Epiphytic lichens in subtropical forest ecosystems in southwest China: Species diversity and implications for conservation

Su Li a,b, Wen-Yao Liu a,∗, Da-Wen Li c

a Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China
b University of Chinese Academy of Sciences, Beijing 100049, China
c National Forest Ecosystem Research Station at Ailao Mountains, Jingdong, Yunnan 676209, China

ARTICLE INFO

Article history:
Received 2 August 2012
Received in revised form 9 December 2012
Accepted 20 December 2012

Keywords:
Conservation
Cyanolichen
Forest characteristic
Primary forest
Secondary forest
Species richness

ABSTRACT

Anthropogenic disturbances can severely impact the abundant lichen epiphyte communities of subtropical forests due to habitat loss, fragmentation and alteration. To assess the potential of anthropogenic secondary forests as conservation sites for epiphytic lichens, we investigated epiphytic lichens in 120 plots of eight forest types that are representative for the subtropical Ailao Mountains, southwest China. A total of 217 epiphytic lichen species were recorded, with 83% occurring in primary forests and 97% in secondary forests. Total species richness was significantly higher in the primary Lithocarpus forest (PLF), the middle-aged oak secondary forest (MOSF), the Populus bonnati secondary forest (PBSF) and the Ternstroemia gymnanthera secondary forest (TGSF) compared to four other forest types. The PLF harbored the highest number of rare species, while the MOSF, the PBSF and the TGSF, which had more pioneer tree species, hosted all cyanolichens found in this area. The Sørensen index of similarity between forest types ranged from 0.39 to 0.90. Ordination analysis showed a distinct lichen species composition in each forest type. Correlation analysis indicated that forest characteristics, such as canopy openness and host diversity, significantly influence lichen richness. These findings demonstrate the importance of primary forests for lichen epiphyte conservation, and suggest that the MOSF, the PBSF and the TGSF help preserve crucial components of the subtropical forest landscape and can play important roles in promoting lichen conservation. At a broad landscape scale, a mosaic of extensive primary forests and small secondary forest fragments is important for biodiversity conservation in subtropical regions.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Epiphyte species diversity and implications for conservation

Epiphytes comprise a highly diverse group and improve the structural complexity and spatial heterogeneity in evergreen broad-leaved forests (Hsu and Wolf, 2009; Li et al., 2011; Xu and Liu, 2005; You, 1983). They are one of the first life forms sensitive to deforestation (Sodhi et al., 2008) and are likely to be dramatically affected by the transformation of primary forests to secondary forests (Zotz and Bader, 2009). Nevertheless, since primary forests are relatively rare, those undisturbed adjacent secondary forests becoming increasingly important habitats for epiphytes; it is therefore necessary to assess the potential conservation value of these secondary forests. If secondary habitats house the same or an additional community of species as primary forests, the preservation of secondary forests alongside primary forest habitats might decrease the local extinction rate.

In subtropical forests, lichens are a nearly ubiquitous group and form a key but poorly understood component of epiphytes. In general, primary or old-growth forests are thought to act as refuges for epiphytic lichens (Ellis, 2012; Marmor et al., 2011; Nascimbene et al., 2010). Studies in the boreal zone have demonstrated that epiphytic lichen richness is lower in secondary forests than in old-growth forests and that their diversity is controlled by stand...
characteristics such as stand age, host composition, tree density and canopy cover (Ellis, 2012; Fritz et al., 2008; Júriado et al., 2003; McMullin et al., 2010). In particular, epiphytic cyanolichens are old-growth associated species and are particularly vulnerable to anthropogenic habitat fragmentation, degradation and loss (Hedenäs and Ericson, 2004; Kuusinen, 1996a; McCune, 1993). In contrast, emerging evidence shows that secondary forests can enrich not only pioneer lichens (Holz and Gradstein, 2005) but also cyanolichens (Fedrowitz et al., 2012; Neitlich and McCune, 1997). Furthermore, some studies from subtropical areas have shown that macrolichen species diversity is distinctly higher in secondary forests, probably due to a constant input of propagules from nearby primary forests, high landscape connectivity, high host species diversity, and moderately open canopies (Li et al., 2007, 2011). Therefore, understanding the conservation value of primary forest remnants and regenerating secondary forests for epiphytic lichens can greatly aid conservation efforts in forest landscapes.

In this study, we examined differences in species diversity and assemblages of epiphytic lichens among eight forest types in the subtropical Ailao Mountains, which are a major feature of Yunnan Province, southwest China. Since the 1980s, a number of natural reserves have been established in Yunnan and deforestation is forbidden in these reserves (Liu et al., 2001). These protected primary and secondary forests are important habitats for epiphytes. To date, more than 450 species of epiphytes (113 angiosperms, 117 ferns, 176 bryophytes and 61 lichens) have been recorded in the Ailao Mountains (Li et al., 2007; Ma et al., 2009; Xu, 2007; Xu and Liu, 2005; You, 1983; Zhu and Yan, 2009). Although the lichen epiphyte community in this region is poorly understood, it is now receiving increasing attention for its biodiversity and the urgent need for conservation. Our objectives were to understand epiphytic lichen diversity among forest types in the subtropical Ailao Mountains and to evaluate the potential of secondary forests for lichen conservation.

2. Materials and methods

2.1. Study area

The study was conducted in the Xujiaiba region (2000–2750 m a.s.l.), a core area of the Ailao National Nature Reserve (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). The NNR, with an area of 677 km², is one of the largest tracts of natural evergreen broad-leaved forest in China (Zhu and Yan, 2009). The mountain range is part of the Indo-Burma biodiversity hotspot and is recognized as a priority area for biodiversity conservation (Myers et al., 2000; Olson and Dinerstein, 1998). The mean annual precipitation is 1947 mm, with 85% falling in the rainy season from May to October. The average annual evaporation is 1192 mm, the annual mean temperature is 11.3 °C, and the mean relative humidity is 85% (Li et al., 2011).

The Xujiaiba region has a gentle undulating topography and consists of eight forest types. About 77.9% of the total area is dominated by primary montane moist evergreen broad-leaved forest also called primary Lithocarpus forest (PLF), 6.7% by primary dwarf mossy forest (PDMF), and less than 16% by secondary forests. The forest landscape is hence characterized by an extensive area of continuous primary forests, archipelagos of small secondary forest fragments and high forest connectivity (You, 1983).

The PDMF is dominated by the tree species Lithocarpus xylocarpus (Kurz) Markgr., L. lanceolata (Benth.) Rehder, Castanopsis watuii (King ex Hook. f.) A. Camus, Schima noronhae Reiw. ex Blume and Stewartsia pteropetiolata Cheng, and is characterized by moist, shaded conditions, and an almost fully closed canopy (Qiu and Xie, 1998). The PDMF only occurs as an “island” of evergreen forest on a mountain top at 2600 m a.s.l. The canopy is exposed to frequent and intense wind and mist events throughout much of the year, and the dominant species are L. crassifolius A. Camus, Rhododendron irroratum Franch., Clethra delavayi Franch., Ilex corallina Franch. and Gaultheria griffithiana Wight. These primary forests are free from anthropogenic disturbances and include large, more than 300 years old trees (Wang, 1983; You, 1983).

The old-aged oak secondary forest (OOSF) experienced clearcutting about 110 years ago but has since been free from human disturbance. It represents the advanced natural succession after cutting (Young et al., 1992). The middle-aged oak secondary forest (MOSF) developed after deforestation in the late 1950s and 1980s. Both secondary forests share most of their tree species with the nearby PLF, but community structure differs significantly between the three forest types (He et al., 2003; Young et al., 1992). The Populus bonatii secondary forest (PBSF) resulted from cutting and grazing in the last century. It is mainly dominated by pioneer P. bonatii Levl. and is associated with L. hancei and Vaccinium duclouxi (H. Lév.) Hand.–Mazz. The PBSF is widely believed to naturally succeed first to secondary oak forest (the MOSF and the OOSF) and finally to the PLF (Qiu and Xie, 1998). The T. gymnanthera secondary forest (TGSF, <20 year) is a very young vegetation adjacent to the MOSF and the PBSF. The tree layer is 3–5 m tall and is dominated by early secondary trees and shrubs such as T. gymnanthera (Wigt et Arn.) Bedd., V. duclouxi and G. forestii Diels (Qiu and Xie, 1998). The TGSF is characterized by shady conditions and small patch size (<0.01 ha). These four secondary forests have been well protected since the foundation of the NNR.

The Alnus nepalensis secondary forest (ANSF) and Pinus yunnanensis secondary forest (PYSF) also resulted from repeated cutting, fires, and grazing. The canopy of the ANSF is dominated by the pioneer tree species A. nepalensis D. Don, while the PYSF is dominated by P. yunnanensis Franch., T. gymnanthera and some Lithocarpus species. These two secondary forests can be described as the first stage of the secondary succession to the PLF and are also protected, but unlawful cutting may occasionally occur (Qiu and Xie, 1998; Wang, 1983).

2.2. Sampling method

Comprehensive fieldwork was carried out from October 2008 to June 2011. We randomly established 120 plots that differed in size due to differently sized forest areas and patches of different forest types in Xujiaiba: 25 plots of 20 × 20 m in the PLF, 10 in the PDMF, 10 in the OOSF, and 15 plots in each of the other five secondary forest types (400 m² in the MOSF and the ANSF, 100–400 m² in the PBSF (plot size and lichen richness was not correlated: $r_{adj}^2 = 0.063, P = 0.367$), 10 × 10 m in the PYSF and 5 × 5 m in the TGSF).

In each plot, we counted and identified each tree with a height > 2 m and diameter at breast height (dbh) > 3.5 cm (dbh > 2 cm in the TGSF), and we then determined dbh, the maximum diameter of the largest tree (mdbh), host density, basal area, deciduous tree richness, deciduous tree density, and host diversity indices (species richness, Shannon–Wiener index and Simpson index). Canopy openness was measured at the beginning of the survey in those plots located in evergreen forests because the presence of deciduous trees had little effect on the canopy openness in these forests (You, 1983), while the canopy openness of the PBSF and the ANSF was measured in May and January. Canopy openness was visually estimated by the first author at 20 random points in each plot, and gave an average value in 10% classes. Additionally, we obtained the age of forests from available documentation (Deng et al., 1993; He et al., 2003; Young et al., 1992), employees of Ailaoshan Station, and the forest management authority.
We recorded 217 epiphytic lichen species belonging to 76 genera from eight forest types in the Ailao Mountains. Approximately 83% (183) of all species occurred in the primary forests, compared to 97% (207) in the secondary forests. One hundred seventy-eight species occurred in the PLF, 91 in the PDMF, 106 in the OOSF, 175 in the MOSF, 158 in the PBSF, 49 in the ANSF, 43 in the PYSF and 166 in the TGSF.

About 17% (37) of all species occurred across all forest types, and 16% (35) of all lichens were rare species (Appendix 2). The number of rare species was highest in the PLF (11) and the TGSF (11), followed by the MOSF (10), the PDSF (10), the PDMF (1) and the ANSF (1), but no rare species were observed in the OOSF or the PYSF. Furthermore, 25 rare species and three common species were unique to a certain forest type: eight in the PLF (Larrea megasperma, Lep- raricia incana, Nephromopsis yunnanensis, Phyllophora cf. farfureaca, Pyrenula dermatodes, P. leucostoma, P. subferruginea and Sticta platy- phillyoides), seven in the PDSF (Buella sp., Fuscopannaria leucosticta, F. praetermissa, Heteroderma szechuanensis, Pertusaria leioplaca, P. ophthalmitza and Sulcaria sulcata V. vulpinoides), five in the TGSF (Anisomeridium sp., Arthonia sp., Callicium lenticulare, Lobaria discolor and Thalloloma anguvinum), five in the PDMF (Collema cf. japonicum, C. fasciculare, Fissurina inabensis, Normandina pulchella and P. car- neopallida), two in the PDSF (Cladonia furcata and Haematomma persoonii) and only one in the ANSF (Parmelia ricasoloides).

The cumulative species curves appeared to reach their asymptotes for each forest type (Fig. 1a and b), indicating that the sampling plots were sufficiently representative for the lichen community. The MOSF and the TGSF curves indicated that these forests were likely to have a higher species richness than the PLF (Fig. 1a), and the richness estimates showed similar results (Fig. 1c). All 217 lichen species were encountered in at least 26 plots (Fig. 1b). The optimized combination of plots that would maximize the number of species included one plot of the PDMF, 10 of the PLF, five of the MOSF, six of the PDSF, one of ANSF, three of TGSF, and their respective contributions to total species would be 23%, 70%, 65%, 64%, 14% and 47%.

The α-diversity differed significantly among forest types (χ² = 102.55, P < 0.001; Fig. 2a). The highest α-diversity occurred in the PDMF and the lowest in the PYSF. For multiple comparisons, significant differences in α-diversity were found between forest types, although in some cases no significant variations were observed (Fig. 2a). For all plots, the α-diversity was significantly and positively related to deciduous tree richness, deciduous tree density and host diversity, and negatively related to canopy openness (Table 1). In the MOSF, α-diversity was significantly and positively related to canopy openness and deciduous tree density, and negatively related to forest age, basal area and mdhb. In the ANSF, α-diversity was significantly and positively related to forest age, basal area, dbh and mdhb, and negatively related to canopy openness, deciduous tree density and host density. In the TGSF, α-diversity was only positively related to host diversity.

Sørensen's similarities between forest types varied from 0.39 to 0.90, with an average of 0.64. The similarity was highest between the PLF and the MOSF, and lowest between the PLF and the PYSF. Similar patterns were observed for similarities in lichen species between pairs of plots (Fig. 3), with a range between 0.34 and 0.96, and an average of 0.60. Plots in the ANSF were most similar (mean ± SE: 0.80 ± 0.01), followed by the PYSF plots (0.78 ± 0.01), the PDSF plots (0.75 ± 0.00), the PDMF plots (0.70 ± 0.01), the MOSF plots (0.70 ± 0.00), the OOSF plots (0.68 ± 0.01), the PLF plots (0.67 ± 0.00) and the TGSF plots (0.62 ± 0.00). Moreover, the NMDS ordination also showed distinct lichen assemblages in each forest type.

3.2. Epiphytic cyanolichens

Altogether we encountered 30 cyanolichens in the 120 plots. While 18 species occurred in primary forests (17 in the PLF and 14 in the PDMF), all species occurred in secondary forests, with 11 species in the OOSF, 23 in the MOSF, 28 in the PBSF, 11 in the ANSF, seven in the PYSF and 26 in the TGSF (Appendix 2). Furthermore, most of the Fuscopannaria, Leptogium, and Panaria species showed a greater preference for deciduous than evergreen trees,
while all Collema species grew exclusively on *Salix daliensis* in the secondary forests. In the ANSF, cyanolichens only occurred on large trunks (dbh > 10 cm). In the PYSF, only *Leioderma sorediatum* occurred on one trunk of *P. yunnanensis*, but all seven species occurred on broad-leaved trees (e.g., *Vaccinium* and *Lithocarpus*).

The $\alpha$-diversity of cyanolichens differed greatly among forest types ($\chi^2 = 91.81, P < 0.001$), and in some cases subsequent pairwise comparisons indicated there were no significant variations between forest types (Fig. 2b). For all plots, the $\alpha$-diversity was significantly and positively related to deciduous tree richness and density, host density and host diversity, and negatively related to forest age, basal area, dbh and mdbh (Table 1). In the OOSF, $\alpha$-diversity was significantly and positively related to host diversity. In the MOSF, $\alpha$-diversity was positively related to canopy openness. In the PBSF, $\alpha$-diversity was positively related to host diversity and negatively related to deciduous tree density. In the ANSF and in the TGSF, the distribution patterns of cyanolichens were similar to those of all lichens.

**4. Discussion**

**4.1. Diversity of epiphytic lichens in subtropical forest ecosystems**

By sampling all eight forest types in our study area we were able to comprehensively understand the distribution patterns of lichen epiphytes in a montane forest landscape, and to obtain a clear picture of the lichen community in each forest type (Fig. 1). At the landscape scale, the total epiphytic lichen richness in the Ailao Mountains is one of the highest in the world (Ellis and Coppins, 2006; Jüriado et al., 2003; Peterson and McCune, 2001; Rhoades,
Recent research has confirmed that landscape attributes such as native vegetation cover and patch isolation are very important in determining species richness distributions (Arroyo-Rodríguez et al., 2009). Moreover, increased spatial heterogeneity of a landscape can promote species richness (Castillo-Campos et al., 2008). Thus, epiphytic lichen communities in this area are likely to benefit from landscape characteristics such as extensive primary forests, small secondary forest fragments and high forest connectivity (Li et al., 2011; You, 1983). Our results also fit the intermediate disturbance hypothesis (Connell, 1978), which predicts a greater species richness in communities subjected to moderate levels of disturbance.

Our study also showed that epiphytic lichen richness and diversity were dependent on forest type, and both were higher in the PLF. These patterns are not only consistent with those of previous studies in the same area (Li et al., 2007, 2011), but also coincide with studies from the temperate/boreal hardwood and conifer forests (Ellis, 2012; Hedénäs and Ericson, 2000; Jüriado et al., 2003) and the tropics (Holz and Gradstein, 2005). The PLF harbored a more heterogeneous lichen community, in accordance with results on macrolichen litter (Li et al., 2011) and forest structure heterogeneity (You, 1983). Moreover, the PLF had the highest number of unique species. These results support the view that primary forests can act as refuges for epiphytic lichens and can provide greater opportunity for the growth of specialists (Ellis, 2012; Sillett and Antoine, 2004). The PDMF, however, harbored lower species diversity, although a thick bryophyte layer, high air humidity and high light availability (You, 1983), which may support the establishment and growth of lichens (Barkman, 1958; Fritz, 2009), were observed in this forest. One possible explanation for our results is altitude, which resulting in foliose and crustose lichen diversity tends to drop with altitude whereas fruticose lichen diversity increases in moss or cloud forests (Rhoades, 1995; Wolf, 1993). Fruticose lichens represent only a very small portion of the entire lichen assemblage in this region, which apparently accelerated the decrease of total lichen richness caused by altitude.

Lichen species richness in the three secondary forests, the MOSF, the PBSF and the TGSF, was very high, even though the TGSF is less than 20 years old and has very small patch size. The estimated species richness in the MOSF and in the TGSF was even higher than in the PLF. Similarly, secondary forests support high cryptogamic epiphyte species richness in the tropics (Holz and Gradstein, 2005) and high epiphytic macrolichen species richness in North America (Netlich and McCune, 1997). In general, the establishment of lichens in secondary forests is thought to be

Table 1
Spearman’s nonparametric correlation test (rho) between plot variables and species richness of epiphytic lichens and cyanolichen group in eight forest types in the Ailao Mountains, southwest China.

<table>
<thead>
<tr>
<th>Variables</th>
<th>All forest types</th>
<th>PDMF</th>
<th>PLF</th>
<th>OOSF</th>
<th>MOSF</th>
<th>PBSF</th>
<th>ANSF</th>
<th>PYSF</th>
<th>TGSF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphytic lichens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.730***</td>
<td>ns</td>
<td>0.636*</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Canopy openness</td>
<td>−0.253**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.737***</td>
<td>ns</td>
<td>−0.828***</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Dbh</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.561*</td>
<td>ns</td>
<td>−0.673**</td>
</tr>
<tr>
<td>Deciduous tree density</td>
<td>0.274**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Deciduous tree richness</td>
<td>0.406***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Forest age</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Mdbh</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.521*</td>
<td>ns</td>
<td>0.721**</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Richness of trees</td>
<td>0.469***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Shannon–Wiener index of trees</td>
<td>0.458***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Simpson index of trees</td>
<td>0.466***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Tree density</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.606*</td>
</tr>
<tr>
<td>Cyanolichen group</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area</td>
<td>−0.282**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.580*</td>
<td>ns</td>
</tr>
<tr>
<td>Canopy openness</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.548*</td>
<td>ns</td>
<td>−0.709***</td>
</tr>
<tr>
<td>Dbh</td>
<td>−0.381***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.686***</td>
</tr>
<tr>
<td>Deciduous tree density</td>
<td>0.573***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.638*</td>
<td>−0.684**</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Deciduous tree richness</td>
<td>0.526***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Forest age</td>
<td>−0.193</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.674**</td>
</tr>
<tr>
<td>Mdbh</td>
<td>−0.268***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Richness of trees</td>
<td>0.189</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.709***</td>
</tr>
<tr>
<td>Shannon–Wiener index of trees</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.646*</td>
<td>ns</td>
<td>0.516*</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Tree density</td>
<td>0.309***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

ns: Not significant.
PDMF: primary dwarf mossy forest; PLF: primary Lithocarpus forest; OOSF: old-aged oak secondary forest; MOSF: middle-aged oak secondary forest; PBSF: Populus bonatii secondary forest; ANSF: Alnus nepalensis secondary forest; PYSF: Pinus yunnanensis secondary forest; TGSF: Ternstroemia gymnanthera secondary forest.

* P < 0.05.
** P < 0.01.
*** P < 0.001.
limited by the absence of adequate propagules and inefficient dispersal (Dettki et al., 2000), but, large trees or old-growth forests are very important propagule sources (Peck and McCune, 1997; Sillett and Goslin, 1999). Thus, the lichen diversity in the secondary forests appears to benefit from landscape attributes in this region (Li et al., 2011; You, 1983). The constant high humidity may also promote the establishment of lichens in secondary forests (Ellis and Coppins, 2006; Li et al., 2011; Qiu and Xie, 1998). Interestingly, the greater prevalence of cyanolichens in the three secondary forests is consistent with the idea that they can emerge earlier in the epiphyte community succession in moist woodlands than in drier woodlands (Ellis and Coppins, 2006). Furthermore, the cyanolichen group showed clear preferences for deciduous trees, indicating that the presence of a deciduous component in evergreen broad-leaved forests helps to increase lichen diversity. These observations are consistent with previous studies demonstrating deciduous trees play a pivotal role in the establishment of epiphytic cyanolichens in conifer forests, which can be attributed to the fact that the cyanolichen group seems to require a substrate pH > 4.5 and many deciduous trees meet this demand (Goward and Arsenault, 2000; Jüriado et al., 2003; Rolstad et al., 2001). Kuusinen (1996b) also realized that cyanolichens are very abundant on deciduous Populus and Salix trees with bark pH above 5.0 in Fennoscandian boreal forests. Moreover, deciduous trees can enhance the bark pH of nearby trees by a dripzone effect, allowing cyanolichens to colonize more acidic barks (Goward and Arsenault, 2000). Likewise, the low diversity of cyanolichens in the PLF may partly be explained by the absence of pioneer deciduous trees.

The OOSF was much poorer in lichen species richness, although it was the oldest secondary forests. The interacting effects of higher humidity, nearly closed canopy and low host diversity have been proposed to explain the dramatic decrease in lichen richness in this forest (Li et al., 2011). These effects could not be excluded, but were insufficient to explain this result. Another possible explanation is the combination of the absence of pioneer deciduous trees and the rarity of late-stage tree species (e.g., L. xylocarpus, C. wattii and S. pteropetiolata) (Li et al., unpublished data; Young et al., 1992).

Similarly, the ANSF and the PYSF had substantially impoverished lichen communities compared to the other forest types. In fact, more than 90% of species that were found in the ANSF and the PYSF can be collected on basal trunks (Li et al., in press). The lowest total richness and the highest similarity between plots indicated that very homogeneous lichen communities occur in the two forests, which may result from the more homogeneous forest structure with lower host diversity and more open canopies (Roo ney et al., 2007). As in other studies (Hedenäls and Ericson, 2000, 2004; McCune, 1993), we found cyanolichens only grew on the basal, more humid part of trunks, indicating most microhabitats (especially canopies) in the ANSF and the PYSF may be generally drier, more sun-exposed and less favorable for this group. Alternatively, the distribution of cyanolichens in the PYSF may indicate that P. yunnanensis is not an appropriate host for many lichens; Fr. spp. are thought to be unsuitable for some epiphytes, possibly due to phenolic substances or resins (Hietz and Hietz-Seifert, 1995), low water retention capacity (Castro-Hernández et al., 1999) and excessively acidic barks (Goward and Arsenault, 2000). The microhabitats in the two forests seem to exclude certain lichen species; for example, same shade (e.g., Graphidion), nitrophytic (e.g., Leconura) and fruticose (e.g., Usnea) species were not found (Barkman, 1958; Hale, 1967). Many lichen species in the ANSF and the PYSF were widespread in the landscape, which were better adapted to survive and reproduce.

These results also allowed us to detect the effects of forest characteristics on epiphytic lichen diversity. Canopy openness is a major factor in determining the distribution of lichen communities (Li et al., 2011; Sillett and Antoine, 2004). In particular, it was one of the causes for the changes of lichen diversity in the ANSF and in the MOSF. Host diversity was another key variable. The alterations in bark properties of different hosts can offer diverse substrates for epiphytes (Ellis, 2012; Kuusinen, 1996b; Sillett and Antoine, 2004). Deciduous tree bark is particularly important for some specialists. Forest age, basal area, dbh and tree density have been linked to lichen richness (Ellis, 2012; Hedenäls and Ericson, 2000; Marmor et al., 2011; McMullin et al., 2010; Rogers and Ryel, 2008) but seemed to have minor influences at our sites. Notably, although the importance of large trees in acting as propagule sources for lichen colonization has been largely weakened by the landscape mosaic (Li et al., 2011; Peck and McCune, 1997; Sillett and Goslin, 1999), they still play an important role in the ANSF.

4.2. Implications for biodiversity conservation

The importance of epiphyte studies for biodiversity conservation has been largely overlooked in China (Li et al., 2011; Ma et al., 2009). This is the first comprehensive study of epiphytic lichen diversity in subtropical forest ecosystems in China, and provides evidence that the conservation of both primary and secondary forests on a broad scale is needed to conserve the maximum species diversity in the landscape.

Our results highlight the importance of primary forests in long-term biodiversity conservation. We believe that the PLF is critical to conserve lichen diversity because this predominant vegetation of subtropical China houses high lichen species richness and may facilitate their re-establishment in secondary forests (Peck and McCune, 1997; Sillett and Goslin, 1999; You, 1983). Its extensive area is particularly likely to lead to a decrease in the risk of local extinction for epiphytes in the landscape (Arroyo-Rodríguez et al., 2009; You, 1983). Although the PDMF – another primary forest – has lower lichen diversity, two species are unique to this forest, and is also an important habitat for other epiphytic groups (especially bryophytes) (Ma et al., 2009; You, 1983). Consequently, the two primary forests need to be preserved in the landscape to ensure the integrity of epiphyte communities in this region.

Different secondary forests were found to have substantially different conservation values. Secondary vegetations have become the predominant environments worldwide and are generally not optimal for biodiversity conservation (Hedenäls and Ericson, 2000; Lundström et al., 2011; Rogers and Ryel, 2008; Zotz and Bad er, 2009). In the Ailao Mountains, however, the MOSF, the PBSF and the TGSF are most likely to contribute positively to total biodiversity. They can provide suitable substrates for lichen specialists not suitably accommodated in primary forests. Thus, we emphasize their potential complementary role in the conservation of forest flora in subtropical forests. Although most deciduous trees are pioneers and are occasionally present in forest edge, riparian areas and early secondary forests (Wang, 1983; Zhu and Yan, 2009), the importance of deciduous trees for lichen conservation is particularly noteworthy in forest practices. On the contrary, we believe that the OOSF, the ANSF and the PYSF have low values for lichen biodiversity conservation because they contribute very little to total species richness.

In conclusion, habitat heterogeneity is important for maintaining lichen diversity in forest landscapes. However, a prerequisite is the presence of primary or old-growth forests functioning as a propagule source to facilitate the restoration of neighboring secondary vegetation within the landscape. Although secondary forests are successional habitats for lichens and their conservation potential is temporally limited, they are also critical for biodiversity conservation. It is very important to stop deforestation, but a mosaic of extensive primary forests and small secondary forest fragments can offer more microhabitats for specialists than
continuous primary forests. Consequently, we strongly emphasize that the maintenance of the forest landscape mosaic is a biodiversity-friendly practice in natural reserves in subtropical China.

Acknowledgments

This project was funded by the National Natural Science Foundation of China (Nos. U1133605, 30870437) and the CAS135 Program (XTBG-F01). We thank the Management Authority of the Ailao Mountain Nature Reserve for the permission to undertake this research. We are grateful to Messrs. Ming-Chun Lu, Ying-Bin Li, Jin-Hua Qi, Lin Chen, Meng-Nan Liu, Guo-Ping Yang and the Ailao Mountains Ecosystem Research Station for their fieldwork assistance. We are also grateful to the reviewers, editors and Dr. Pelin Kayaalp for constructive comments on the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocen.2012.12.027.

References


