

Species composition and life forms of epiphytic bryophytes in old-growth and secondary forests in Mt. Ailao, SW China

MA Wen-Zhang^{a,b,d}, LIU Wen-Yao^{a,c*} & LI Xing-Jiang^d

^a*Xishuangbanna Tropical and Botanical Garden, Chinese Academy of Sciences
Kunming, Yunnan, P. R. China, 650223,*

^b*Graduate University of Chinese Academy of Sciences, Beijing, P. R. China, 100049*

^c*Curtin University of Technology, Perth, WA 6845, Australia*

^d*Kunming Institute of Botany, Chinese Academy of Sciences Heilongtan,
Kunming, Yunnan, China, 650204*

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Abstract – Epiphytes constitute a major component of tropical forests. However, human caused disturbances can alter the structure and diversity of epiphyte community. We surveyed and compared the diversity and distribution of epiphytic bryophytes on host tree trunks within 0-2m above ground in two old-growth and three secondary forests in Xujiaba, Mt. Ailao, SW China, in order to see whether disturbed forests have lower diversity and to identify environmental variables that can influence epiphyte distribution.

We recorded 176 species in total 38 families. Meteoriaceae was the dominant families in terms of species richness (24 species). Species richness did not differ between old-growth and secondary forests, however, beta diversity indexes were severely reduced in secondary forests. The life forms differed in preferences to some forest types: fan (moss) and rough mat (moss) preferred old-growth forests, while turf (moss) was commoner in secondary forests.

The degree of abundance of CWD (Coarse Woody Debris), atmospheric relative humidity, the roughness and water-holding capacity of host bark were the four environmental variables found to be significantly influencing the distribution of life forms in epiphytic bryophytes in the study area. Although secondary forests were similar to old-growth forests in epiphytic diversity, the absence of particular bark features in trees in secondary forest limited the growth of certain life form groups. Besides retaining CWD in old-growth forest, forest management should encourage the protection and rehabilitation of trees with special bark features to enhance the diversity of epiphytic bryophytes.

Species composition / life forms / epiphytic bryophytes / old-growth forests / secondary forests / Mt. Ailao / SW China / Coarse Woody Debris

Résumé – Les épiphytes constituent un élément majeur des forêts tropicales. Cependant, des causes anthropiques peuvent en altérer la diversité et la structure de croissance. Nous avons relevé la présence de bryophytes épiphytes sur des troncs entre 0 et 2 m de hauteur, dans trois forêts secondaires récemment exploitées et deux forêts matures du sud-ouest de

* Correspondence and reprints : liuwuy@xtbg.ac.cn

la Chine, à Xujiaba, Mont Ailao. Les bryophytes observées ont été échantillonnées et comparées entre ces différentes forêts, afin d'observer si les forêts exploitées présentent une diversité de bryophytes épiphytes plus faible, et afin d'identifier les facteurs environnementaux qui pourraient influencer leur distribution et leur structure.

Au total, sur l'ensemble des forêts étudiées, 176 espèces et 38 familles ont été observées, avec une prédominance des Meteoriaceae (24 espèces). On n'a pas constaté de différence significative de richesse spécifique entre les forêts matures et les forêts secondaires. Toutefois, la diversité- β au niveau sub-échantillon est considérablement réduite en forêt secondaire.

Les formes de croissance montrent des préférences d'habitat : les formes en éventail (« fan », mousses) et les formes en matelas grossier (« rough mat », mousses) préfèrent les forêts matures, alors que les formes en gazon (« turf », mousses) sont davantage présentes dans les forêts secondaires.

L'abondance de débris ligneux grossiers (CWD, « coarse woody debris »), l'humidité relative de l'air en forêt, la rugosité et la capacité de rétention en eau des écorces des arbres-hôtes sont les quatre variables environnementales qui influencent de façon significative la distribution des formes de croissance des bryophytes épiphytes. Bien que les forêts secondaires et les forêts matures présentent une richesse spécifique similaire, l'absence d'écorce avec ces caractéristiques particulières dans les forêts secondaires limite la croissance de certains groupes.

Au-delà de laisser les débris ligneux en place dans les forêts matures, la sylviculture devrait encourager dans les forêts secondaires la protection et la réhabilitation des arbres à l'écorce présentant ces caractéristiques particulières, afin de favoriser la diversité des bryophytes épiphytes.

Composition spécifique / forms de vie / bryophytes épiphytes / forêts matures / forêts secondaires / Mt. Ailao / SW Chine / Abondance de débris ligneux

INTRODUCTION

The epiphyte community is an important constituent of tropical and subtropical montane forests. However, anthropogenic disturbances in these forests have adversely affected the habitat quality for epiphytes, particularly the cryptogamic species (Söderström, 1988). Being a vital component of the cryptogam flora, epiphytic bryophytes not only contribute significantly to water and nutrient cycling in montane forests, but also serve as reliable indicators of minor variations in habitat quality (Cooper-Ellis, 1998). Many epiphytic bryophytes are disturbance-sensitive and they can not grow in secondary forest because of the unsuitable substrates or lack of appropriate microclimatic conditions (Vellak & Paal, 1999). Thus, old-growth forests are important for habitat specialists (Acebey *et al.*, 2003; Wolf, 2005), especially for dispersal-limited species. However, with increasing loss, degradation and alteration of primary old-growth forests, secondary forests are acquiring added significance for the conservation of biodiversity (Chazdon, 2008), and presumably for epiphytes as well.

The concept of life form in bryology, according to Bates (1998), refers to the combination of 1) “the morphological characters of a plant as defined by the position of its growing points, its mode of branching, leaf orientation, *etc.*”; as well as 2) “the assembly of shoots into colonies”; and 3) “the modification of the resultant form by local environmental conditions.” This concept has received much attention because it generalized the ecological knowledge on bryophytes. Also, data collected on life forms is more reliable than classification to species, as species identification is a major constraint.

About 74.5% of the bryophyte flora in China is preserved in Yunnan, SW China (Gao & Cao, 2000; Li, 2002, 2005). But few studies deal with how epiphytic bryophytes distribute in forests experienced disturbances, and how potential environmental variables regulate their distributions. Located in the central part of Yunnan, Mt. Ailao National Nature Reserve (NNR) is home to a large pristine montane forest (3.2×10^3 ha, see also You, 1983) and has several secondary fragmented forests under different successional stages of growth resulting from human disturbances (Qiu & Xie, 1998). Therefore this site provides an ideal condition to compare the diversity and distribution of epiphytic bryophytes between old-growth and secondary forests.

In an attempt to further the ecological knowledge on epiphytic bryophytes and provide effective suggestions for future biodiversity management in this region, this study focuses on epiphytic bryophytes in subtropical montane evergreen broad-leaved old-growth forests and nearby secondary forests, with two main objectives to be addressed: (1) to compare the diversity and distribution of epiphytic bryophytes in old-growth and secondary forests; and (2) to assess how the selected environmental variables affect the distribution of epiphytic bryophytes' life forms.

MATERIAL AND METHODS

Study sites

The study was conducted in the Xujiaba region (24°31'35" N, 101°00'03" E), Mt. Ailao NNR (Fig. 1), with altitude ranging from 2,450-2,650m. The mean annual precipitation for a period of ten years from 1992-2002 is 1,931mm, with 85% of the rains fallen from May to October. The average annual temperature is 11°C and relative humidity is 86% (Yang *et al.*, 2007). Five types of forest within NNR were chosen to compare their epiphyte composition.

Secondary Alnus association (SAA)

SAA was heavily disturbed in the middle of last century by clear cutting, fires and grazing. This forest type was dominated by *Alnus nepalensis* D. Don., which can be considered as the first stage of secondary succession towards the evergreen broad-leaved forest in this area (Qiu & Xie, 1998). The epiphytic bryophytes mainly grew at trunk base.

Secondary Populus association (SPA)

SPA also suffered heavy human impact in the past, but can be considered a later successional stage than SAA, as it was dominated by more mature trees, including *Populus bonatii* Levl. and *Lithocarpus* spp. The epiphytic bryophytes were basically distributed in the understorey canopy with few species sparsely covering along the higher part of tree trunk.

Secondary Lithocarpus association (SLA)

This forest experienced clear felling by local people about 110 years ago and was free from human disturbance since (Young *et al.*, 1992). It was the oldest secondary forest in this region and shared many dominate tree species with



Fig. 1. Location of the study site.

nearby old-growth forest. The majority of host trees were abundantly covered with moss mats.

Old-growth Lithocarpus forest (OLF)

OLF within NNR remain free of human disturbances historically and is dominated by *Lithocarpus hancei* (Benth.) Rehd., *Castanopsis rufescens* (Hook. f. et Th.) Huang et Y.T. Chang, *L. xylocarpus* Markg. and *Manglietia insignis* (Wall.) Blume, ranging in height from 18-25m in the upper canopy and has been categorized as old-growth or over mature forest (Yang *et al.*, 2007). This forest is especially rich in epiphytic flora (You, 1983).

Old-growth dwarf mossy forest (ODMF)

This type of forest in Xujiaba is also free of anthropogenic disturbance and largely restricted to elevation above 2,600m, exposing to strong and constant winds. *Lithocarpus pachyphyloides* Y. C. Hsu and *Rhododendron decorum* Fr. in small DBH (diameter at breast height) class dominated this forest type. ODMF is heavily loaded with epiphytic materials, mainly bryophytes (You, 1983).

Sampling methods

Field survey was carried out in 2005 (April, August and September), 2007 (January and May), and 2008 (July and August). In total 25 sampling sub-plots, of dimensions 30 × 30 m, were set up to study the epiphytic bryophytes. Among these sub-plots, 8 were in OLF, 4 in ODMF, 4 in SAA, 4 in SPA and 5 in SLA.

12-15 most epiphyte-loaded trees in each sub-plot were targeted as sampling phorophytes. The epiphytic bryophytes were sampled within a 20 × 20 cm (or 40 × 10 cm) metal-frame-quadrat (with 256 standard-square shaped grids equal in size) on host trunks (a total of 1945 quadrats in all forest types).

All epiphytic bryophytes found in the field were estimated for coverage based on a cover class scale ranging from 1-9 (1 = 0-1.0%; 2 = 1.1-2.5%; 3 = 2.6-5.0%; 4 = 5.1-10.0%; 5 = 10.1-20.0%; 6 = 20.1-40.0%; 7 = 40.1-60.0%; 8 = 60.1-80.0%; 9 = 80.1-100%). Each quadrat was placed 2-5 times from tree base to 2 m above ground of the phorophyte trunk where epiphytes were abundant. Unfamiliar species were mainly identified in the laboratory with the help of the third author. Nomenclature followed Gao & Cao (2000) for liverworts and 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. Voucher specimens were deposited in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences.

Life form classification

Bryophytes were first divided into moss and liverworts and then classified into 8 life forms using Bates (1998) and Schofield (1985) with minor modification (Table 1).

Collection of environmental variables

Host character traits

For all phorophytes sampled, DBH was measured with a DBH tape and height was measured with the help of a clinometer. Bark roughness of host tree was determined on a 1-9 scale modified from Male & Roberts (2005) (1 = very smooth; 3 = smooth but with fissures; 5 = shallowly furrowed; 7 = with deep fissures; 9 = with crevices abundantly across the surface; while 2, 4, 6, 8 were the cases in-between). Bark samples were collected from the dominant host tree species in each forest type after careful removal of the epiphytes, and later taken to laboratory for measurement of the moisture content and water-holding

Table 1. Definitions of life form classification in epiphytic bryophytes.

<i>Life form</i>	<i>Definitions</i>
Cushion	<i>dome-shaped colonies formed by regeneration from a central point of origin</i>
Dendroid	<i>resemble miniature trees and possess an erect main stem from which the erect gametophores emerge</i>
Fan	<i>on vertical substrate, creeping, with branches in one plane and leaves usually flat</i>
Rough mat	<i>shoots creep over the substrate with rhizoids adhering to substratum, with many lateral branches erect</i>
Smooth mat	<i>shoots creep over the substrate with rhizoids adhering to substratum, with branches lie flat</i>
Pendant	<i>formed of shoots that hang down from branches</i>
Turf	<i>with stems erect, parallel and close together; often covering extensive areas</i>
Weft	<i>loosely interwoven, often ascending growth form</i>

capacity. The moisture content (C_m) and water-holding capacity (C_{wh}) were calculated using the following formulas:

$$C_m = [(W_{\text{fresh}} - W_{\text{dry}}) / W_{\text{fresh}}] \times 100\%$$

$$C_{wh} = [(W_{\text{soaked}} - W_{\text{dry}}) / W_{\text{dry}}] \times 100\%$$

where W_{fresh} refers to the fresh weight of bark sample weighed immediately after collecting; W_{dry} refers to the dry weight of bark after being dried in the oven for 24 h; W_{soaked} refers to the weight of bark after being soaked in water for 24 h with no water dripping.

Plot character traits

According to Rouvinen *et al.* (2002), coarse woody debris classified in decay class 3 (knife blade could penetrate 1-1.5 cm into woody debris) and 4 (knife blade could penetrate 2-3 cm into woody debris) were chosen as intermediate-decayed coarse woody debris (All CWD hereafter refer to intermediate-decayed CWD). CWD were assessed at two scales, one was to measure their biomass at sub-plot level, which were used for another paper (Yang *et al.*, 2007), while the other was to estimate the abundance of CWD in a 3m-radius circle with each sampling host as the centre. CWD data explored from the latter were used for multivariate analysis in this study. Vascular epiphytic plants were also recorded from the host trees under surveyed. The density of vascular epiphytes on host trees was later treated as an environmental variable in an attempt to explore the potential interaction between vascular plants and the bryophytes.

The average relative atmospheric humidity was measured by placing an auto data logger (Thermo Recorder TR-71U) on host tree trunks at 1.5m above ground. In each type of forest, 3 hosts from different sub-plots were randomly selected (by random numbers) as the humidity measuring points. The same data logger was placed on one measuring point for at least 48 hours and then moved to the next two points successively. There was about 8 hours in the time lag when installing separately these 5 data loggers in all forest types, and we took the simultaneously part of hourly data to calculate the mean humidity representing each forest type. The measurement was first done during April, 2005, and later repeated during the following August.

Plot shadiness was evaluated by applying the "crown illumination index" defined by Clark & Clark (1992). Each index value was converted to percentage of shadiness (1 = 95%; 1.5 = 80%; 2 = 70%; 2.5 = 60%; 3 = 50%; 4 = 30%; 5 = 10%) before submitting to ordination.

Data analysis

All data were submitted to Shapiro-Wilk normality test and Bartlett homoscedasticity test before applying the parametric (ANOVA and LSD) or non-parametric statistical methods (Kruskal-Wallis rank sum test and Pairwise Wilcoxon rank sum test). Analysis of variance test ($P < 0.05$) was used to determine whether or not there were significant differences exist in species richness, bryophyte coverage, diversity indexes, and life form frequencies among forest types.

Species diversity in each sub-plot (30 × 30 m) level was determined by calculating both α (H' , Shannon-Wiener diversity Index) and β diversity indexes (1-Ij) using the formulas below:

$$H' = \sum (p_i) \cdot (\log_2 p_i)$$

$$I_j = a / (a + b + c)$$

where H' is the Shannon-Wiener diversity index; p_i = refers to proportion of total sample belonging to i th species. I_j refers to the similarity coefficient of Jaccard index; a refers number of species in sample A and sample B; b = Number of species in sample B but not in sample A; c = Number of species in sample A but not in sample B (Krebs, 1999).

Indicator species analysis (ISA, Dufrêne & Legendre, 1997) was used to determine species indicative of each forest type. Calculations were done in package “labdsv” (Roberts, 2006).

Detrended correspondence analysis (DCA, Hill & Gauch, 1980) was used to analyze the variation of species composition among forest types. In order to diminish the disproportionate effects of rare species on site scores, epiphytic bryophytes that with frequencies less than 5% across all sampling quadrats were excluded. Canonical Correspondence Analysis (CCA, ter Braak, 1986) was employed to analyze the potential effects that the selected environmental variables may have on the life form distribution of bryophytes. “Vegetation matrix” was formed by entering the absolute frequencies of each life form of bryophytes (root square transformed) per sub-plot. Sampling hosts were treated as “sites” in CCA, and host whose total frequencies of all life forms less than 10% were excluded from CCA test. Meanwhile, environmental variables were submitted to “forward selection” before the creation of “environmental matrix”. Both ordination techniques were performed in package “vegan” (Oksanen *et al.*, 2008). All the calculation and statistical analyses were performed with the help of R 2.8.1 (R Development Core Team, 2008).

RESULTS

There were significant variations in all environmental variables measured among forest types (Table 2). Generally, old-growth forests had much greater amount of CWD, slightly higher density of vascular epiphytes, and relative higher atmospheric humidity than secondary forests.

Table 2. The environmental variables (mean \pm SE) measured in each forest and P value from LSD or Pairwise Wilcoxon rank sum test.

<i>Environmental variables</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>P</i>
Abundance of CWD (kg·h ⁻¹)	28.6 \pm 7.9	51.4 \pm 32.0	44.4 \pm 20.5	32.3 \pm 8.0	1888.4 \pm 441.4	< 0.001
Bark roughness	8.4 \pm 0.8	4.3 \pm 1.6	4.1 \pm 0.8	5.4 \pm 1.6	4.7 \pm 0.6	< 0.001
Bar moisture content (%)	55.4 \pm 2.8	56.2 \pm 7.7	53.1 \pm 7.7	39.6 \pm 3.7	54.5 \pm 9.3	0.003
Bark water-holding capacity	93.6 \pm 6.3	67.6 \pm 13.2	91.7 \pm 25.7	85.5 \pm 4.8	92.4 \pm 30.3	< 0.001
Density of vascular epiphytes per host	0.4 \pm 0.2	0.2 \pm 0.1	0.7 \pm 0.3	2.7 \pm 1.3	2.1 \pm 0.7	0.001
Host DBH (cm)	26.5 \pm 2.6	29.9 \pm 2.4	28.5 \pm 4.4	17.6 \pm 1.8	29.6 \pm 3.6	< 0.001
Host height (m)	13.8 \pm 1.2	14.4 \pm 1.1	16.1 \pm 0.8	6.3 \pm 0.6	18.8 \pm 1.0	< 0.001
Plot shadiness (%)	74.5 \pm 13.2	85.9 \pm 9.4	83.8 \pm 9.1	88.4 \pm 6.1	84.3 \pm 7.3	< 0.001
Relative atmospheric humidity (%)	72.6 \pm 5.0	79.9 \pm 7.4	84.4 \pm 5.7	89.1 \pm 8.9	81.1 \pm 3.7	< 0.001

In all, there were 176 epiphytic bryophytes (117 mosses and 59 liverworts) belonging to 83 genera, 38 families collected in both old-growth and secondary forests. The most speciose moss family was Meteoriaceae (24 spp.), and among liverworts was Porellaceae (15 spp.). The most frequently recorded species in SAA were *Pterobryopsis acuminata* (Hook.) Fleisch., *Brachythecium noguchii* Tak. and *Ptychanthus striatus* (Lehm. & Lindenb.) Nees.; in SPA were *Plagiochila arbuscula* (Brid. ex Lehm.) Lindenb. and *Homaliodendron flabellatum* (Sm.) Fleisch.; in SLA were *H. flabellatum* and *Plagiochila assamica* Steph; in ODMF were *P. arbuscula*, *Sinskea phaea* (Mitt.) Buck., and *H. flabellatum*., and in OLF were *H. flabellatum*, *H. scalpellifolium* (Mitt.) Fleisch. and *P. arbuscula*. From DCA results (Fig. 3), it is obvious that besides two sub-plots in SAA, there were no distinct differentiation in species composition among all sub-plots.

Between old-growth forests (OF) and secondary ones (SF), the species richness (OF: 136; SF: 141), α diversity (Shannon diversity index, OF: 4.282, SF: 4.370) and mean coverage per sub-plot (OF: $62.2 \pm 1.3\%$; OS: $64.7 \pm 1.5\%$) were similar. There were also no significant differences observed among each type of forests except for β diversity values (Kruskal-Wallis $\chi^2 = 213.7$, $P < 0.001$) (Fig. 2).

Species with indicator values higher than 0.200 for each type of forest were: 1) SAA: *Brachythecium noguchii* (0.367), *Pterobryopsis acuminata* (Hook.) Fleisch. (0.341), *Spruceanthus semirepandus* (Nees) Verd. (0.317), *Tayloria subglabra* (Griff.) Mitt. (0.295) and *Frullania bolanderi* Aust. (0.239); 2) SPA: *Neckera crenulata* Harv. in Hook. (0.201); 3) ODMF: *Sinskea phaea* (0.301); 4) OLF: *Homaliodendron flabellatum* (0.205). No species meet the above criteria in SLA and all species listed above were significant with 1000 randomly conducted Monte-Carlo simulations.

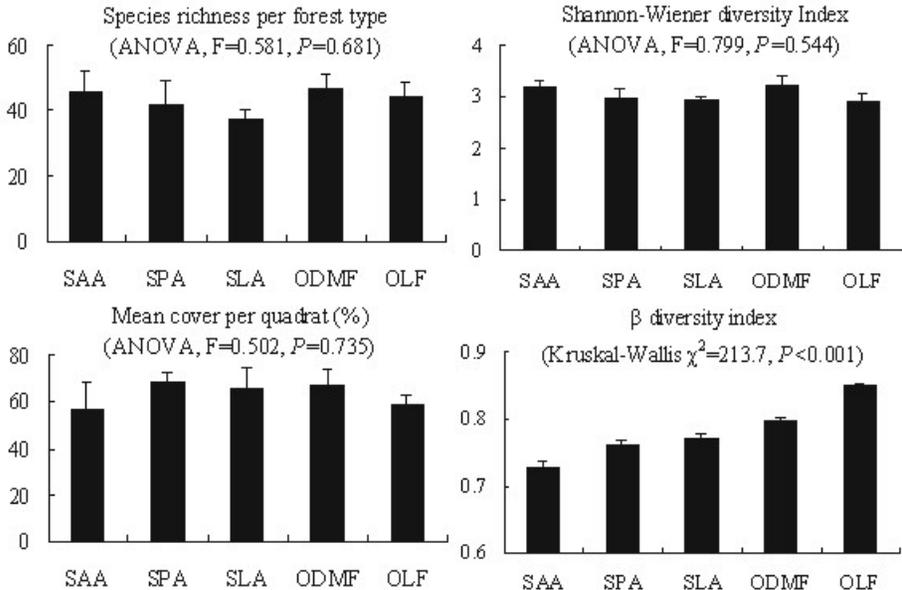


Fig. 2. Comparison of epiphytic bryophytes' species richness, cover, α and β diversity among forest types.

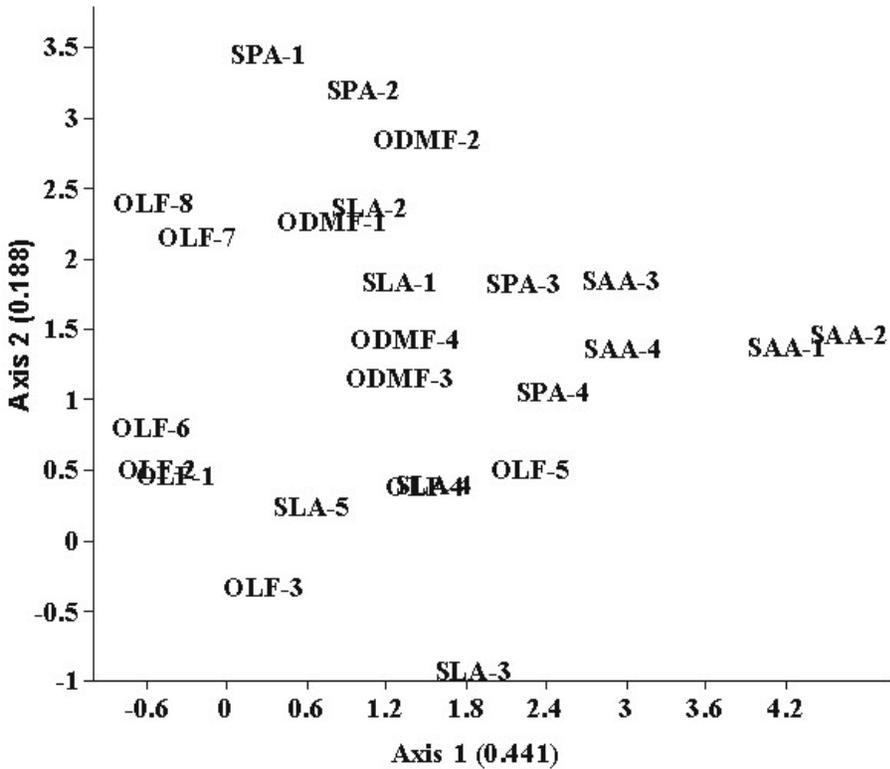


Fig. 3. Biplot of detrended correspondence analysis for epiphytic bryophytes in all sub-plots. (With eigenvalues in brackets)

There were no significant differences in any life form's frequencies among forest types. However, the division of bryophytes into mosses and liverworts yielded clearer trends: the fan-shaped mosses show a preference for old-growth forests, and the turf-form mosses appear more frequently in young secondary forests (Fig. 4). While among hepatics, rough mat life form occurs significantly more often in old-growth forests than in secondary counterparts (Fig. 5).

Several environmental factors have influenced the distribution of epiphytic bryophytes as shown by the CCA results (Fig. 6). The degree of abundance of CWD, the relative humidity of atmosphere, and roughness of bark of host tree turned out to be the most influential environmental variables in determining the life form composition of epiphytic bryophyte communities. Both high atmospheric humidity and abundant CWD showed a strong influence on the distribution of weft species. Pendant life form may be positively favored by the barks' water-holding capacity of the host tree, and turf life form may be regulated by the gradient in the barks' roughness of the host tree. The first axis (eigenvalue 0.527) in Fig. 6 probably stood for the successional gradient, as many hosts from old-growth forests (dots in black) appeared on the left side of this axis, although no distinct segregation between host trees from old-growth and secondary forests were observed.

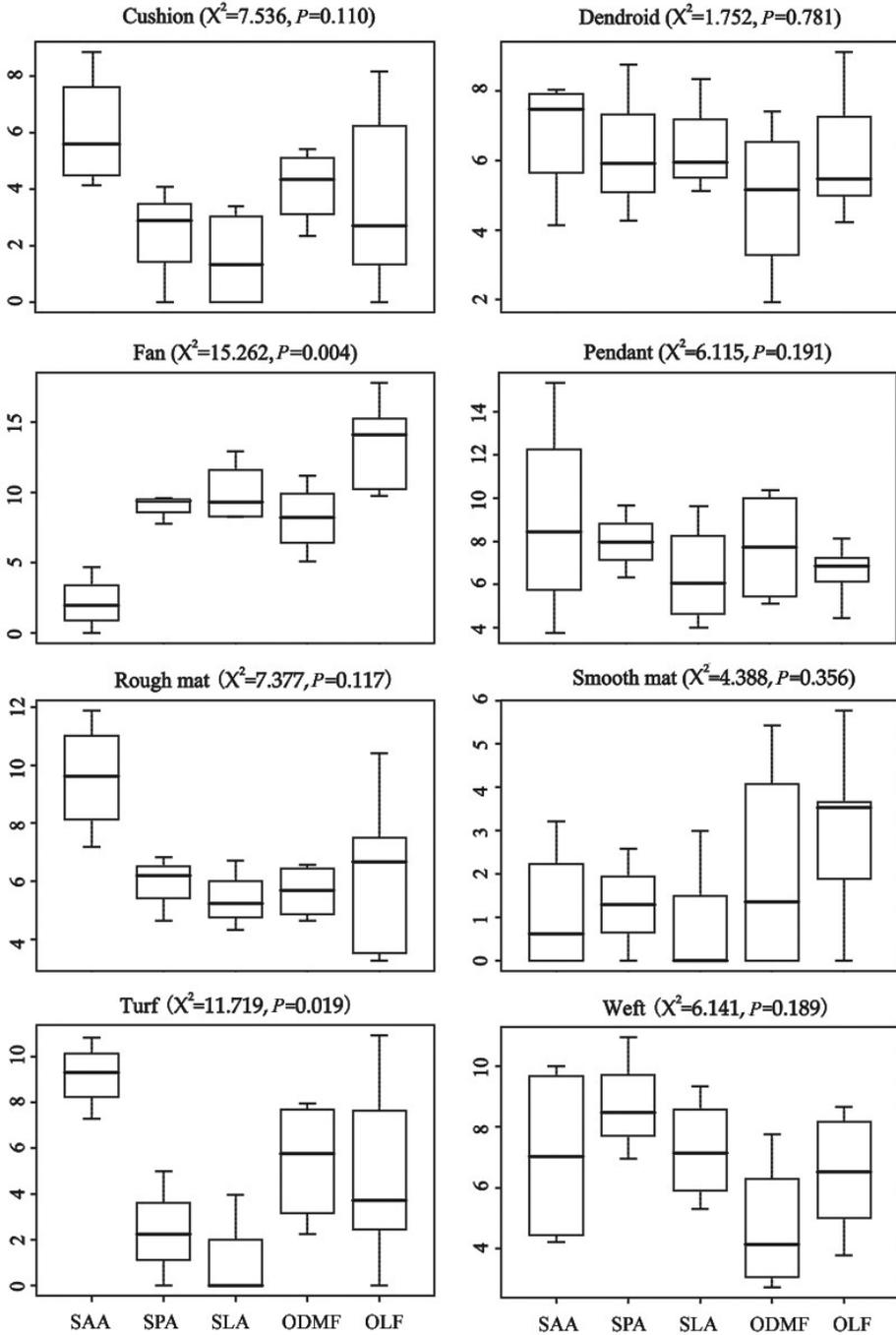


Fig. 4. Box-plot of frequencies by epiphytic moss'life forms in all forest types, with Kruskal-Wallis χ^2 and P value in brackets. (All vertical axes refer to percentage frequency).

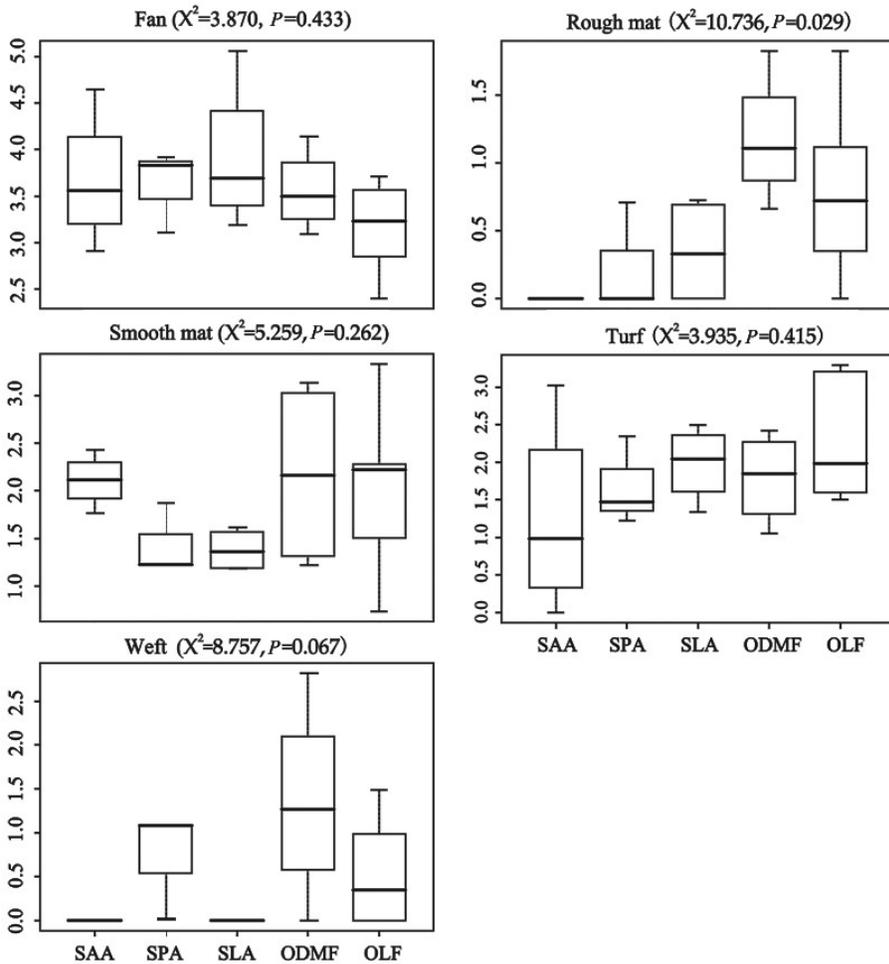


Fig. 5. Box-plot of frequencies by epiphytic hepatics' life forms in all forest types, with Kruskal-Wallis χ^2 and P value in brackets (All vertical axes refer to percentage frequency).

DISCUSSION

Species diversity

Previous studies have reported lower levels of α diversity in secondary forest when compared with old-growth forests (Barthlott *et al.*, 2001; Wolf, 2005). Whereas we found that species richness was similar in both forest types, as shown by Holz and Gradstein (2005). This may be due to the following reasons: firstly, since the substrates in old-growth forests were, in general, occupied by strong competitors during long period of time, this has made it difficult for newly arrived species to colonize the substrates. *Homaliodendron flabellatum* and

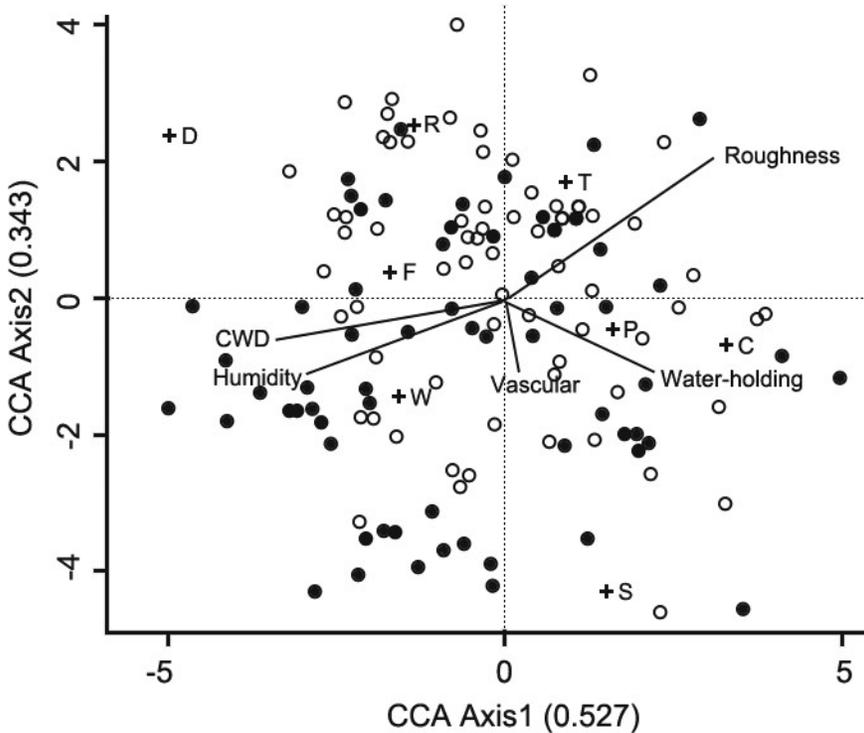


Fig. 6. CCA of epiphytic bryophytes (categorized by life forms) and environmental variables. (“CWD” refers to the degree of abundance of CWD; “Humidity” refers to relative humidity; “Vascular” refers to the abundance of vascular plants; “Water-holding” refers to water-holding capacity of host barks; “Roughness” refers to the roughness of host bark; “•” represent hosts in old-growth forests; “o” represent hosts in secondary associations; “+” stand for life forms; “D” means dendroid; “F” means fan; “R” means rough mat; “T” means turf; “P” means pendant; “C” means “cushion”; “S” means “smooth mat”; “W” means “weft”)

H. scalpellifolium were just the typical representatives of these strong competitors. Secondly, drought-tolerant epiphytic bryophytes had made up a large proportion of the assemblage in secondary forests. This evidently explained why turf, rough mat and smooth mat life forms were more frequently encountered in secondary forests. Thirdly, some host trees in a secondary forest had particular bark character traits that favored certain epiphytic species. For example, the rough bark of *Alnus nepalensis* in SAA (Table 2) favored turf species (Fig. 6), and the high water-holding capacity of *Schefflera shweliensis* W. W. Smith ($191.6 \pm 14.9\%$) and *Symplocos ramosissima* Wall. ex G. Don ($129.3 \pm 23.4\%$) in SPA and SLA (unpublished data) had promoted pendant life form. Lastly, the overall air humidity in all forest types was rather high. Despite significant differences in humidity existed among all forest types, the lowest relative humidity recorded in SAA could still be considered high ($72.6 \pm 5.0\%$). Besides, this figure only depicted the situation in dry seasons, while our measurements yielded almost the same values (ca 99%) in the relative humidity among all forest types during rainy seasons. High air humidity must be rather important in sustaining the epiphytes in secondary forests. Many epiphytic bryophytes associated with old-growth

forests were also recorded in younger forests with high humidity (González-Mancebo *et al.*, 2004). That may explain why some dominant species, such as *Homaliodendron flabellatum* and *Plagiochila arbuscula*, with morphologically drought-sensitive features, could also flourish in nearby secondary forests.

Although α diversity did not differ among forest types, old-growth forests showed a significantly higher value in β diversity. The β diversity, or species turn over rate, was reported high in neotropical, old-growth forests because of the high degree of niche partitioning (Gentry & Dodson, 1987). Similarly, Flores-Palacios & García-Franco (2008) found the β diversity of epiphytes were lower in isolated forests due to uniform environmental conditions. The reduced β diversity meant the loss of habitat heterogeneity for the epiphytes. Indeed, compared with secondary forests, old-growth stands are structurally more complex as demonstrated by taller canopy heights, more branching of host trees, more abundant presence of dead wood, and higher density of vascular epiphytes, at least in the areas where we conducted this study. This complexity has created diversified substrates for individual species to explore. Accordingly, high β diversity in old-growth forests had resulted from the gradual accumulation of species from one host to another (Wolf & Flamenco, 2003). On the other hand, the low β diversity in present study in secondary forests reflected the fact that species were clustered within a limited number of host trees species, since our survey was biased on “most epiphyte-loaded” phorophytes.

Take SAA for instance, the high number of the bryophyte indicator species demonstrated that these species were either niche-breadth-narrowed or dispersal-limited (Mills & Macdonald, 2005). Whatever the case, epiphytic bryophytes in secondary forests were more vulnerable to disturbance as they tended to cluster their distribution on certain preferred hosts.

Life form distribution

In a broader sense, the species richness of a bryophyte community could not tell the whole story about the quality of epiphytic habitats without the information on their various life forms. The classification of bryophyte life forms provides increased accuracy, although less in species specific, in data collection due to the difficulty of identifying some bryophytes to the species level in the field.

Bryophytes with different life forms are indicative of the habitats where they are found because of their strong reliance on transient water supplies. According to Gimingham & Birse (1957), mat, turf and cushion could be roughly considered as xeric life forms with increasing drought-tolerance. Furthermore, dendroid, weft, fan and pendants are life forms indicative of wet environments (Smith, 1982), especially the pendant, which has been considered very desiccation-sensitive (Bates, 1998).

In present study, among the 13 life forms categorized by moss and liverworts seen in the five forest types, only fan (moss), turf (moss) and rough mat (liverworts) exhibited a pronounced preference for a definitive forest type. The differentiation in the distribution pattern of fan and turf among forest types were largely shown by the SAA, since SAA had significantly lower frequency of desiccation-sensitive life-form (fan) than in other forest types. This pattern corresponded to the fact that human-disturbed forests would initiate a loss of drought-intolerant epiphytic bryophytes (Acebey *et al.*, 2003). Meanwhile, SAA also had significantly higher frequency of drought-tolerant life form (turf). This may reflect the comparatively dry environment there.

The dramatic decline in frequencies of fan (moss), rough mat (liverworts) and weft (liverworts) in secondary forests reflected also, in addition, the fact that these forests did not provide many suitable epiphytic substrates for moss plants to grow as compared to the old-growth counterparts.

Environmental variables

Although there were significant differences in all environmental variables measured among forest types, much of the variation in epiphytic bryophytes can be explained by four gradients: the roughness of the bark of host tree, degree of abundance of CWD, relative air humidity, and water-holding capacity of host barks.

Barks with dense fissures are expected to favor the establishment and growth of epiphytic bryophytes (Znotiņa, 2003). Because of retention of more stem flow on rough barks ensure higher success of spore anchorage (Schofield, 1985). In our study, the distribution of turf life form turned out to be strongly affected by the roughness of host barks. This partly agreed with van Leerdam *et al.* (1990) who maintained that rough barks were better at fostering turf species than smooth barks. The positive association of turf species with rough bark (*e. g. Alnus nepalensis* and *Populus boantii*) was not by accident in secondary forests, especially in SAA. The relatively open and dry environments in SAA probably excluded life forms other than turf, a drought-tolerant group. This goes to show that a combination of physical environments and host bark character traits had produced this pattern of life form distribution.

Likewise, both the degree of abundance of CWD and relative humidity had influenced the distribution of weft life form, which is an indicator of humid environments (Bates, 1998). Among the weft species, majority of them also grow on dead wood. For instance, *Thuidium* spp. and *Macrothamnium* spp. dominated the epixylic communities in the region. Their dominance is primarily observed in OLF, because not much CWD was present in secondary forests (Table 2). Since high humidity may speed up colonization of epiphytes (González-Mancebo *et al.*, 2004), it can be postulated that given ample water supply, the ecological significance of dead wood habitat would expand from “increasing the habitat heterogeneity” to “being the dispersal center that help epixylic bryophytes to colonize epiphytic substrates”.

The water-holding capacity of host tree bark is reported a crucial determinant of epiphytic bryophytes (Turner & Pharo, 2005). In our survey, we found this factor to be regulating the distribution of pendant life form (Fig. 6). Because of their hanging growth form, pendant bryophytes are extremely sensitive to air humidity (Bates, 1998), and they play important roles in the water cycling in tropical montane forests (Romero, 1999). But pendant life form in this study did not show a strong reliance on air humidity. The possible explanation might be that the reduced air humidity in the secondary forest had not reached the lowest threshold required for the survival of pendant bryophytes. In case when overall water availability is not the limiting factor, barks of trees with strong water-holding capacity became beneficial to epiphytes during the temporary shortage of water. Pendant bryophytes growing on wet tree trunks are more likely to be favored as they have relatively larger proportion of their body coming into direct contact with the bark substrate.

CONCLUSION

Secondary forests in Xujiaba, Mt. Ailao NNR, not only play a role in providing suitable habitats for a diversified flora of epiphytic bryophytes with a wide range of ecological amplitudes, but also harbor unique species composition as shown by large number of indicator species with limited range of local distribution. So, this forest type deserves our conservation attention. But secondary forests can not replace the old-growth forest due to the loss of β diversity in epiphytic communities. Besides, ecological functions such as providing habitat for fan (moss), rough mat (liverworts) are also weakened in secondary forests.

Host bark character traits (roughness and water-holding capacity) and forest stand characters (degree of abundance of CWD and relative atmospheric humidity) were shown in our study to be important environmental variables influencing the distribution of specific epiphytic bryophytes categorized by life forms. This information has shed new light on the conservation of epiphytic bryophyte diversity. In practice, the retaining of CWD in old-growth forests and the introduction of host tree species with high moisture retaining bark features should be added and integrated in the forest management.

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REFERENCES

- ACEBEY A., GRADSTEIN S.R. & KRÖMER T., 2003 — Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of tropical ecology* 19: 9-18.
- BARTHLOTT W., SCHMITT-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 ecology* 152: 145-156.
- BATES J.W., 1998 — Is ‘life-form’ a useful concept in bryophyte ecology? *Oikos* 82: 223-237.
- CHAZDON R.L., 2008 — Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* 320: 1458-1460.
- CHEN P.-C., LI X.-J. & WU P.-C., 1963 — *Genera Muscorum Sinicorum* (Pars Prima). Beijing: Science Press.
- CHEN P.-C., LI X.-J. & WU P.-C., 1978 — *Genera Muscorum Sinicorum* (Pars Secunda). Beijing: Science Press.
- CLARK D.A & CLARK D.B., 1992 — Life history of canopy and emergent trees in a neotropical rain forest. *Ecological monograph* 62: 315-344.
- COOPER-ELLIS S., 1998 — Bryophytes in old-growth forests of western Massachusetts. *Journal of the Torrey botanical society* 125: 117-132.
- DUFRENE M. & LEGENDRE P., 1997 — Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs* 67: 345-366.
- FLORES-PALACIOS A. & GARCÍA-FRANCO J.G., 2008 — Habitat isolation changes the beta diversity of the vascular epiphyte communities in lower montane forest, Veracruz, Mexico. *Biodiversity conservation* 17:191-207.

- GAO C. & CAO T., 2000 — *Flora Yunnanica Tomus 17, Bryophyta: Hepaticae, Anthocerotae*. Beijing: Science Press.
- GENTRY A.H. & DODSON C.H., 1987 — Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri botanical garden* 74: 205-233.
- GIMINGHAM C.H. & BIRSE E.M., 1957 — Ecological studies on growth-form in bryophytes: I. Correlations between growth-form and habitat. *Journal of ecology* 45: 533-545.
- GLIME, J.M., 2007 — *Bryophyte Ecology*. Vol. 1. Physiological Ecology (Chapter 4-5). E-book sponsored by Michigan Technological University and the International Association of Bryologists. [Accessed on 18th, July, 2009 at <http://www.bryoecl.mtu.edu>.]
- GONZÁLEZ-MANCEBO J., ROMAGUERA F., LOSADA-LINA A., SUÁREZ A., 2004 — Epiphytic bryophytes growing on *Laurus azorica* in three laurel forest areas in Tenerife (Canary Islands). *Acta oecologica* 25: 159-167.
- GROLLE R., 1983 — Nomina generica Hepaticarum: references, types and synonymies. *Acta botanica fennici* 121: 1-62.
- HILL M. O. & GAUCH H. J., 1980. — Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- HOLZ I. & GRADSTEIN S.R., 2005 — Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica — species richness, community composition and ecology. *Plant ecology* 178: 89-109.
- KREBS C.J., 1999 — *Ecological Methodology*. Menlo Park, Addison-Welsey Educational Publishers, pp. 375-445.
- LI X.-J., 2002 — *Flora Yunnanica, Tomus 18, Bryophyta: Musci*. Beijing: Science Press.
- LI X.-J., 2005 — *Flora Yunnanica, Tomus 19, Bryophyta: Musci*. Beijing: Science Press.
- MALE T.D. & ROBERTS G.E., 2005 — Host association of the strangler fig *Ficus watkinsiana* in a subtropical Queensland rain forest. *Austral ecology* 30: 229-236.
- MILLS S.E. & MACDONALD S.E., 2005 — Factors influencing bryophyte assemblage at different scales in the Western Canadian Boreal Forest. *The bryologist* 108: 86-100.
- OKSANEN J., KINDT R., LEGENDRE P., O'HARA B., SIMPSON G.L., SOLYMOS P., STEVENS M.H.H. & WAGNER H., 2008 — Vegan: Community Ecology Package. R package version: 1.15-0, <http://vegan.r-forge.r-project.org/>
- QIU X.-Z. & XIE S.-C., 1998 — *Studies on the forest ecosystem in Ailao Mountains, Yunnan* (in Chinese with English summary). Kuming: Yunnan Sciences and Technology Press.
- R. DEVELOPMENT CORE TEAM., 2008 — R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- ROBERTS D.W., 2006 — labdsv: Ordination and multivariate analysis for ecology. R package version: 1.3-1. <http://ecology.msu.montana.edu/labdsv/R>
- ROMERO C., 1999 — Reduced-impact logging effects on commercial non-vascular pendant epiphyte biomass in a tropical montane forest in Costa Rica. *Forest ecology and management* 118: 117-125.
- ROUVINEN S., KUULUVAINEN T. & KARJALAINEN L., 2002 — Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. *Canadian journal of forestry research* 32: 2184-2200.
- SCHOFIELD W.B., 1985 — *Introduction to Bryology*. New York, Macmillan Press. pp. 316-319.
- SCHUSTER R.M., 1966 — *The Hepaticae and Anthocerotae of North America*. New York, Columbia University Press.
- SMITH A.J.E., 1982 — *Epiphytes and epiliths*. In Smith A.J.K. (ed), *Bryophyte Ecology*. London, Chapman and Hall, pp. 191-227.
- SÖDERSTRÖM L., 1988 — The occurrence of epixylic bryophytes and lichen species in an old natural and managed forest stand in northeast Sweden. *Biological conservation* 45: 169-178.
- TER BRAAK C.J.F., 1986 — Canonical correspondence analysis, a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- TURNER P.A.M. & PHARO E., 2005 — Influence of substrate type and forest age on bryophyte species distribution in Tasmanian mixed forest. *The bryologist* 108: 67-85.
- VAN LEERDAM A., ZAGT R.J. & VENEKLAAS E.J., 1990 — The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. *Vegetatio* 87: 59-71.
- VELLAK K. & PAAL J., 1999 — Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. *Biodiversity and conservation* 8: 1595-1620.
- WOLF J.H.D. & FLAMENCO A., 2003 — Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of biogeography* 30: 1-9.
- WOLF J.H.D., 2005 — The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest ecology and management* 212: 376-393.

- YANG L., LIU W. & MA W., 2007 — Woody debris stocks in different secondary and primary forests in the subtropical Ailao Mountains, SW China. *Ecological research* 23: 805-812.
- YOU C.-X., 1983. — Classification of vegetation in Xujiaba region Ailao Mts. In: WU Z.-Y. (ed.) *Research of Forest Ecosystem on Ailao Mountains, Yunnan*. Yunnan Science and Technology Press, pp. 74-117.
- YOUNG S.-S., CARPENTER C. & WANG Z.-J., 1992 — A study of the structure and composition of an old growth and secondary broad-leaved forest in the Ailao Mountain of Yunnan, China. *Mountain research and development* 12: 269-284.
- ZNOTIČA V., 2003 — Epiphytic bryophytes and lichens in boreal and northern temperate forests. *Proceeding of the Latvian academy of science* 57: 1-10.

Appendix. List of epiphytic bryophytes found in three secondary forests (SAA, SPA and SLA) and two old-growth forests (OMDF and OLF), with frequency (%) of occurrence in each forest.

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>OMDF</i>	<i>OLF</i>	<i>Life form</i>
Herbertaceae						
<i>Herbertus dicranus</i> (Tayl.) Trev.	5.56	7.79	-	0.83	-	Turf
<i>Herbertus fragilis</i> (Steph.) Herz.	-	-	-	1.65	1.99	Turf
<i>Herbertus huerlimannii</i> Mill.	-	-	-	2.07	-	Turf
<i>Herbertus angustissimus</i> (Herz.) Mill.	-	-	-	7.43	-	Turf
<i>Herbertus decurrens</i> (Steph.) Mill.	-	0.41	-	-	-	Turf
Lepidoziaceae						
<i>Bazzania fauriana</i> (Steph.) Hatt.	-	-	-	-	0.66	Rough mat
<i>Bazzania himalayana</i> (Mitt.) Schiffn.	-	1.64	-	10.33	0.66	Weft
<i>Bazzania ovistipula</i> (Steph.) Mizut.	-	1.64	1.99	19.83	20.53	Smooth mat
<i>Bazzania praerupta</i> (Reinw. et al.) Trev.	-	-	-	3.31	-	Rough mat
<i>Bazzania sikkimensis</i> (Steph.) Herz.	-	0.41	-	10.33	0.33	Weft
<i>Bazzania tricrenata</i> (Wahlenb.) Trev.	-	-	-	2.07	-	Weft
<i>Bazzania tridens</i> (Reinw. et al.) Trev.	-	3.28	2.39	13.22	8.61	Weft
<i>Bazzania yashinagana</i> (Steph.) Steph.	-	-	-	-	0.99	Smooth mat
<i>Lepidozia trichodes</i> (Reinw. et al.) Nees	-	0.82	-	0.83	0.33	Weft
<i>Lepidozia reptans</i> (L.) Dum.	-	1.23	-	1.65	5.30	Weft
Lophoziaceae						
<i>Chandonanthus birmensis</i> Steph.	0.40	-	-	-	-	Smooth mat
<i>Chandonanthus hirtellus</i> (Web.) Mitt.	1.19	0.41	-	-	-	Smooth mat
Scapaniaceae						
<i>Scapania ciliata</i> Sande Lac.	-	1.64	-	-	1.99	Turf
Geocalyceae						
<i>Heteroscyphus zollingeri</i> (Gott.) Schiffn	1.59	5.74	11.95	1.65	12.25	Smooth mat
<i>Heteroscyphus</i> sp.	-	-	-	-	1.32	Smooth mat
Plagiochilaceae						
<i>Plagiochila fruticosa</i> Mitt.	-	1.23	1.99	20.66	5.96	Fan
<i>Plagiochila assamica</i> Steph.	-	2.05	37.85	14.88	26.16	Fan
<i>Plagiochila semidecurrans</i> (Lehm. et Lindenb.) Lindenb.	15.87	7.38	0.40	-	0.99	Turf
<i>Plagiochila pseudorenitens</i> Steph.	-	5.74	-	1.65	4.64	Turf
<i>Plagiochila secretifolia</i> Mitt.	2.78	6.56	-	1.24	0.99	Turf
<i>Plagiochila ovilifolia</i> Mitt.	1.59	0.82	23.51	15.29	16.56	Turf
<i>Plagiochila subtropica</i> Steph.	33.33	16.39	17.13	12.81	10.60	Fan
<i>Plagiochila trabeculata</i> Steph.	-	10.66	18.33	2.89	25.83	Turf
<i>Plagiochila sciophila</i> Nees.	-	-	0.40	0.41	1.66	Turf

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
<i>Plagiochila flexuosa</i> Mitt.	-	-	4.38	10.33	1.32	Fan
<i>Plagiochila arbuscula</i> (Brid. ex Lehm.) Lindenb.	21.83	40.57	31.08	37.60	34.77	Fan
Acrobolbaceae						
<i>Marsupidium knightii</i> Mitt.	-	-	-	-	0.66	Turf
Radulaceae						
<i>Radula complanata</i> (L.) Dum.	-	-	0.40	1.65	0.99	Smooth mat
Porellaceae						
<i>Porella pinnata</i> L.	-	-	-	0.83	-	Fan
<i>Porella obtusiloba</i> var. <i>macroloba</i> (Steph.) Hatt. et Zhang	0.79	0.41	1.20	0.41	0.99	Fan
<i>Porella nitens</i> (Steph.) Hatt.	-	-	7.97	-	-	Fan
<i>Porella chinensis</i> f. <i>hastata</i> (Steph.) Hatt.	-	0.82	-	-	-	Fan
<i>Porella revoluta</i> (Lehm.) Trev. var. <i>revoluta</i>	15.08	-	3.19	0.41	6.29	Fan
<i>Porella handelii</i> Hatt.	-	4.10	7.17	-	0.66	Fan
<i>Porella longifolia</i> (Steph.) Hatt.	-	-	-	2.48	1.66	Fan
<i>Porella oblongifolia</i> Hatt.	-	2.87	3.19	0.41	2.98	Fan
<i>Porella obtusiloba</i> Hatt.	1.98	-	-	-	1.32	Fan
<i>Porella plumosa</i> (Mitt.) Inoue	-	1.64	-	-	1.32	Fan
<i>Porella caespitens</i> (Steph.) Hatt.	-	0.41	1.20	0.41	-	Fan
<i>Porella acutifolia</i> subsp. <i>tosana</i> (Steph.) Hatt.	-	-	0.40	-	-	Fan
<i>Porella campylophylla</i> (Lehm. et Lindb.) Trev. var. <i>campylophylla</i>	0.79	7.38	-	17.36	5.96	Fan
<i>Porella campylophylla</i> var. <i>ligulifera</i> (Tayl.) Hatt.	-	-	12.75	-	3.97	Fan
<i>Porella perrottetiana</i> (Mont.) Trev. var. <i>clatodentata</i> (Chen et Wu) Hatt.	1.19	1.23	-	-	0.66	Fan
Frullaniaceae						
<i>Frullania bolanderi</i> Aust.	22.62	-	-	-	-	Smooth mat
<i>Frullania nepalensis</i> (Spreng.) Lehm. et Lindenb.	15.87	6.15	-	11.98	2.32	Smooth mat
<i>Frullania inouei</i> Hatt.	-	1.64	-	-	-	Smooth mat
<i>Frullania handelii</i> Verd.	1.59	1.64	0.40	9.92	6.62	Smooth mat
Lejeuneaceae						
<i>Ptychanthus striatus</i> (Lehm. et Lindenb.) Nees	36.91	31.15	6.37	7.44	5.30	Fan
<i>Caudalejeunea reniloba</i> (Gott.) Steph.	-	-	-	-	0.66	Fan
<i>Spruceanthus semirepandus</i> (Nees) Verd.	28.97	5.74	-	1.65	1.66	Fan
<i>Leucolejeunea turgida</i> (Mitt.) Verd.	0.79	0.41	-	5.37	5.30	Smooth mat
<i>Lejeunea</i> sp.	-	-	2.39	-	0.33	Smooth mat

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
Metzgeriaceae						
<i>Apometzgeria pubescens</i> (Schrank) Kuwah.	-	1.64	-	-	-	Smooth mat
<i>Metzgeria conjugata</i> Lindb.	0.40	7.38	3.19	8.26	4.30	Smooth mat
Dicranaceae						
<i>Campylopus schimperi</i> Mild.	11.51	-	-	-	-	Turf
<i>Dicrandontium denudatum</i> (Brid.) Britt. ex Williams	-	4.51	0.40	10.74	6.29	Turf
<i>Dicranodontium tenii</i> Broth. et Herz.	-	-	-	1.65	-	Turf
<i>Dicranodontium</i> sp.	1.98	-	-	-	-	Turf
<i>Symblepharis vaginata</i> (Hook.) Wijk et Marg.	2.78	-	-	-	-	Turf
<i>Dicranum crispifolium</i> Muell.Hal.	-	-	0.40	0.41	1.32	Turf
<i>Dicranum japonicum</i> Mitt.	-	0.41	-	10.33	0.99	Turf
<i>Dicranum muehlenbeckii</i> B.S.G.	2.38	-	-	0.41	-	Turf
<i>Dicranum diplospiniiferum</i> C.Gao et Auo	-	-	-	2.89	1.32	Turf
<i>Dicranum</i> sp.	-	-	-	11.57	-	Turf
Leucobryaceae						
<i>Leucobryum juniperoideum</i> (Brid.) Muell.Hall.	0.40	5.33	4.78	19.01	21.85	Cushion
Fissidentaceae						
<i>Fissidens geppii</i> M.Fleisch.	-	-	-	3.72	-	Turf
<i>Fissidens ceylonensis</i> Dozy et Molk.	-	-	0.80	-	-	Turf
<i>Fissidens taxifolius</i> Hedw.	-	-	-	-	1.32	Turf
<i>Fissidens dubius</i> P.Beauv.	-	3.69	-	-	5.30	Fan
<i>Fissidens anomalus</i> Mont.	-	-	10.36	4.55	8.61	Fan
Calymperaceae						
<i>Syrhropodon gardneri</i> (Hook.) Schwaegr.	-	-	-	-	5.63	Turf
Pottiaceae						
<i>Leptodontium flexifolius</i> (With.) Hampe	0.40	0.41	0.80	-	3.97	Turf
<i>Leptodontium viticulosoides</i> (P. Beauv.) Wijk et Marg	8.33	2.46	0.40	2.89	-	Turf
<i>Leptodontium warnstorffii</i> M.Fleisch.	-	-	-	-	0.66	Turf
<i>Trichostomum cuspidatum</i> (Dozy et Molk.) Dozy et Molk.	9.92	0.41	-	-	3.31	Turf
Splachnaceae						
<i>Tayloria rudolphiana</i> (Garov.) B.S.G.	-	-	0.80	0.83	-	Turf
<i>Tayloria subglabra</i> (Griff.) Mitt.	23.81	6.97	-	0.83	3.97	Turf
Bryaceae						
<i>Brachymenium capitulatum</i> (Mitt.) Kindb.	-	-	-	-	1.66	Turf
<i>Brachymenium nepalense</i> Hook.	21.43	1.23	-	-	-	Turf
<i>Brachymenium</i> sp.	1.59	-	-	-	-	Turf
<i>Rhodobryum giganteum</i> (Schwaegr.) Par.	-	0.82	-	-	-	Cushion

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
Mniaceae						
<i>Orthomnion bryoides</i> (W. Griff.) Norkett.	10.71	-	-	-	1.66	Rough mat
<i>Plagiomnium maximoviczii</i> (Lindb.) T.Kop.	2.78	17.62	17.13	5.79	7.28	Rough mat
<i>Plagiomnium</i> sp.	-	-	-	-	0.33	Rough mat
Orthotrichaceae						
<i>Macromitrium ferriei</i> Card. et Thér.	13.10	-	-	-	-	Rough mat
<i>Macromitrium</i> sp.	1.19	-	-	-	-	Rough mat
<i>Macrocoma tenue</i> (Hook. et Grev.) Vitt subsp. <i>sullivantii</i> (Muell.Hal.) Vitt.	2.38	-	-	-	-	Rough mat
Hedwigiaceae						
<i>Hedwigia ciliata</i> (Hedw.) Ehrh. ex P. Beauv.	0.40	-	-	-	-	Rough mat
Trachypodaceae						
<i>Trachypus bicolor</i> Reinw. et Hornsch.	-	3.69	-	3.72	2.32	Dendroid
<i>Trachypus humilis</i> Lindb.	1.19	-	3.98	0.83	6.95	Dendroid
<i>Duthiella formosana</i> Nog.	-	-	-	4.96	-	Dendroid
<i>Trachypodopsis serrulata</i> (P. Beauv.) M.Fleisch. var. <i>crispatula</i> (Hook.) Zant.	-	-	1.20	0.41	1.32	Dendroid
Pterobryaceae						
<i>Calypothecium hookeri</i> (Mitt.) Broth.	-	1.23	0.80	2.48	14.57	Pendant
<i>Pterobryopsis acuminata</i> (Hook.) M.Fleisch.	39.29	2.46	13.55	2.07	1.32	Dendroid
<i>Meteoriella soluta</i> (Mitt.) Okam.	0.40	-	3.59	1.24	-	Pendant
<i>Symphysodontella tortifolia</i> Dixon	-	-	-	0.83	0.99	Pendant
Meteoriaceae						
<i>Aerobryidium aureo-nitens</i> (Schwaegr.) Broth.	20.24	1.23	-	0.83	-	Pendant
<i>Aerobryidium crispifolium</i> (Broth. et Geh.) M.Fleisch. ex Broth.	-	3.28	-	-	-	Pendant
<i>Aerobryidium filamentosum</i> (Hook.) M.Fleisch. ex Broth.	-	-	-	2.07	-	Pendant
<i>Aerobryidium levieri</i> (Ren. et Card.) S.H. Lin	1.98	-	-	0.41	0.66	Pendant
<i>Aerobryum speciosum</i> Dozy et Molk	1.19	-	-	-	-	Pendant
<i>Barbella chrysonema</i> (Muell.Hal.) Nog.	-	1.23	-	-	-	Pendant
<i>Chrysocladium retrorsum</i> (Mitt.) M.Fleisch.	0.79	0.41	-	5.79	0.33	Pendant
<i>Floribundaria walkeri</i> (Ren. et Card.) Broth.	26.98	18.03	-	9.09	21.52	Pendant
<i>Meteoriopsis reclinata</i> (Muell.Hal.) M.Fleisch. ex Broth.	21.43	-	19.12	-	-	Pendant
<i>Meteoriopsis squarrosa</i> (Hook.) M.Fleisch	-	-	-	-	-	Pendant
<i>Meteorium cucullatum</i> S.H. Lin et & S.H. Wu	-	-	0.40	-	0.33	Pendant
<i>Meteorium longipilum</i> Nog.	-	3.28	-	-	-	Pendant
<i>Meteorium miquelianum</i> (Muell.Hal.) Fleisch.	-	-	-	0.83	0.33	Pendant

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
<i>Meteorium subpolytrichum</i> (Besch.) Broth.	-	0.82	-	-	0.66	Pendant
<i>Neodiciadiella pendula</i> (Sull.) Buch.	-	1.23	-	2.48	2.98	Pendant
<i>Neonoguchia auriculata</i> (Copp. ex Ther.) S.H. Lin	-	1.64	0.40	1.24	0.33	Pendant
<i>Papillaria chrysoclada</i> (Muell.Hal.) Jaeg.	5.16	-	-	-	0.99	Pendant
<i>Papillaria feae</i> M.Fleisch.	2.78	2.05	-	-	1.32	Pendant
<i>Papillaria fuscescens</i> (Hook.) Jaeg.	19.84	21.31	0.80	12.81	6.95	Pendant
<i>Pseudobarbella angustifolia</i> Nog.	-	0.41	8.37	-	-	Pendant
<i>Pseudobarbella attenuata</i> (Thwaites et Mitt.) Nog.	0.40	-	0.80	-	-	Pendant
<i>Sinskea phaea</i> (Mitt.) W.R.Buck	-	4.10	-	26.86	0.33	Pendant
<i>Trachycladiella aurea</i> (Mitt.) Menzel	-	-	-	-	1.32	Pendant
<i>Trachycladiella sparsa</i> (Mitt.) Menzel	6.35	-	-	0.41	0.66	Pendant
Neckeraceae						
<i>Nerkeria pennata</i> Hedw.	-	0.41	-	-	2.98	Fan
<i>Neckeria yezoana</i> Besch.	-	-	5.98	-	2.32	Fan
<i>Neckeria crenulata</i> Harv. in Hook.	3.97	31.97	-	16.12	17.55	Fan
<i>Homaliodendron exiguum</i> (Bosch et Sande Lac.) M.Fleisch.	-	-	25.90	-	3.31	Fan
<i>Homaliodendron flabellatum</i> (Sm.) M.Fleisch.	-	36.48	-	35.12	75.17	Fan
<i>Homaliodendron scalpellifolium</i> (Mitt.) M.Fleisch.	1.98	20.08	57.37	23.14	54.30	Fan
Hookeriaceae						
<i>Hookeria acutifolia</i> Hook. et Grev.	-	0.41	15.94	-	15.23	Fan
Symphyodontaceae						
<i>Symphyodon echinatus</i> (Mitt.) Jaeg.	1.19	-	-	-	0.99	Rough mat
<i>Symphyodon perrottetii</i> Mont.	-	4.10	-	-	2.98	Rough mat
Hypopterygiaceae						
<i>Cyathophorella hookeriana</i> (Griff.) M.Fleisch.	0.40	4.92	-	8.26	4.30	Fan
<i>Cyathophorella tonkinensis</i> (Broth. et Par.) Broth.	-	-	9.96	-	3.97	Fan
<i>Cyathophorella spinosa</i> (Muell.Hal.) M.Fleisch.	-	-	-	-	2.65	Fan
<i>Cyathophorella subspinosa</i> P.C. Chen.	0.79	-	3.19	-	0.99	Fan
Leskeaceae						
<i>Regmatodon declinatus</i> (Hook.) Brid.	5.95	-	0.80	-	-	Rough mat
<i>Lindbergia serrulatus</i> C.Gao et W.H. Wang	2.78	-	-	-	-	Rough mat
Thuidiaceae						
<i>Claopodium</i> sp.	-	2.05	-	-	-	Weft
<i>Cyrtio-hypnum haplohymenium</i> (Harv.) W.R.Buck et H.A. Crum	2.38	-	-	-	-	Weft
<i>Thuidium assimile</i> (Mitt.) Jaeg.	11.91	4.92	-	0.83	0.33	Weft
<i>Thuidium cymbifolium</i> (Dozy et Molck.) Dozy et Molck.	8.33	11.89	-	8.26	25.83	Weft
<i>Thuidium kanedae</i> Sak.	-	15.57	25.10	9.09	8.94	Weft
<i>Thuidium philibertii</i> Limpr.	-	11.07	5.58	2.07	1.66	Weft

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
Brachytheciaceae						
<i>Palamocladium euchloron</i> (Muell.Hal.) Wijk et Mang.	-	-	1.99	-	0.66	Rough mat
<i>Brachythecium noguchii</i> Tak.	39.29	-	-	-	-	Rough mat
<i>Eurhynchium laxirete</i> Broth.	-	2.87	-	-	10.60	Rough mat
<i>Eurhynchium squarrifolium</i> (Lindb.) SandeLac.	-	-	4.78	-	0.33	Weft
<i>Rhynchostegium ovalifolium</i> Okam.	-	9.02	-	-	-	Rough mat
Entodontaceae						
<i>Entodon viridulus</i> Card.	5.56	-	3.59	-	-	Rough mat
<i>Entodon acutifolius</i> R. L. Hu	5.95	-	-	-	-	Rough mat
<i>Entodon obtusatus</i> Broth.	-	0.82	-	0.41	0.33	Rough mat
<i>Entodon micropodus</i> Nog.	-	-	-	-	0.33	Rough mat
<i>Entodon</i> sp.	-	0.82	-	-	-	Rough mat
Plagiotheciaceae						
<i>Plagiothecium neckeroideum</i> B.S.G.	-	-	-	-	20.86	Fan
<i>Plagiothecium formosicum</i> Broth. et Yas.	-	1.23	-	0.41	0.33	Fan
<i>Plagiothecium laetum</i> B.S.G.	-	1.23	0.80	5.79	1.32	Fan
<i>Plagiothecium nemorale</i> (Mitt.) Jaeg.	-	-	2.39	-	3.97	Fan
Sematophyllaceae						
<i>Struckia argentata</i> (Mitt.) Muell.Hal.	24.60	-	-	-	-	Cushion
<i>Gammiella pterogonioides</i> (Griff.) Broth.	0.40	0.41	-	-	-	Rough mat
<i>Wijkia deflexifoia</i> (Ren. et Card.) H.A.Crum	1.98	15.57	-	20.66	12.25	Rough mat
<i>Wijkia tanytricha</i> (Mont.) H.A.Crum	-	-	4.78	-	0.66	Weft
<i>Trismegistia undulata</i> Broth. et Yas.	-	-	-	0.83	10.93	Dendroid
<i>Hageniella micans</i> (Mitt.) B.C.Tan et Jia Yu	-	6.15	5.58	-	1.32	Turf
<i>Brotherella erythrocaulis</i> (Mitt.) M.Fleisch.	-	-	-	-	6.29	Rough mat
<i>Brotherella nictans</i> (Mitt.) Broth.	-	1.64	-	4.55	7.28	Smooth mat
<i>Brotherella henonii</i> (Duby) M.Fleisch.	-	-	-	4.13	1.99	Smooth mat
<i>Pylaisiadelpha yokohamae</i> (Broth.) W.R.Buck.	2.78	0.41	0.40	0.41	-	Smooth mat
<i>Sematophyllum subpinnatum</i> (Brid.) Britt.	-	-	-	0.83	3.64	Smooth mat

Appendix (continued)

<i>Taxa</i>	<i>SAA</i>	<i>SPA</i>	<i>SLA</i>	<i>ODMF</i>	<i>OLF</i>	<i>Life form</i>
Hypnaceae						
<i>Taxiphyllum taxirameum</i> (Mitt.) M.Fleisch.	-	3.28	1.59	0.83	0.33	Weft
Hylocomiaceae						
<i>Macrothamnium javense</i> M.Fleisch.	15.48	-	1.20	-	0.66	Weft
<i>Macrothamnium macrocarpum</i> (Reinw et Hornsch.) M.Fleisch.	0.79	12.30	-	6.20	8.28	Weft
<i>Macrothamnium setschwanicum</i> Broth.	5.56	-	17.93	-	-	Weft
Polytrichaceae						
<i>Pogonatum cirratum</i> (Sw.) Brid. subsp. <i>fuscatum</i> (Mitt.) Hyvoenen	-	-	-	-	0.66	Turf