ORIGINAL ARTICLE

Liang Song · Wen-yao Liu · Wen-zhang Ma
Zheng-hong Tan

Bole epiphytic bryophytes on *Lithocarpus xylocarpus* (Kurz) Markgr. in the Ailao Mountains, SW China

Abstract Epiphytic bryophytes growing on *Lithocarpus xylocarpus* (Kurz) Markgr. trunks of different diameter classes in primary (132 plots) and secondary (84 plots) *Lithocarpus* forests in the Ailao Mountains, SW China, were surveyed and analyzed to determine species composition and richness, and to identify environmental variables that may affect it. Among the 65 species (belonging to 32 genera, 19 families) found, 28 occurred in both forests, with *Syrrhopodon gardneri* (Hook.) Schwaegr. predominanting. Species richness and total coverage in primary forest were significantly higher than in secondary forest. We suggest that a period of perhaps much more than 110 years is necessary for the recovery of epiphytic bryoflora in montane forest of SW China. Fan, turf, and smooth mat are the most important life forms, with high occurrences in both forests. The life form composition of epiphytic bryophytes is determined mainly by microhabitat and host age. Tree age, the presence of primary forest, bark pH, and plot exposure are the environmental variables that have significantly influenced the composition of epiphytic bryophytes. Tree age explained most variations in epiphytic bryoflora. Bark pH is another important parameter that significantly influenced the epiphytic bryophyte community, but seemed indirectly correlated with tree age. Primary forest is a favorable habitat for epiphytes, due mainly to its diversified canopy structure and the presence of large diameter hosts. Moisture-laden southwest trade winds and forest structure could differentiate microclimate and impel a distinct composition of epiphytes in windward and leeward exposures.

Keywords Epiphytic bryophyte · Richness · Life form · Recovery · Bark pH · Diameter · Humidity · Aspect

L. Song · W. Liu (✉) · Z. Tan
Key Laboratory of Tropical Forest Ecology,
Xishuangbanna Tropical Botanical Garden,
Chinese Academy of Sciences, No. 88 Xuefu Road,
Kunming 650223, Yunnan, People's Republic of China
E-mail: liuwy@xtbg.ac.cn
Tel.: +86-871-5153787
Fax: +86-871-5160916

L. Song · Z. Tan
Graduate University of Chinese Academy of Science,
Beijing 100049, People's Republic of China

W. Liu
School of Environmental Biology,
Curtin University of Technology,
Perth, WA 6845, Australia

W. Ma
Kunming Institute of Botany, Chinese Academy of Sciences,
Heilongtan, Kunming 650204, Yunnan, People's Republic of China

Introduction

Environmental parameters such as biogeographic region, and especially forest type, can influence the distribution and composition of epiphytes (Kenkel and Bradfield 1986; González-Mancebo et al. 2004). Some authors have claimed that species richness and diversity in primary forests are significantly higher than in secondary forests because many epiphytes are sensitive to disturbance and cannot grow in secondary forest as it lacks the appropriate microclimatic conditions and suitable substrates (Turner et al. 1994; Vellak and Paal 1999; da Costa 1999). Others have argued that some secondary forests are not necessarily less diverse in epiphytes than primary forests due to high air humidity and habitat heterogeneity (Nkongmeneck et al. 2002; Holz and Gradstein 2005).

Individual characteristics of the phorophytes may affect the epiphytic community to different degrees. Among phorophyte traits it is possible to distinguish: diameter (size), height, stem flow, plot exposure to light and trade winds, bark water-holding capacity, bark pH value, bark roughness, and bark nutrient content (Bates 1992; Bergstrom and Tweedie 1998; González-Mancebo et al. 2003; Loppi and Frati 2004).

Many studies have found a positive relationship between host size and epiphyte diversity (Hietz and Hietz-Seifert 1995; Zotz and Vollrath 2003; Burns and Dawson 2005). Culberson (1955) suggested that bark-factors were the most important determinants of epiphytic communities in upland forests. According to Barkman (1958), epiphytic vegetation was controlled mainly by humidity as tree bark, generally retaining little water, was a drier habitat than other substrates. Bark acidity was another factor that may explain the composition and distribution of epiphytic flora (Bates and Brown 1981; Studlar 1982; Kuusinen 1996). In addition, changes in epiphytic composition along the height gradient of a tree trunk have been documented for bryophytes (Kenkel and Bradfield 1981); while plot exposure may affect bryophyte species composition on the same host species (González-Mancebo et al. 2003).

Ma et al. (2009) found that relative humidity, bark roughness, and water-holding capacity of host barks were important environmental parameters that explained much of the variation in life forms of epiphytic bryophytes in the Ailao Mountains (Mts.) of SW China. However, how these parameters and others, especially tree age, bark pH, plot exposure, influence communities of epiphytic bryophytes is still unclear. Different phorophyte species usually support distinct epiphytic assemblages (Kuusinen 1996). For a specific host tree species, variation in the species composition of their associated epiphytes might be expected between sites because of habitat differentiation (Kenkel and Bradfield 1986). In the present study, epiphytic bryophytes on the basal trunks of *Lithocarpus xylocarpus* (Kurz) Markgr., one of the most abundant tree species with a wide distribution throughout the Ailao Mts. region, were surveyed and analyzed in both primary and secondary *Lithocarpus* forests within a National Nature Reserve (NNR) in the Ailao Mts., SW China. The main objectives were: (1) to compare species richness and composition (in terms of species and life forms) between primary and secondary forest (ca. 110 years old) in subtropical evergreen broad-leaved forest (considering different tree age classes); and (2) to assess which environmental variables (forest type, diameter class, plot exposure, height, bark pH, bark roughness, and bark water-holding capacity) affect the composition of the epiphytic bryoflora.

Methods

Study site

This study was conducted in the Xujiaba region (24°32′N, 101°01′E)—a protected section with 5,100 ha of pristine montane moist evergreen broad-leaved forest, in Ailao Mts. NNR (23°35′–24°44′N, 100°54′–101°01′E,

Fig. 1). The altitude ranges from 2,450 to 2,650 m. The climate is influenced mainly by the southwest monsoon. Meteorological observations during 1991–1995 show an average annual temperature of 11.3°C (averages of 5.4°C in January to 16.4°C in July). The annual mean precipitation is 1,931.1 mm, with 85% of the rain in the rainy season (May–October). The annual mean evaporation is 1,485.5 mm and the annual mean relative humidity is 86%. The frost-free period is ca. 200 days (Qiu and Xie 1998). Typical plots of primary and secondary *Lithocarpus* forest within the NNR were chosen to investigate and analyze the epiphyte composition on *L. xylocarpus* in this study. Study sites were located at similar altitudes but with different degrees of human disturbance.

Primary *Lithocarpus* forest

Primary *Lithocarpus* forest (PLF), which covers nearly 85% of the Xujiaba region, is the most extensive forest type in the study area (Young et al. 1992). It is co-dominated primarily by *Lithocarpus hancei* (Benth.) Rehder, *Castanopsis rufescens* (Hook.f.et Th.) Huang et Y.T.Chang, and *L. xylocarpus* (You 1983). This forest has been classified to be an old-growth forest according to the presence of large, old trees, and the absence of widespread human disturbance (Yang et al. 2008). It is especially rich in epiphytic flora (You 1983).

Secondary *Lithocarpus* forest

This secondary *Lithocarpus* forest (SLF) experienced clear cutting by local people about 110 years ago but has been free from human disturbance since then (Young et al. 1992). It is dominated by *L. hancei*, *L. xylocarpus* and *Vaccinium ducrouxii* (Levl.) Hand.-Mazz., and shares many dominate tree species with nearby primary forest (Young et al. 1992). Based on stand age and the growth rate of major species (Yang et al. 2008), it represents the advanced natural succession after cutting. The majority of host trees are loaded with epiphytic bryophytes (Ma et al. 2009).

Average diameter at breast height (DBH) in the canopy is 50.9 cm and 26.1 cm for the PLF and SLF, respectively. The former has a wider range of size classes in the canopy; the latter is much more even-aged. The host height in the PLF is significantly ($P < 0.01$) higher than in the SLF (average height of canopy in the PLF, 23.3 m; SLF, 20.5 m). Woody species diversity was higher in the PLF. In contrast, the SLF maintains a higher density of tree individuals (Young et al. 1992).

Sampling method

Field survey was carried out from April to July 2009. *L. xylocarpus* was sampled based on six diameter classes

Fig. 1 Location of the study site in the Ailao Mountain National Nature Reserve (NNR), SW China
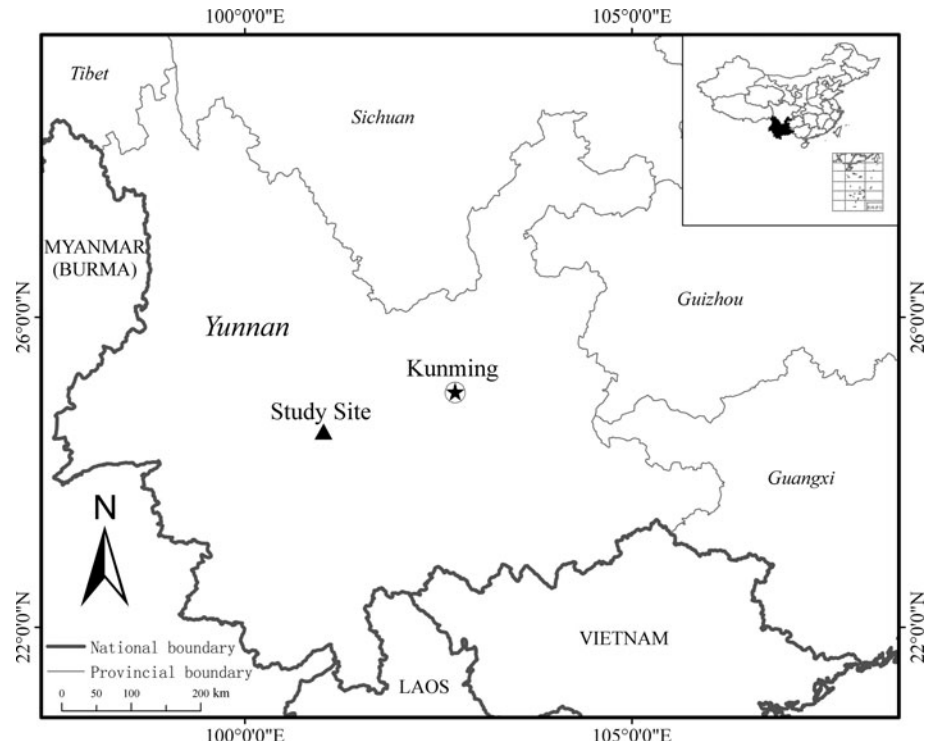
(1 = 5.0–12.0 cm; 2 = 12.1–20.0 cm; 3 = 20.1–30.0 cm; 4 = 30.1–40.0 cm; 5 = 40.1–60.0 cm; 6 > 60.0 cm). We chose one *L. xylocarpus* individual belonging to diameter class 6 (DBH > 60.0 cm) as the circle center first, then we established a round-shaped plot within a 25 m-radius-circle and tried to find one tree per diameter class (five trees in total for diameter classes 1–5) randomly in the PLF. Only plots that boasted at least one tree per diameter class were surveyed for their epiphytic bryophytes. A similar method was used in the SLF, but hosts belonging to class 5 and 6 were not sampled because no big trees were present. In total, six typical 25 m-radius-circle plots were selected in each type of forest. The epiphytic bryophytes were sampled from two height intervals [from the forest floor to 0.5 m (base section) and from 1.5 to 2 m (trunk section)] and two aspects [both the windward (southwest) and leeward (northeast) exposures]. For this purpose we divided the tree into two exposure zones: southwest, ranging from southeast (135°) around to northwest (315°), and northeast, ranging from northwest (315°) around to southeast (135°) (individuals belonging to diameter class 1 were not divided into different exposures because of their small perimeters) (González-Mancebo et al. 2004). The epiphytic bryophytes were investigated using 20 cm × 20 cm or 10 cm × 40 cm metal-frame-quadrats with 256 standard square-shaped grids equal in size.

A total of 132 quadrats (400 cm^2) in the PLF and 84 in the SLF were investigated. At each plot, both coverage of all epiphytic bryophytes and each species were collected (calculated as the percentage of grids occupied by the species from the total 256 grids of the plot). We also recorded the height and plot exposure for each plot. Unfamiliar species were identified in the laboratory by W.-Z.M. and voucher specimens were deposited in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences. Nomenclature followed that of Gao and Cao (2000) for liverworts, Li (2002, 2005) for mosses, and taxonomic arrangement refers to Chen et al. (1963, 1978) for mosses, and Schuster (1966) and Grolle (1983) for liverworts. Bryophytes were classified into eight life forms (cushion, dendroid, fan, rough mat, smooth mat, pendant, turf, and weft) according to Ma et al. (2009).

Measurement of environmental variables

For all phorophytes sampled, diameter was measured with a DBH tape at 1.3 m from the ground. Bark roughness of each plot was determined on a 1–9 scale (1 = very smooth; 3 = smooth but with fissures; 5 = shallowly furrowed; 7 = with deep fissures; 9 = with crevices abundantly across the surface; with 2, 4, 6, 8 being in-between cases) (Male and Roberts 2005). Bark samples were collected from the boles within each plot and small pieces (2 g) were incubated in 25 ml distilled water for 24 h and then the pH value of the extract was measured with a standard pH meter (PHS-3C, Shanghai Precision and Scientific Instrument Co., China) (Kuusinen 1996). Similarly sized (3 × 3 cm) bark samples were collected per plot, and later taken to the

laboratory for measurement of water-holding capacity (C_{wh}). Samples were first cleared carefully of epiphytes with a toothbrush (Hauck et al. 2006). The average relative air humidity was measured by placing an auto data logger (Thermo Recorder TR-71U, T and D Corporation, Japan) on host tree trunks at 1.5 m above ground level in both types of forest simultaneously. Three hosts were selected randomly as measuring points for relative air humidity. The measurements were first taken during April 2005, and repeated during the following August.

Data analysis

The important value (IV) of epiphytic bryophytes was calculated using the formula below:

$$IV = (R_{cov} + R_{fre})/2 \times 100\% \qquad (1)$$

where R_{cov} is the relative coverage of a certain species, and R_{fre} refers to relative frequency of a certain species.

Water-holding capacity was calculated using the following formula:

$$C_{wh} = \left[(W_{soaked} - W_{dry})/W_{dry} \right] \times 100\% \qquad (2)$$

where W_{dry} refers to the dry weight of bark after being dried in the oven at 105°C for 24 h; W_{soaked} refers to the weight of bark after being soaked in water for 24 h with no water dripping (Hauck et al. 2006).

All data were submitted to normality and homoscedasticity tests before applying further statistical methods. As all assumptions were met, ANOVA was conducted to determine whether forest type had a significant influences on species richness and total coverage of epiphytic bryophyte on different diameter classes of host trees. Pearson correlation analysis was conducted among environmental variables including diameter class, height, bark water-holding capacity, bark roughness and bark pH.

Canonical correspondence analysis (CCA) (Ter Braak 1986) was applied to relate species composition to selected environmental variables. This analysis was performed with the CANOCO package (Ter Braak and Smilauer 1998), all analyses using 'Automatic selection' (forward selection). CCA was run with abundance data (coverage of each epiphytic bryophyte species in each plot). We entered the environmental data, including forest type, diameter class, height, windward, leeward, bark pH, and bark water-holding capacity where the plot was positioned. Bark roughness was strongly linearly correlated with diameter class, and thus was excluded from the CCA ordination. Since host trees of class 1 were too small to be divided into windward and leeward exposures, plots sampled from them were excluded. Species with less than three occurrences were removed to lessen the disproportionate effects of rare species on site scores.

Results

Bryophyte flora

Sixty-five epiphytic bryophytes (36 mosses and 29 liverworts) belonging to 32 genera, 19 families were found on all the trunks sampled. The richest moss families were Sematophyllaceae (eight species) and Dicranaceae (seven species), and Plagiochilaceae (eight species) and Lepidoziaceae (seven species) among liverworts. The most dominant species recorded in the PLF were *Syrrhopodon gardneri* (Hook.) Schwaegr. (R_{fre}: 8.86%, R_{cov}: 11.52%), *Bazzania ovistipula* (Steph.) Mizut. (R_{fre}: 6.01%, R_{cov}: 11.76%), and *Plagiochila assamica* Steph. (R_{fre}: 5.38%, R_{cov}: 12.35%); while in the SLF they were *S. gardneri* (R_{fre}: 8.95%, R_{cov}: 18.27%), *Lejeunea subacuta* Mitt. (R_{fre}: 9.47%, R_{cov}: 13.08%), and *Brotherella erythrocaulis* (Mitt.) Fleisch (R_{fre}: 8.95%, R_{cov}: 11.86%) (see Appendix).
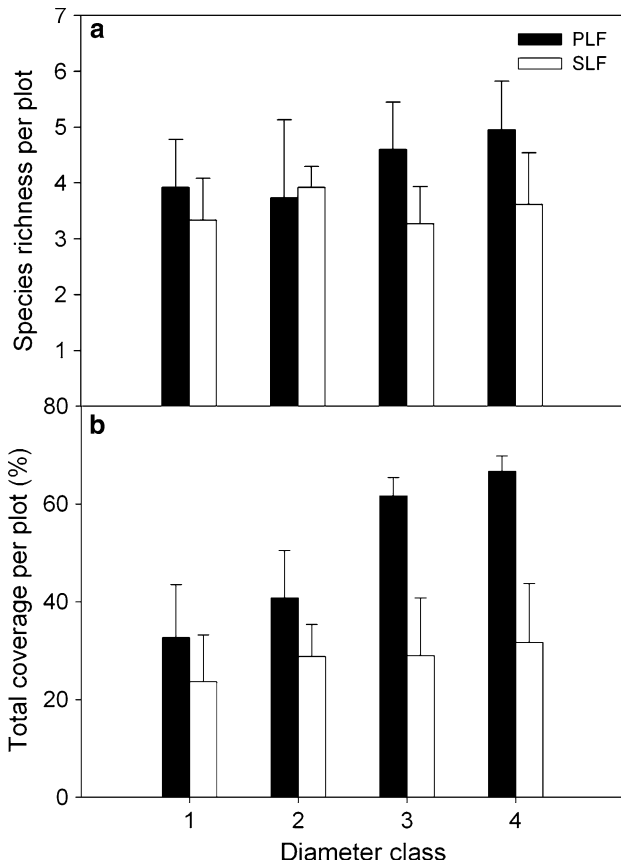
Species richness and total coverage

The species composition, richness, and total coverage of epiphytic bryophytes differed greatly between PLF and SLF. Species richness of samples was higher in the PLF than in the SLF. Considering only individuals of diameter class 1–4, 47 epiphytic bryophytes were collected in the PLF, while only 37 were found in the SLF. However, if trees of diameter class 5 and 6 in the PLF were considered, 56 bryophytes were recorded. There were 28 species that occurred exclusively in the PLF, including *Bazzania sikkimensis* (Steph.) Herz., *Porella plumose* (Mitt.) Inoue, and *Dicranodontium denudatum* (Brid.) Britt, etc. Species number and total coverage of epiphytic bryophytes per plot in the PLF were markedly higher than in the SLF on phorophytes in different diameter classes except for class 2, on which bryophyte species numbers per plot in the two forest types were nearly the same (Table 1, Fig. 2). The results of ANOVA showed that species richness ($F = 9.119$, $P < 0.01$, $df = 1$) and total coverage ($F = 72.085$, $P < 0.01$, $df = 1$) of epiphytic bryophytes per tree were significantly higher in the PLF.

Life form composition

Epiphytic bryophytes were classified into eight life forms; all eight were recorded in the two types of forest. Comparison of life form composition including all diameter classes showed that fan (accounting for 25.0%) dominated in the PLF, and was also the most common life form in the SLF (24.3%). Smooth mat was another important life form, with high occurrences both in the PLF (21.4%) and SLF (21.6%). Turf species in the PLF (25.0%) were more abundant than in the SLF (21.6%, Table 2). Comparisons separating each diameter class in

Table 1 Comparison of community characteristics between primary *Lithocarpus* forest (PLF) and secondary *Lithocarpus* forest (SLF). *DBH* Diameter at breast height

Community characteristics	PLF	SLF
Elevation (m)	2,540	2,560
Canopy cover (%)	89	90
Average tree height (m)	23.3	20.5
Species richness (tree number 4000 m^{-2})	91	84
Mean DBH (cm)	50.9	26.1
Dominant canopy tree species	*Lithocarpus xylocarpus*, *Lithocarpus hancei*, *Castanopsis rufescens*	*Lithocarpus xylocarpus*, *Lithocarpus hancei*, *Vaccinium duclouxii*
Average relative humidity (%)	84.4	81.1
Total number of epiphytic species	56	37

Fig. 2 Comparison (mean ± SD) of species number (**a**) and total coverage (**b**) of epiphytic bryophytes on host trees of the common diameter classes [diameter at breast height (DBH) range of diameter classes 1–4: *1* 5.0–12.0 cm; *2* 12.1–20.0 cm; *3* 20.1–30.0 cm; *4* 30.1–40.0 cm] between the primary *Lithocarpus* forest (PLF) and secondary *Lithocarpus* forest (SLF)

the PLF showed that some life forms are clearly related to diameter class. For example, weft and cushion species were distributed on all hosts except diameter class 1, while pendant forms were present only in the youngest trees. We also found that fan was scarce (accounting for only 4.5%) but turf was abundant (accounting for 40%) in diameter class 6 in the PLF (Fig. 3).

Table 2 Proportions of life form (in percentages) in PLF and SLF

Life form	PLF (%)	SLF (%)
Cushion	1.8	2.7
Dedroid	1.8	2.7
Fan	25.0	24.3
Pendant	7.1	5.4
Rough mat	3.6	8.1
Smooth mat	21.4	21.6
Turf	25.0	21.6
Weft	14.3	13.5
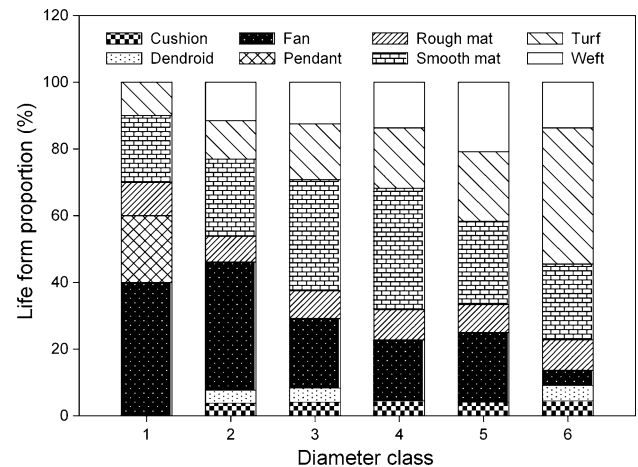
Fig. 3 Life form proportions on trunks of different diameter classes in PLF

Environmental variables and bryophytes

High atmospheric relative humidity was recorded in the two types of forest throughout the whole measuring period. The average relative humidity in the SLF was 84.4% in dry seasons, which was even higher than in the PLF (81.1%, see Table 1), while the values of relative humidity were nearly the same (ca. 99%) between the two forest types during rainy seasons.

Pearson correlation analysis was conducted among environmental variables including diameter class, height, bark water-holding capacity, bark roughness and bark pH, with all plots of the two localities used together. The

results showed that bark roughness and diameter class were significantly positively correlated ($r = 0.924$, $P < 0.01$, $n = 192$), while bark pH was significantly negatively correlated ($r = -0.360$, $P < 0.01$, $n = 192$) to diameter class. Bark water-holding capacity and bark roughness were significantly negatively correlated to height of bryophyte on the tree ($r = -0.198$, $P < 0.01$, $n = 192$; $r = -0.159$, $P < 0.05$, $n = 192$), but no significant correlation was found between height and bark pH.

The ordination of all sample plots and bryophyte species from two forest types indicated that the majority of variation in the species composition of bryophytes was explained by both diameter class and the presence of primary forest (Fig. 4). Diameter class was the most influential environmental factor. Species such as *Trismegistia undulata* Broth. et Yas. and *Bazzania tridens* (Reinw. et al.) Trev. tended to dwell on hosts with a large diameter. The presence of pristine forest significantly affected epiphytic bryflora. Many species—*Bazzania himalayana* (Mitt.) Schiffn., *Wijkia deflexifolia* (Ren. et Card.) Crum, *Plagiothecium neckeroideum*

B. S. G., and *P. assamica*—had a higher coverage in the PLF, while species such as *Wijkia tanytricha* (Mont.) Crum were correlated to the SLF. Bark pH was another important factor that was related to the composition of epiphytic bryophytes, and the distribution of species such as *Homaliodendron scalpellifolium* (Mitt.) Fleisch was determined mainly by this factor (Fig. 4).

We also analyzed the two forest types including all diameter classes individually (Figs. 5, 6). In the PLF, diameter class and bark pH explained a significant amount of epiphytic bryophyte variation for communities; while in the SLF, plot exposure was significantly related to the composition of epiphytic bryophytes along axis 2 in addition to diameter class and height (axis 1). *Trimegistia undulata* and *B. tridens* were related mainly to diameter class in the PLF, but, in the SLF, other species such as *S. gardneri* and *L. subacuta* were associated with diameter class. In the PLF, *Thuidium cymbifolium* (Doz.et Molk.) Doz. et Molk., *Pylaisiadelpha yokohamae* (Broth.) Buck., and *H. scalpellifolium* depended mainly on bark pH. *Wijkia tanytricha* and *T. cymbifolium* were determined mainly by plot exposure in the SLF. However, the importance of bark water-holding capacity and sampling height was highlighted if the CCA calculations were performed without data from diameter class 5 or 6 in the PLF (Fig. 7). The first two ordination axes accounted for a relatively high
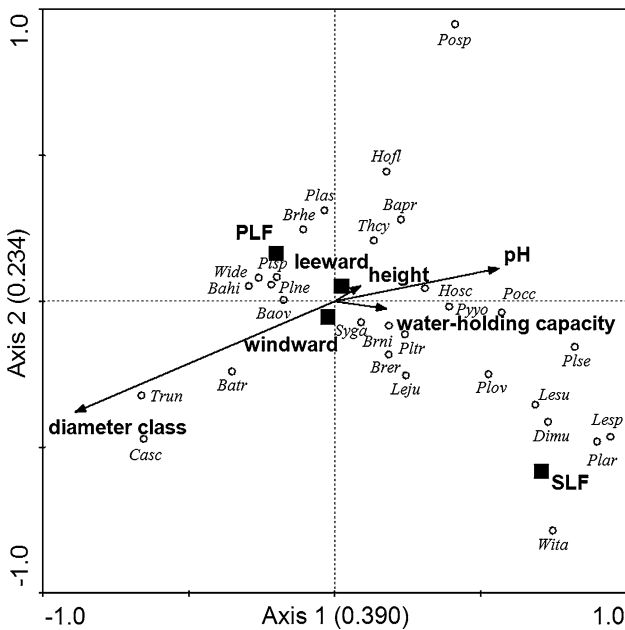

Fig. 4 Canonical correspondence analysis (CCA) ordination of all sample plots and bryophyte species: biplot for the first two canonical axes of species and environmental variables (with eigenvalues in *brackets*). The cumulative percentage variance for the first two axes was 77.0%. Bryophyte species are indicated by the first two letters of the generic and the specific epithet. *Circles* refers to species. *Square centroids* are presented instead of *arrows* because these variables are categorical, not numerical. Nominal variables: *PLF* plot in primary forest, *SLF* plot in secondary forest, *Windward* southwest side of trunk, *Leeward* northeast side of trunk. *Diameter class* Diameter class of the host tree; diameter was measured at 1.3 m. Height refers to sample height. Water-holding capacity refers to bark water-holding capacity where the plot was located. pH refers to the bark pH value where the plot was located
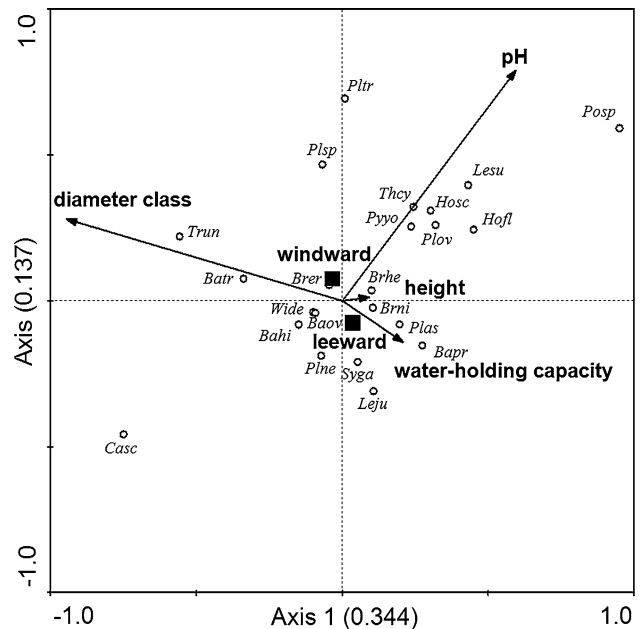

Fig. 5 CCA of all sample plots and bryophyte species of PLF: biplot for the first two canonical axes of species and environmental variables (with eigenvalues in *brackets*). Cumulative percentage variance for the first two canonical axes was 75.6%. Bryophyte species abbreviations, environmental variables, and symbols are as in Fig. 4
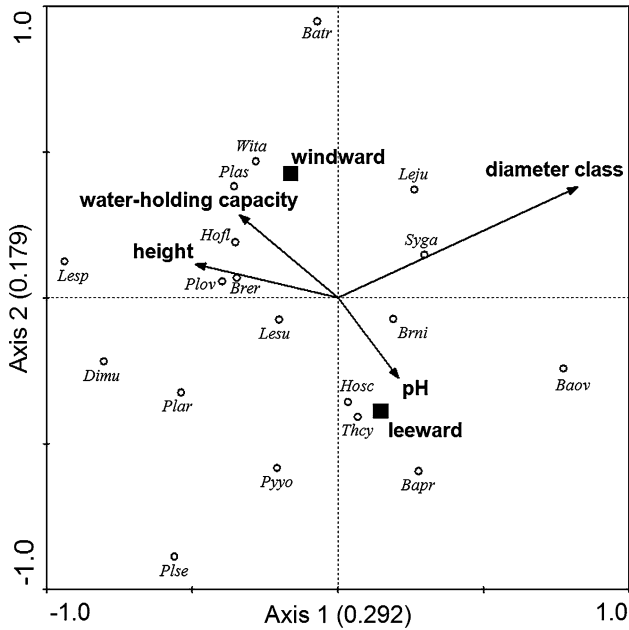
Fig. 6 CCA of all sample plots and bryophyte species of SLF: biplot for the first two canonical axes of species and environmental variables (with eigenvalues in *brackets*). Cumulative percentage variance for the first two canonical axes was 67.3%. Bryophyte species abbreviations, environmental variables, and symbols are as in Fig. 4
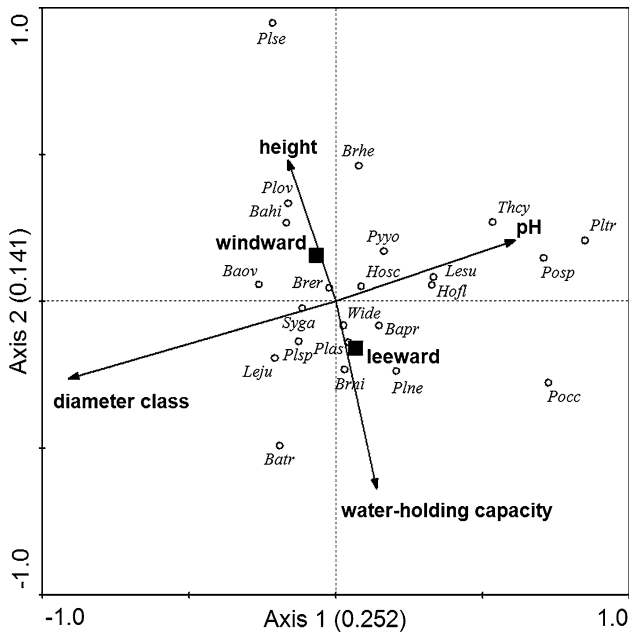

Fig. 7 CCA of sample plots and bryophyte species of diameter classes 2–4 of PLF: biplot for the first two canonical axes of species and environmental variables (with eigenvalues in *brackets*). Cumulative percentage variance for the first two canonical axes was 69.0%. Bryophyte species abbreviations, environmental variables, and symbols are as in Fig. 4

percentage of the species–environment relation, but the eigenvalues were relatively low, especially in the SLF (Figs. 4–7).

Discussion

Sampling accuracy

Several studies have suggested that sampling of three to five trees may yield over 75% of the total epiphytic bryophyte diversity of homogeneous forest stands in the tropical and subtropical regions (Gradstein 1992, 1996; Acebey et al. 2003; Patiño et al. 2009a). Gradstein et al. (2003) proposed that sampling five trees within a 1-ha plot of forest would allow rapid and representative analysis of epiphyte diversity for bryophytes. In the present study, we sampled six trees per diameter class within each forest stand. Almost all of the species–trunks curves for different diameter classes both in the PLF and SLF (Fig. 8) showed that species richness tends to be stable after six trunks were sampled. We thus concluded that our sampling size yielded a good representation of the actual richness of epiphytic bryophytes that occurs in different diameter classes in the two types of forest.

Comparison of species richness

Our results showed that species richness of epiphytic bryophytes on the trunks of *L. xylocarpus* in the primary forest was much higher than that of secondary forest. Similar results were reported by Vellak and Paal (1999), Barthlott et al. (2001), and Acebey et al. (2003); however, their conclusions were based on surveys of different host species, different study locations, and different forest types. If the comparison were made on hosts of diameter classes (1–4) common to both forests, ten more epiphytic species were recorded in the primary forest. This result indicates that primary forest greatly favors certain epiphytes. According to Vellak and Paal (1999), many epiphytic bryophytes are disturbance-sensitive and cannot grow in secondary forest because of unsuitable substrates or lack of appropriate microclimatic conditions. Besides, secondary forest yielded phorophytes with only limited complexity in structure (Barthlott et al. 2001). The long period of succession in primary forest, on the other hand, had stimulated the hosts in primary forest to develop a diversified canopy structure, including wide range of size classes, high diversity of phorophytes, and the presence of higher trees. This structure had, in turn, made it possible for epiphytic bryophytes with different niches to co-exist on same host. In addition, if larger individuals (diameter classes 5–6) in the primary forest were considered in the comparison, this advantage of primary forest was more obvious, increasing the number of species from 10 to 19. As diameter is positively linearly correlated to tree age for *L. xylocarpus* (Xie et al. 1983), we supposed that tree age plays an important role in bryophyte richness. Lack of large diameter phorophytes seemed to be one of the main reasons for the low richness observed in secondary forest.

Fig. 8 Species–trunks curves for diameter classes 1–6 (**a**–**f**) in PLF and diameter classes 1–4 (**g**–**j**) in SLF
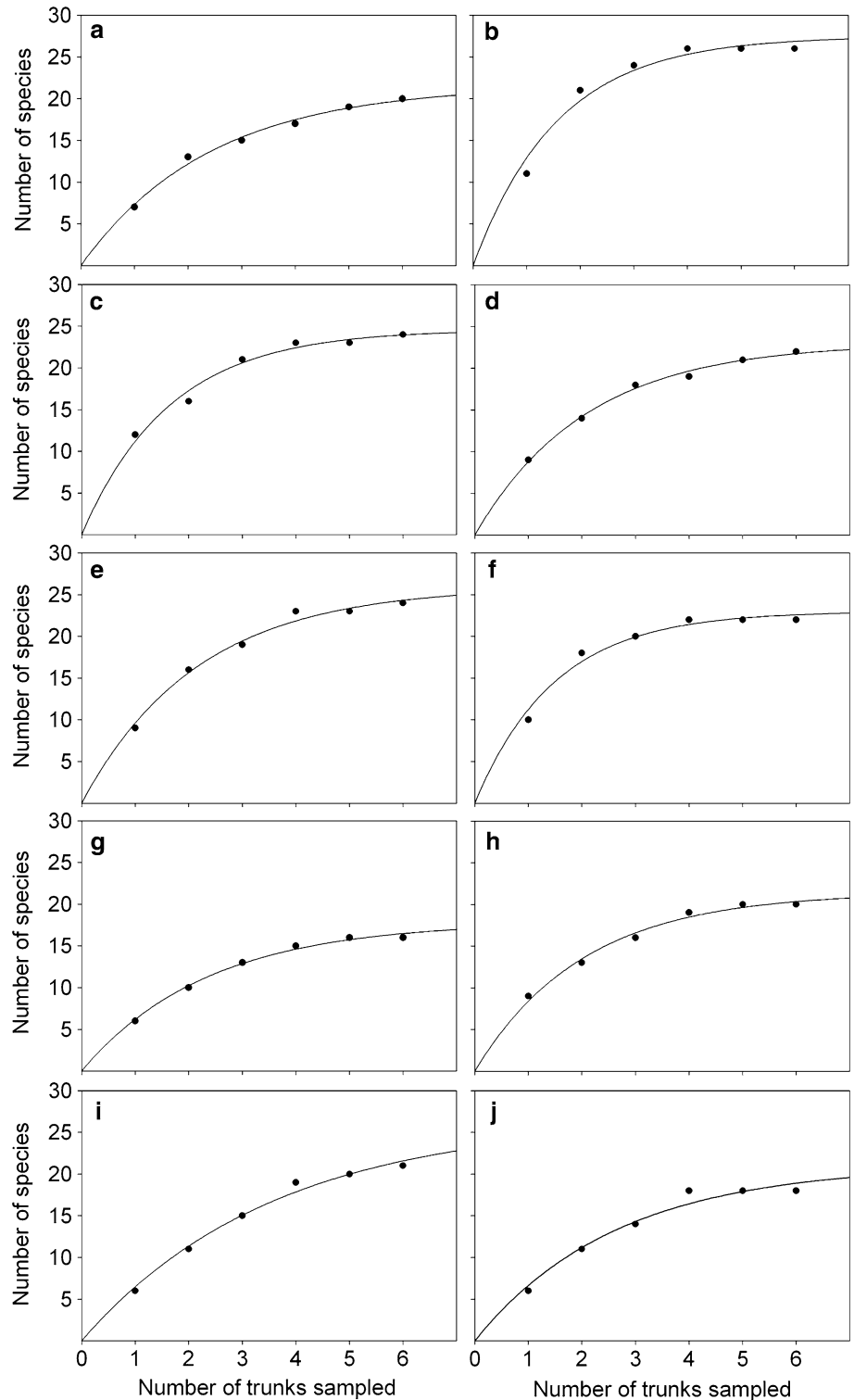
Recovery of epiphytic bryophytes

Many researchers have documented that once destroyed, epiphytic flora is rather difficult to recover. Few bryophytes had returned after 25 years in subtropical rain forests of Australia (Chapman and King 1983). Sillett et al. (1995) found that, on remnant isolated trees, only about half of the original bryophytes remained 30 years after clear felling. In subtropical montane cloud forests in Spain, some hosts like *Laurus novocanariensis* experienced a gradual increase of epiphytic richness during a 60-year succession (Patiño et al. 2009a). These latter

authors concluded that the current rotation periods (< 30 years) used to manage laurel forests in this region are not adequate for a complete reestablishment of epiphytic bryoflora (Patiño et al. 2009b). Secondary upper montane forests in Costa Rica, which were only 10–15 years old, harbored a similar diversity of epiphytes as primary forest in the same region, but the species composition was markedly different even after 40 years of succession (Holz and Gradstein 2005). In the lowland rainforests of Brazil, after 20–45 years of succession many epiphytic bryophyte species had not yet returned, but after 80 years the bryoflora was similar to that of primary forest (da Costa 1999). Nevertheless, this does not mean that 80 years would be enough for a satisfactory recovery of epiphytes. In this study, we found that the average number of species per plot as well as total species richness were markedly lower in secondary forest compared with primary forest. CCA ordination results indicated a notable difference in species composition between the distinct types of forest (Fig. 2). After nearly 110 years of succession, one-half (28 species) of the primary forest species still had not re-established in the secondary forest. Furthermore, total coverage of epiphytic bryophytes in the primary forest was significantly higher than in the secondary forest. All these results indicate that the epiphytic bryoflora has not completely recovered in the secondary forest. Slow recovery rates in epiphytes have also been recorded in other tropical forests (Acebey et al. 2003), as well as in temperate (Norris 1987) and boreal (Kuusinen and Siitonen 1998) forests. Most of these studies argue that at least 100 years are needed for the regeneration of most non-vascular epiphytes in regrowing forest (Zotz and Bader 2009). We suggest that an even longer period, perhaps much more than 110 years, is needed for the reinvasion of epiphytic species and re-establishment of microhabitats and epiphytic communities in subtropical montane forests of SW China.

Life form composition and environmental conditions

Life form is defined as "the modification of the resultant form by local environmental conditions" (Bates 1998). Habitat conditions have been shown to be associated with life form representation in bryophytes (Gimingham and Birse 1957). Different life forms of bryophytes reflect distinct moisture status and light intensity of their habitats (Bates 1998). Life form seems to be more sensitive than species to environmental conditions, especially water availability. Fan was one of the life forms that indicated wet environments (Smith 1982). Thus, abundant fan species in both primary and secondary forests reflected the ample water supply in the study regions, which was supported by the measured relative humidity data. Acebey et al. (2003) presumed that the smooth mat was usually interpreted as an adaptation to smooth bark; however, this could not be used to explain the plentiful smooth mat bryophytes on *L. xylocarpus*

because it has rough bark. Kürschner (2004) argued that mats, wefts, tails or fans dominated in shady and humid sites. Sampled trunks had a high proportion of smooth mats in both forest types, probably because they were low under the canopy, with dark and highly humid conditions that were more favorable for this life form. In the primary forest, pendant forms were present only in the youngest trees, which might be related to the fact that pendant species usually occur in the canopy as well as on trunks in young trees where the canopy does not have a good structure. In addition, weft and cushion species were not found on small diameter hosts while abundant turf species were recorded on hosts with the largest diameter. We thus proposed that tree age (represented by diameter class) has an important influence on the composition of life forms.

Epiphyte composition and environmental variables

CCA ordinations (Figs. 4–6) showed that tree age, bark pH, the presence of primary forest, and plot exposure significantly influenced the composition of epiphytes. Tree age was the most important environmental variable that affected the composition of epiphytic bryophytes. By comparing Figs. 5 and 7, we found that the presence of larger diameter hosts in the primary forest played an important role in maintaining the distribution pattern of epiphytes. Epiphyte composition may depend on local moisture conditions and tree diameter on the same tree species at different sites as was mentioned by McCune and Antos (1982), Wolf (1995), and González-Mancebo et al. (2004). As relative humidity was nearly the same in primary and secondary sites, tree diameter may become the determinant of epiphyte composition. Bates and Brown (1981) held that the epiphyte flora respond to variations in bark acidity. Studlar (1982) found that species richness decreased with bark pH. We also found that bark pH was an important factor that significantly influenced the composition of epiphytic bryophytes in our study, but seemed only indirectly correlated with tree age. As trees grow, diameters become bigger, along with changing bark characteristics such as higher roughness and lower pH, which may cause variations in epiphytic community composition. As also observed by González-Mancebo et al. (2004), the differences in species composition between forest types seemed to be more influenced by forest age than humidity condition. Compared with secondary forest, primary forest is a more favorable habitat for epiphytes. As mentioned above, the diversified canopy structure and the presence of large host trees in the old primary forest was favorable for the development of epiphytic communities. Glime and Hong (2002) suggested that there was no clear north/south differentiation in community structure of epiphytes in a humid conifer forest on the Queen Charlotte Islands, Canada. But in the Keweenaw Peninsula of Michigan in the United States, bryophytes dominated on the south side of trees at breast height,

presumably due to strong winds from the north and greater light on the south during humid periods of early spring and fall (Trynoski and Glime 1982). In open forests, circumferential variation at a given height tends to be correlated with aspect (Gough 1975). We found that plot exposure played an important role in species composition in secondary forest. The influence of the moisture-laden southwest trade winds and forest structure such as tree density and height could be possible explanations. Similar results were found by González-Mancebo et al. (2003) for trade winds coming from the opposite direction. Nevertheless, the micro-environmental factors involved can be very complicated, reflecting simultaneous variation in water availability, light intensity, and substrate quality, etc. (Kenkel and Bradfield 1986). Despite the first two ordination axes accounting for a high percentage (see legends to Figs. 4–7) of the species–environment relation, the low eigenvalues imply that much of the variation in bryophyte species composition still cannot be explained by the measured variables.

In conclusion, species richness and total coverage on *L. xylocarpus* trunks in primary forest are significantly higher than those of secondary forest. Species composition is distinct between the two forest types. We thus suggest that a very long period, perhaps much more than 110 years, is needed for the recovery of epiphytic bryoflora in montane forest of SW China. Microhabitat and host age have a considerable influence on life form composition of epiphytic bryophytes. Tree age was the most important environmental variable affecting the composition of epiphytic bryophytes.

Appendix

See Table 3.

Table 3 Epiphytic bryophytes found in the primary *Lithocarpus* forest (PLF) and secondary *Lithocarpus* forest (SLF), with numbers of important value in each forest

Taxa	PLF	SLF	Life form
Liverworts			
Herbertaceae			
Herbertus fragilis (Steph.) Herz.	0.27	–	Turf
Lepidoziaceae			
Bazzania oshimensis (Steph.) Horik.	0.42	–	Weft
Bazzania sp.	0.51	–	Weft
Bazzania praerupta (Reinw. et al.) Trev.	2.25	1.86	Smooth mat
Bazzania tridens (Reinw. et al.) Trev.	1.75	1.29	Weft
Bazzania sikkimensis (Steph.) Herz.	0.51	–	Weft
Bazzania himalayana (Mitt.) Schiffn.	7.47	0.49	Weft
Bazzania ovistipula (Steph.) Mizut.	8.89	3.76	Smooth mat
Geocalycaceae			
Heteroscyphus zollingeri (Gott.) Schiffn	0.36	–	Smooth mat
Plagiochilaceae			
Plagiochila assamica Steph.	8.87	1.15	Fan
Plagiochila pseudorenitens Steph.	0.17	–	Turf
Plagiochila ovalifolia Mitt.	0.65	3.34	Turf
Plagiochila secretifolia Mitt.	0.17	1.26	Turf
Plagiochila arbuscula (Brid. ex Lehm.) Lindenb	–	4.40	Fan
Plagiochila trabeculata Steph.	0.38	0.71	Turf
Plagiochila sp.	0.74	0.29	Turf
Plagiochila fruticosa Mitt.	0.34	0.40	Fan
Porellaceae			
Porella campylophylla (Lehm. et Lindb.) Trev. var. *campylophylla*	0.98	0.67	Fan
Porella oblongifolia Hatt.	0.23	–	Fan
Porella sp.	0.54	–	Fan
Porella nitens (Steph.) Hatt.	0.18	–	Fan
Porella plumosa (Mitt.) Inoue	0.36	–	Fan
Frullaniaceae			
Frullania handelii Verd.	–	0.80	Smooth mat
Lejeuneaceae			
Lejeunea discreta Lindenb.	0.20	–	Smooth mat
Lejeunea subacuta Mitt.	1.53	11.28	Smooth mat
Leucolejeunea turgida (Mitt.) Verd.	0.18	–	Smooth mat
Lejeunea curviloba Steph.	0.20	–	Smooth mat

Table 3 continued

Taxa	PLF	SLF	Life form
Lejeunea sp.	0.18	1.57	Smooth mat
Ptychanthus striatus (Lehm.& Lindenb.) Nees	–	1.30	Fan
Mosses			
Dicranaceae			
Dicranodontium denudatum (Brid.) Britt.	0.80	–	Turf
Dicranum sp.	0.21	–	Turf
Dicranum japonicum Mitt.	0.17	–	Turf
Dicranum japonicum Mitt. vat. *japonicum*	–	0.46	Turf
Dicranum diplospiniferum Gao et Auo	0.55	–	Turf
Dicranum muehlenbeckii B. S. G.	0.18	0.64	Turf
Campylopus schimperi Mild.	1.53	0.61	Turf
Leucobryaceae			
Leucobryum juniperoideum (Brid.) C. Muell.	2.87	7.40	Cushion
Calymperaceae			
Syrrhopodon japonicus (Bsch.) Broth.	0.26	–	Turf
Syrrhopodon gardneri (Hook.) Schwaegr.	10.19	13.61	Turf
Mniaceae			
Plagiomnium maximoviczii (Lindb.) T. Kop.	–	0.33	Rough mat
Meteoriaceae			
Sinskea phaea (Mitt.) Buck.	0.38	–	Pendant
Neonoguchia auriculata (Copp. ex Ther.) S. H. Lin	0.20	–	Pendant
Papillaria fuscescens (Hook.) Jaeg.	–	0.36	Pendant
Pseudobarbella attenuata (Thwait. et Mitt.) Nog.	–	0.33	Pendant
Barbella chrysonema (C. Muell.) Nog.	0.17	–	Pendant
Floribundaria walkeri (Ren. et Card.) Broth.	0.17	–	Pendant
Neckeraceae			
Homaliodendron scalpellifolium (Mitt.) Fleisch	4.03	5.56	Fan
Homaliodendron flabellatum (Sm.) Fleisch.	7.39	4.00	Fan
Hookeriaceae			
Hookeria acutifolia Hook. et Grev.	0.17	–	Fan
Hypopterygiaceae			
Cyathophorella tonkinensis (Broth. et Par.) Broth.	0.22	–	Fan
Cyathophorella hookeriana (Griff.) Fleisch.	0.17	–	Fan
Thuidiaceae			
Thuidium cymbifolium (Doz.et Molk.) Doz. et Molk.	2.57	3.00	Weft
Thuidium kanedae Sak.	0.17	–	Weft
Thuidium philibertii Limpr.	0.28	–	Weft
Plagiotheciaceae			
Plagiothecium neckeroideum B. S. G.	2.85	0.33	Fan
Plagiothecium laetum B. S. G.	0.37	0.34	Fan
Sematophyllaceae			
Trismegistia undulata Broth. et Yas.	5.79	0.29	Dendroid
Brotherella erythrocaulis (Mitt.) Fleisch	6.14	10.40	Rough mat
Brotherella nictans (Mitts.) Broth.	5.13	7.70	Smooth mat
Pylaisiadelpha yokohamae (Broth.) Buck.	1.83	2.67	Smooth mat
Wijkia tanytricha (Mont.) Crum	–	5.20	Weft
Brotherella henonii (Duby) Fleisch	2.02	1.59	Smooth mat
Wijkia deflexifolia (Ren. et Card.) Crum	4.60	0.31	Rough mat
Sematophyllum subpinnatum (Brid.) Britt.	0.24	–	Smooth mat
Hypnaceae			
Taxiphyllum taxirameum (Mitt.) Fleisch.	–	0.30	Weft

References

Acebey A, Gradstein SR, Kromer T (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. J Trop Ecol 19:9–18. doi:10.1017/S026646740300302X

Barkman JJ (1958) Phytosociology and ecology of cryptogamic epiphytes: including a taxonomic survey and description of their vegetation units in Europe. Koninklyke Van Gorcum, Assen

Barthlott W, Schmit-Neuerburg V, Nieder J, Engwald S (2001) Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol 152:145–156. doi:10.1023/A:1011483901452

Bates JW (1992) Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. J Ecol 80:163–179. doi:10.2307/2261073

Bates JW (1998) Is 'life-form' a useful concept in bryophyte ecology? Oikos 82:223–237. doi:10.2307/3546962

Bates JW, Brown DH (1981) Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* trees in a maritime area of South West England. Plant Ecol 48:61–70. doi:10.1007/BF00117362

Bergstrom DM, Tweedie CE (1998) A conceptual model for integrative studies of epiphytes: nitrogen utilisation, a case study. Aust J Bot 46:273–280. doi:10.1071/BT96104

Burns KC, Dawson J (2005) Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. Aust Ecol 30:891–899. doi:10.1111/j.1442-9993.2005.01532.x

362

Chapman WS, King GC (1983) Floristic composition and structure of a rainforest area 25 years after logging. Aust Ecol 8:415–423. doi:10.1111/j.1442-9993.1983.tb01338.x

Chen PC, Li XJ, Wu PC (1963) Genera Muscorum Sinicorum (Pars Prima). Science Press, Beijing

Chen PC, Li XJ, Wu PC (1978) Genera Muscorum Sinicorum (Pars Secunda). Science Press, Beijing

Culberson WL (1955) The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Ecol Monogr 25:215–231. doi:10.2307/1943551

da Costa DP (1999) Epiphytic bryophyte diversity in primary and secondary lowland rainforests in southeastern Brazil. Bryologist 102:320–326

Gao C, Cao T (2000) Flora Yunnanica Tomus 17, Bryphyta: Hepaticae, Anthocerotae. Science Press, Beijing

Gimingham CH, Birse EM (1957) Ecological studies on growth-form in bryophytes: I. Correlations between growth-form and habitat. J Ecol 45:533–545. doi:10.2307/2256934

Glime JM, Hong WS (2002) Bole epiphytes on three conifer species from Queen Charlotte Islands, Canada. Bryologist 105:451–464. doi:10.1639/0007-2745(2002)105[0451:BEOTCS]2.0.CO;2

González-Mancebo JM, Losada-Lima A, McAlister S (2003) Host specificity of epiphytic bryophyte communities of a laurel forest on Tenerife (Canary Islands, Spain). Bryologist 106:383–394. doi:10.1639/04

González-Mancebo JM, Romaguera F, Losada-Lima A, Suárez A (2004) Epiphytic bryophytes growing on Laurus azorica (Seub.) Franco in three laurel forest areas in Tenerife (Canary Islands). Acta Oecol 25:159–167. doi:10.1016/j.actao.2004.01.005

Gough LP (1975) Cryptogam distributions on Pseudotsuga menziesii and Abies lasiocarpa in the Front Range, Boulder County, Colorado. Bryologist 78:124–145

Gradstein SR (1992) The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates JW, Farmer AR (eds) Bryophytes and lichens in a changing environment. Clarendon, Oxford, pp 234–258

Gradstein SR (1996) Corticolous bryophytes. In: Gradstein SR et al (eds) How to sample the epiphytic diversity of tropical rain forest. Ecotropica, vol 2, pp 63–65

Gradstein SR, Nadkarni NM, Krömer T, Holz I, Nöske N (2003) A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana 24:105–111

Grolle R (1983) Nomina generica Hepaticarum: references, types and synonymies. Acta Bot Fenn 121:1–62

Hauck M, Hofmann E, Schmull M (2006) Site factors determining epiphytic lichen distribution in a dieback-affected spruce-fir forest on Whiteface Mountain, New York: microclimate. Ann Bot Fenn 43:1–12

Hietz P, Hietz-Seifert U (1995) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. J Veg Sci 6:487–498. doi:10.2307/3236347

Holz I, Gradstein RS (2005) Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica—species richness, community composition and ecology. Plant Ecol 178:89–109. doi:10.1007/s11258-004-2496-5

Kenkel NC, Bradfield GE (1981) Ordination of epiphytic bryophyte communities in a wet-temperate coniferous forest, South-Coastal British Columbia. Plant Ecol 45:147–154. doi:10.1007/BF00054669

Kenkel NC, Bradfield GE (1986) Epiphytic vegetation on Acer macrophyllum: a multivariate study of species–habitat relationships. Plant Ecol 68:43–53. doi:10.1007/BF00031579

Kürschner H (2004) Life strategies and adaptations in bryophytes from the Near and Middle East. Turk J Bot 28:73–84

Kuusinen M (1996) Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. Lichenologist 28:443–463. doi:10.1006/lich.1996.0043

Kuusinen M, Siitonen J (1998) Epiphytic lichen diversity in old-growth and managed Picea abies stands in southern Finland. J Veg Sci 9:283–292. doi:10.2307/3237127

Li XJ (2002) Flora Yunnanica, Tomus 18, Bryophyta: Musci. Science Press, Beijing

Li XJ (2005) Flora Yunnanica, Tomus 19, Bryophyta: Musci. Science Press, Beijing

Loppi S, Frati L (2004) Influence of tree substrate on the diversity of epiphytic lichens: comparison between Tilia platyphyllos and Quercus ilex (central Italy). Bryologist 107:340–344. doi:10.1639/0007-2745(2004)107[0340:IOTSOT]2.0.CO;2

Ma WZ, Liu WY, Li XJ (2009) Species composition and life forms of epiphytic bryophytes in old-growth and secondary forests in Mt. Ailao, SW China. Cryptogam Bryol 30:477–500

Male TD, Roberts GE (2005) Host associations of the strangler fig Ficus watkinsiana in a subtropical Queensland rain forest. Aust Ecol 30:229–236. doi:10.1111/j.1442-9993.2005.01442.x

McCune B, Antos JA (1982) Epiphyte communities of the Swan Valley, Montana. Bryologist 85:1–12. doi:10.2307/3243136

Nkongmeneck BA, Lowman MD, Atwood JT (2002) Epiphyte diversity in primary and fragmented forests of Cameroon, Central Africa: a preliminary survey. Selbyana 23:121–130

Norris DH (1987) Long-term results of cutting on the bryophytes of the Sequoia sempervirens forest in northern California. Symp Biol Hung 35:467–473

Patiño J, González-Mancebo JM, Fernández-palacios JM (2009a) Epiphytic bryophytes in canarian subtropical montane cloud forests: the importance of the time since disturbance and host identity. Can J For Res 39:48–63. doi:10.1139/X08-155

Patiño J, González-Mancebo JM, Fernández-palacios JM, Arévalo JR, Bermúdez A (2009b) Short-term effects of clear-cutting on the biomass and richness of epiphytic bryophytes in managed subtropical cloud forests. Ann For Sci 66:609–621. doi:10.1051/forest/2009042

Qiu XZ, Xie SC (1998) Studies on the Forest Ecosystem in Ailao Mountains, Yunnan, China (in Chinese with English summary). Yunnan Sciences and Technology Press, Kunming

Schuster RM (1966) The Hepaticae and Anthocerotae of North America 1. Columbia University Press, New York

Sillett SC, Gradstein SR, Griffin D III (1995) Bryophyte diversity of Ficus tree crowns from cloud forest and pasture in Costa Rica. Bryologist 98:251–260. doi:10.2307/3243312

Smith AJK (1982) Epiphytes and epiliths. Chapman and Hall, London

Studlar SM (1982) Host specificity of epiphytic bryophytes near Mountain Lake, Virginia. Bryologist 85:37–50. doi:10.2307/3243139

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179. doi:10.2307/1938672

Ter Braak CJF, Smilauer P (1998) CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power. Ithaca, New York

Trynoski SE, Glime JM (1982) Direction and height of bryophytes on four species of northern trees. Bryologist 85:281–300. doi:10.2307/3243047

Turner IM, Tan HTW, Wee YC, Ibrahim AB, Chew PT, Corlett RT (1994) A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. Conserv Biol 8:705–712. doi:10.1046/j.1523-1739.1994.08030705.x

Vellak K, Paal J (1999) Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. Biodivers Conserv 8:1595–1620. doi:10.1023/A:1008927501623

Wolf JHD (1995) Non-vascular epiphyte diversity patterns in the canopy of an upper montane rain forest (2550–3670 m), central cordillera, Colombia. Selbyana 16:185–195

Xie SC, Qiu XZ, Jin GF (1983) A preliminary study on the growth rate of the major species composition in Lithocarpus xylocarpus forest in Xujiaba region, Ailao Mts. Yunnan Science and Technology Press, Kunming

Yang LP, Liu WY, Ma WZ (2008) Woody debris stocks in different secondary and primary forests in the subtropical Ailao Mountains, southwest China. Ecol Res 23:805–812. doi:10.1007/s11284-007-0442-4

You CX (1983) Classification of vegetation in Xujiaba region Ailao Mts. In: Zhengyi W (ed) Research of forest ecosystem on Ailao Moutains, Yunnan. Yunnan Science and Technology Press, Kunming

Young SS, Carpenter C, Wang ZJ (1992) A study of the structure and composition of an old growth and secondary broad-leaved forest in the Ailao Mountains of Yunnan, China. Mt Res Dev 12:269–284. doi:10.2307/3673670

Zotz G, Bader MY (2009) Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Prog Bot 70:147–170. doi:10.1007/978-3-540-68421-3_7

Zotz G, Vollrath B (2003) The epiphyte vegetation of the palm Socratea exorrhiza-correlations with tree size, tree age and bryophyte cover. J Trop Ecol 19:81–90. doi:10.1017/S0266467403003092