichens. This explains why a higher α-diversity and most of the cyanolichens existed in the relatively exposed MOSF. This pattern is in accordance with a previous

study in the same area (Li et al., 2007). Similar observations have also been documented in boreal forests (McCune, 1993; Peterson and McCune, 2003; Sillett and Antoine, 2004).

However, the combination of the highest atmospheric humidity (Ma et al., 2009), nearly closed canopy and low diversity of phorophytes (Fig. 4) may result in the low species richness of lichens observed in the OOSF.

In addition, the results of β-diversity analysis indicate that a slightly more heterogeneous community occurred in the PF than in secondary forests, which may result from limitations of forest area, understory structure and topography in the latter.

4.3. Biomass in primary and secondary forests

The litterfall of epiphytic lichen in the four forest types ranged from 11 to 31 kg ha^{-1} year^{-1}, which falls within the range of those reported in other studies on coniferous forests in Europe (Dettki and Esseen, 1998), northern America (Sillett and Goslin, 1999; Price
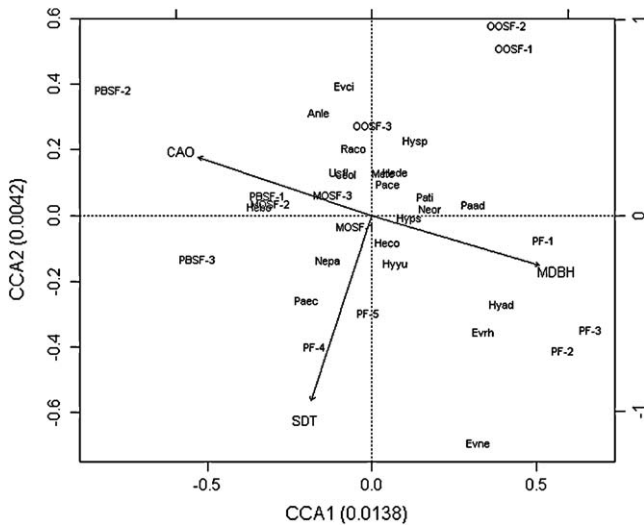
Fig. 4. Epiphytic macrolichen species and environmental variables on the biplot of CCA of axis 1 and axis 2 (*S. sulcata* at leftmost, not shown). The inertia is 0.0373 and the eigenvalues are labeled in parentheses. Abbreviations are the first two letters of genus and species names given in Table 2.

and Hochachka, 2001; Lehmkuhl, 2004) and *Nothofagus* forests in Argentina (Caldiz and Brunet, 2006). These forests supported a biomass of hundreds of times more chlorolichen than cyanolichen. This may be partly because the species richness was nearly three times higher for chlorolichens than cyanolichens. Alternatively, chlorolichens tend to be more tolerant of desiccation and are able to reactivate photosynthesis with humid air in dry periods whereas cyanolichens require hydration by liquid water (Lange et al., 1993; Rhoades, 1995; Sillett and Antoine, 2004). Hence, because of high air humidity during the dry season, the chlorolichens probably had longer periods of hydration in this region, and this accelerated the accumulation of their biomass.

According to many studies, epiphytic lichen abundance also increased with forest age and heterogeneity (McCune, 1993; Lehmkuhl, 2004; Caldiz and Brunet, 2006). In contrast, in the Ailao

Mountains, younger forests had significantly more biomass than older forests, with the exception of the OOSF. These results are largely due to the biomass of foliose *E. cirrhatum* and fruticose *U. florida* that accumulated dramatically in the MOSF and then decreased during subsequent successions. In addition, the relative contribution of cyanolichens and fruticose chlorolichens to the total litterfall was reduced significantly during succession, whereas foliose chlorolichens showed the opposite trend (Table 3; Fig. 3). As mentioned previously, young forests, which form wet and exposed habitats, certainly favor the accumulation of macrolichen biomass. Alternatively, the benefits of increased light availability may have exceeded the costs of heat or desiccation stress. Similar explanations have also been proposed to explain higher lichen biomass in old boreal forests (McCune, 1993; Boudreault et al., 2009).

4.4. Community structure and environmental variables

The MRPP showed significant differences in the macrolichen community structure between primary and secondary forests in the Ailao Mountains, although most lichens were common, and only a few species were restricted to particular forests. These findings indicate that the recovery of epiphytic lichens was still incomplete in terms of both biomass and community composition and that at least a few hundred years were needed for their complete recovery. The secondary forests (except for the OOSF) generally offered appropriate, but unstable, environmental conditions for lichens; however, unpredictable changes likely occur during subsequent succession stages.

Interestingly, the visual interpretation of CCA ordination also corroborates these results. In CCA ordination, the low eigenvalues may suggest that the four forest types tended to separate along relatively short gradients. Moreover, the CCA strongly indicated that the most important factors were likely canopy openness and the size of the largest trees, which represented forest structural heterogeneity and were closely related to axis 1 (Fig. 4). The first axis is interpreted as an environmental gradient from exposed to sheltered habitats that strongly controls lichen community structure, which is consistent with other studies (McCune et al., 2000; Sillett and Antoine, 2004; Williams and Sillett, 2007). The PBSF and the PF
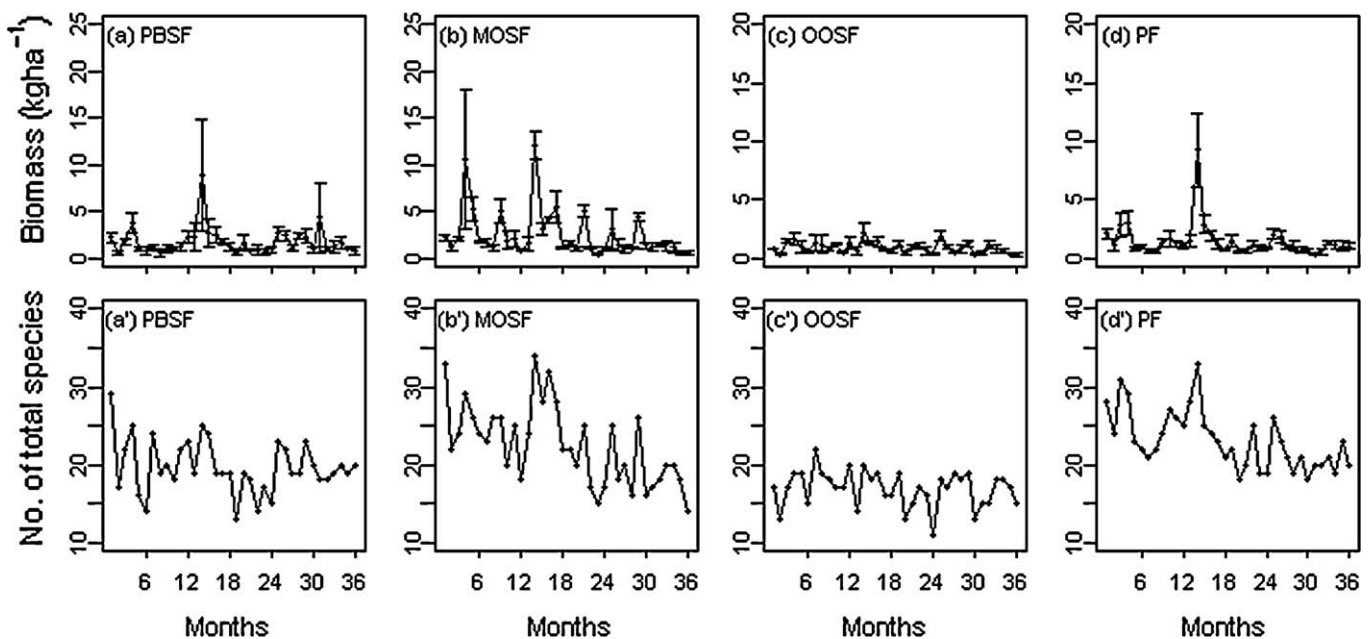

Fig. 5. Monthly dynamics of litterfall biomass (a–d, mean ± standard error) and total species (a′–d′) of epiphytic macrolichens in four forest types during 36 months in the Ailao Mountains, SW China.

represent the two most extreme forest types. The most dominant species preferred the MOSF, which had moderately open canopies and medium-sized trees. The MOSF also had the highest number of indicator species characteristic to the forest type. Although oldest or largest trees were thought to be very important in acting as propagule sources for the colonization of lichens in secondary forests (Peck and McCune, 1997; Sillett and Goslin, 1999), it was not the case in the study. Considered the largest trees in the MOSF, however, the oldest or largest trees seemed less important for lichens in these secondary forests. This may be because their importance and effectiveness were largely weakened by a mosaic of primary and secondary forests in our study. The second axis that associated with the species diversity of phorophytes explained 11.25% of variation. Apparently, it has emphasized the importance of host species, which corresponds to other studies (Kuusinen, 1996b; Li et al., 2007; Jüriado et al., 2009). In general, the alterations in bark properties of different phorophytes offered various microhabitats for lichen growth. The concentrated distribution of lichens around the centroid in the CCA ordination may also partly result from the similar diversity of trees in these forests of the Ailao Mountains. Again, we proposed that young forests with high structural heterogeneity and high tree diversity had the opportunity for maintaining most lichen species.

4.5. Indicator species in primary and secondary forests

Although epiphytic lichens are useful as subjects for environmental monitoring and forest ecosystem management, it is difficult to monitor most species (Nascimbene et al., 2010). Thus, indicators provided measurable surrogates for estimating total biodiversity (Hedenås and Ericson, 2000; Holz and Gradstein, 2005; Rogers and Ryel, 2008). According to Hedenås and Ericson (2000), many cyanolichens that are conservation indicators respond to succession in aspen stands. Rogers and Ryel (2008) found five species that were significant indicators for particular succession groups in the southern Rocky Mountains. In Costa Rica, five lichen indicators also occurred in tropical primary and recovering upper montane oak forests (Holz and Gradstein, 2005). In our study, MOSF had the highest number of forest type specific indicator species, and most of these indicators were probably typical pioneer species or early colonizers. Four indicator species of the PF were presumably dependent on microclimates of late-seral communities. Likewise, the co-occurrence of cyanolichen and chlorolichen indicators in the PBSF indicates that the forest can provide distinct microhabitats for lichens. The only cyanolichen indicator, *Leptogium saturninum*, may indicate that the OOSF was too wet for most lichens.

4.6. Limitations of the study

In our study, the data of biomass, species diversity and community structure of epiphytic lichens were collected only from 14 plots, which cannot capture comprehensive information on canopy lichen assemblages within the four forest types. Large-scale studies are desirable to address the changes in the epiphyte communities of the subtropical forests. Further, gaps which resulted from natural disturbances may also be important in maintaining epiphytic lichen biomass and diversity. Further research is needed to explore distribution patterns of epiphytic lichens in these gaps with different size and different succession stage.

5. Conclusion

Compared to primary forests, secondary forests, especially the MOSF, are also critical for epiphytic macrolichens of the Ailao Mountains. Higher litterfall biomass, more indicators and more rare species occurred in the MOSF. The secondary forests offered appropriate, but unstable, habitats for lichens and indicated that a long period following disturbance is needed for the complete recovery of lichen communities in the subtropical montane forests. Canopy openness, the DBH of the largest tree and diversity of trees were important factors influencing epiphytic lichen communities. Indicator species analysis determined 19 indicators that can be used in environmental monitoring of this region. Moreover, the maintenance of the forest mosaic can make important contributions to the promotion of lichen biodiversity and biomass accumulation in the forest management of this region.

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