Composition and Diversity Patterns of Epiphytic Bryophytes in Xishuangbanna Tropical Rainforest and Tropical Montane Evergreen Broad-Leaved Forest: Postprint

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Date: 2020-05-28T00:00:00+00:00

Abstract

This study aims to investigate and analyze trunk epiphytic mosses in two vegetation types—tropical rainforest and tropical montane evergreen broad-leaved forest—in Xishuangbanna, to reveal the composition, diversity patterns, and formation and maintenance mechanisms of epiphytic mosses within these two vegetation types. The study site was located in Mengla County, Xishuangbanna. For each vegetation type, 10 quadrats of 20 m × 20 m were established, and approximately 10 sample trees were selected in each quadrat for trunk epiphytic moss survey. The results showed that: (1) A total of 60 species belonging to 39 genera and 20 families were recorded in this survey, among which epiphytic mosses in tropical rainforest comprised 48 species in 33 genera and 19 families, while those in tropical montane evergreen broad-leaved forest comprised 19 species in 14 genera and 9 families, with 6 shared species; (2) The most dominant family in tropical rainforest was Neckeraceae, while that in tropical montane evergreen broad-leaved forest was Sematophyllaceae; (3) Tropical rainforest exhibited higher species richness, -diversity, and -diversity than tropical montane evergreen broad-leaved forest; (4) The coverage of epiphytic mosses differed significantly among hosts of different diameter classes and bark roughness, whereas species richness showed no significant difference; (5) The life forms of moss plants exhibited preferences for vegetation types, with pendant, fan, interwoven, and coarse mat types aggregating in tropical rainforest, while tufted, cushion, and fine mat types aggregating in tropical montane evergreen broad-leaved forest; (6) Direct ordination results indicated that host characteristics, particularly bark roughness, significantly influenced the composition and distribution of moss life forms. Tropical rainforest can provide more diverse microhabitats than tropical montane evergreen broad-leaved forest, thus fostering more species-rich epiphytic moss communities. Given that different vegetation types or host characteristics nurture mosses with different life form compositions, moss life forms can serve as an important indicator for future forest monitoring.

Full Text

Preamble

Composition and Diversity Patterns of Epiphytic Bryophytes in Tropical Rain Forest and Tropical Mountain Evergreen Broad-Leaved Forest in Xishuangbanna

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Funding: This study was supported by the 135 Program of CAS (2017XTBG-F03, 2017XTBG-F01), the National Natural Science Foundation of China (31670452), the Lancang-Mekong Cooperation (LMC) Special Fund, and the CAS “Light of West China” Program.

Abstract

This study investigated bole epiphytic bryophytes in tropical rain forest and tropical mountain evergreen broad-leaved forest in Xishuangbanna to reveal their composition, diversity patterns, and underlying mechanisms. The study site was located in Mengla County, Xishuangbanna, where ten 20 m × 20 m plots were established in each vegetation type. Approximately ten sample trees per plot were selected for bole epiphytic bryophyte surveys. The results showed: (1) A total of 60 species belonging to 39 genera and 20 families were recorded, including 48 species (33 genera, 19 families) in tropical rain forest and 19 species (14 genera, 9 families) in tropical mountain evergreen broad-leaved forest, with six shared species; (2) Neckeraceae was the dominant family in tropical rain forest, while Sematophyllaceae dominated in tropical mountain evergreen broad-leaved forest; (3) Tropical rain forest exhibited higher species richness, diversity, and diversity than tropical mountain evergreen broad-leaved forest; (4) Bryophyte coverage differed significantly among host trees of different diameter classes and bark roughness, while species richness showed no significant differences; (5) Bryophyte life forms demonstrated distinct preferences for vegetation types, with pendant, fan, weft, and rough mat types aggregating in tropical rain forest, while turf, cushion, and smooth mat types concentrated in tropical mountain evergreen broad-leaved forest; (6) Direct ordination revealed that host characteristics, particularly bark roughness, significantly influenced the composition and distribution of bryophyte life forms. Tropical rain forests provide more diverse microhabitats than tropical mountain evergreen broad-leaved forests, thus supporting richer epiphytic bryophyte communities. Given that different vegetation types and host characteristics harbor distinct life form assemblages, bryophyte life forms should be considered an important indicator for future forest monitoring and management.

Keywords: Xishuangbanna, biodiversity, epiphyte, life form, distribution pattern

Introduction

Bryophytes were among the first green plants to colonize land successfully from aquatic algal ancestors approximately 470–550 million years ago (Morris et al., 2018). In terms of species diversity, bryophytes represent the second largest group of higher plants after angiosperms and constitute a vital component of biodiversity (Crosby et al., 2000). Although bryophytes have evolved significantly in morphological structure and reproductive characteristics compared to green algae, their lack of differentiated roots (Ligrone et al., 2008), reliance on water and nutrient absorption through the gametophyte surface, dependence on water for sexual reproduction (Steinhorst & Kudla, 2017), and poikilohydric nature make them highly sensitive to climatic conditions and environmental change (Azuelo et al., 2011; Song et al., 2012; He et al., 2016; Shi et al., 2017). Species vary in their capacity to respond to environmental change (Willis & MacDonald, 2011; Jaeschke et al., 2013; Bocedi et al., 2014), and the combined effects of habitat fragmentation and climate change may cause substantial shifts in community composition and diversity (Mantyka-Pringle et al., 2015). In this context, bryophyte communities may exhibit pronounced changes (Frego, 2007; Sporn et al., 2010; Löbel et al., 2018).

Bryophyte life forms reflect morphological and structural characteristics shaped by long-term adaptation to specific habitats (Table 1) (Mägdefrau, 1982; Bates, 1998; Glime, 2017). As a survival strategy, bryophyte life forms are closely related to moisture and light conditions in the environment and serve as important indicators of environmental conditions (Bates, 1998; Oishi, 2009; Glime, 2017). Generally, cushion and turf types dominate in well-lit, dry environments, while dendroid, weft, pendant, and fan types typically occupy shaded, moist habitats. Mat types are common in relatively dry environments, with smooth mats preferring shaded conditions and rough mats occurring in well-lit environments (Bates, 1998; Glime, 2017; Löbel et al., 2018). Thus, bryophyte life forms are intimately linked to habitat environmental conditions, reflecting selective pressures and adaptive significance (Glime, 2017).

Bryophytes constitute an important component of epiphytic communities (Nadkarni, 1984). The assembly of epiphytic communities is influenced by dispersal capacity, geographic isolation, vegetation type, and host characteristics (Campos et al., 2006; Klimes et al., 2012). Different vegetation types create distinct internal environmental conditions that directly affect bryophyte species composition and distribution (Wang et al., 2012; Gehrig-Downie et al., 2013). Additionally, host trees provide various substrates and microhabitats within a single tree (Sanger & Kirkpatrick, 2016), and epiphytic community composition and abundance vary with host size, height, and bark characteristics (Song et al., 2015a; Wang et al., 2016; Patiño et al., 2018). For example, larger host diameter may indicate longer colonization time, greater available surface area, and higher microhabitat heterogeneity, while higher bark roughness typically implies stronger water absorption and retention capacity, potentially providing richer humus and colonization space for epiphytes (Sáyago et al., 2013; Wagner et al., 2015; Taylor & Burns, 2015). These host characteristics directly influence epiphytic bryophyte species and their life forms.

Xishuangbanna is part of the Eastern Himalaya and Indo-Myanmar biodiversity hotspot, representing a critical region for global biodiversity conservation (Myers et al., 2000; Tordoff et al., 2012; Corlett, 2014) and harboring China’ s largest tropical forest area (Zhu et al., 2015). Tropical rain forest is the main zonal vegetation in Xishuangbanna. Due to the mountainous plateau topography, a series of vertical zonal vegetation types have developed above the tropical rain forest, with tropical mountain (low mountain) evergreen broad-leaved forest—also known as monsoon evergreen broad-leaved forest—representing the primary mountain vegetation type (Zhu et al., 2015). However, human activities such as slash-and-burn agriculture, rubber plantation establishment, and understory economic cultivation are destroying forest vegetation across large areas, leading to rapid biodiversity loss (Zhu et al., 2015). Nevertheless, investigations of bryophyte diversity across different vegetation types in Xishuangbanna remain scarce (Song et al., 2015a; Shen et al., 2019), which is detrimental to future conservation efforts. Therefore, this study surveyed the species and life form composition and distribution patterns of epiphytic bryophytes in two typical vegetation types in Xishuangbanna to address: (1) What are the characteristics of epiphytic bryophyte composition and distribution patterns in the two vegetation types? (2) To what extent are these patterns influenced by host diameter at breast height (DBH) and bark roughness?

1.1 Study Area Overview

Xishuangbanna Dai Autonomous Prefecture (99°56 -101°50 E, 21°08 -22°36 N) is located in southern Yunnan Province, belonging to the southern extension of the Wuliang and Nushan mountain ranges of the Hengduan Mountains. The terrain is characterized by high surrounding areas and low central regions, dominated by mountains interspersed with broad valleys, ring-shaped low hills, and lowlands, creating a complex and highly undulating topography. The climate belongs to the western tropical monsoon type, primarily controlled by the Indian Ocean monsoon, with mean annual temperatures of 15.1–21.7 °C and annual precipitation of 1,193–2,491 mm. Precipitation is unevenly distributed temporally and spatially, with distinct dry and wet seasons—February being the driest month and July–August the wettest, with higher rainfall in the east than in the west. Fog is common in winter and spring, particularly from November to February when foggy days exceed 70% and fog precipitation can reach 0.1–0.3 mm·d ^{1}. Forest vegetation includes 32 typical formations belonging to seven major vegetation types: tropical rain forest, tropical seasonal moist forest, tropical monsoon forest, tropical mountain (low mountain) evergreen broad-leaved forest, tropical palm forest, warm coniferous forest, and bamboo forest (Zhu et al., 2015).

The tropical rain forest in Xishuangbanna develops under tropical monsoon climate conditions, representing a tropical rain forest at the limits of moisture, heat, and altitude. It is further divided into two subtypes: tropical seasonal rain forest distributed in valley rain forest margins and low hills below 800 m, which is relatively dry and seasonally variable compared to typical tropical rain forest; and tropical mountain rain forest occurring at the upper margin of seasonal rain forest, dominated by tropical species but mixed with subtropical tree species, showing transitional characteristics between tropical seasonal rain forest and southern subtropical monsoon evergreen broad-leaved forest in both ecological features and floristic composition. Tropical mountain evergreen broad-leaved forest refers to evergreen broad-leaved forests on non-limestone tropical mountains, where evergreen trees account for over 90% of both species number and individual count, creating a perennially green forest canopy (Zhu et al., 2015).

1.2 Sample Plot Setup and Survey Methods

This study was conducted in plots located in Mengla County, Xishuangbanna, managed by the Xishuangbanna Forest Ecosystem National Observation and Research Station. Two vegetation types—tropical rain forest and tropical mountain evergreen broad-leaved forest—were selected as study objects. Ten 20 m × 20 m plots were established in each vegetation type, with ten sample trees selected per plot. Sample trees were prioritized based on DBH > 20 cm, with smaller trees selected only when insufficient large trees were available. DBH and bark roughness information were recorded for each sample tree (Table 2). On each sample tree, a 20 cm × 20 cm grid (16 × 16 cells) was placed on the southwest-facing side at 1.5 m height to survey bole epiphytic bryophytes, recording species, life forms, and number of grid cells occupied (Song et al., 2015a).

DBH was measured at 1.3 m above ground level and classified into five diameter classes: 1 = <20 cm; 2 = 20–30 cm; 3 = 30–40 cm; 4 = 40–60 cm; 5 = 60 cm. Bark roughness was visually assessed following Male and Roberts (2005), using a nine-level scale: 1 = very smooth; 3 = smooth with cracks; 5 = shallow fissures; 7 = deep grooves; 9 = deeply undulating grooves; and 2, 4, 6, 8 as intermediate levels. Based on bryophyte life form classification standards (Glime, 2017) and field conditions, epiphytic bryophyte life forms in the two vegetation types were classified into seven types: fan, rough mat, smooth mat, pendant, weft, cushion, and turf. Species composition, life form classification, and frequency data for epiphytic bryophytes in both vegetation types are provided in the Appendix.

1.3 Specimen Identification and Nomenclature System

Bryophyte specimens were primarily identified using *Flora Yunnanica* Volumes 17-19 (Gao & Cao, 2000; Li, 2002, 2005). Unidentified species were verified by consulting relevant experts. Voucher specimens are stored in the Laboratory of Restoration Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. The Goffinet system (Goffinet, 2009) was adopted for arranging taxonomic units at family and genus levels.

1.4 Data Analysis

Since individual bryophyte numbers are difficult to measure, epiphytic bryophyte abundance was represented by coverage, calculated from the grid area occupied by each species. All data analyses were performed using R 3.6.1 (R Development Core Team, 2019).

1.4.1 Important Value Due to the unique characteristics of bryophytes, dominance measurement must consider both coverage and frequency. Therefore, the Important Value (IV) was calculated for dominant families, genera, and species using:

$$IV = \text{Relative Frequency} + \text{Relative Coverage}$$

where Relative Frequency (F) = frequency of a given epiphytic bryophyte / sum of frequencies of all epiphytic bryophytes, and Relative Coverage (C) = coverage of a given species / sum of coverage of all species.

1.4.2 Species Accumulation Curves Species accumulation curves were generated using the `specaccum` function in the vegan package in R 3.6.1 to assess whether sample size adequately represented actual epiphytic bryophyte species richness in the forests.

1.4.3 Diversity Indices , , and diversity indices were used to measure epiphytic bryophyte diversity in the two forest types:

diversity indices included mean species richness per plot (S), Margalef index (d), Shannon-Weiner index (H), and Simpson index (D):

$$d = \frac{S-1}{\ln N}$$

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

$$D = 1 - \sum_{i=1}^{S} P_i^2$$

where S = total number of epiphytic bryophyte species, N = sum of coverage of all species, and P_i = relative coverage of the i-th species.

diversity was measured using the Whittaker index:

$$\beta = \frac{\gamma}{\alpha}$$

diversity represented the total number of epiphytic bryophyte species in each forest type (Li et al., 2013). Diversity indices were calculated using the `alpha` function in the psych package in R (Revelle et al., 2018).

1.4.4 Between-Group Difference Tests

Differences in epiphytic bryophyte species and life form distribution patterns between the two vegetation types, as well as species richness and coverage across different DBH classes and bark roughness levels, were tested. Prior to analysis, data were subjected to Shapiro-Wilk normality tests and Bartlett' s homogeneity of variance tests. t-tests were used for data meeting both normality and homogeneity assumptions, non-parametric Pairwise Wilcoxon rank-sum tests and Kruskal-Wallis tests for non-normal data, and approximate t-tests for normal data with heterogeneous variances.

1.4.5 Ordination Analysis

Ordination analysis was performed to assess the influence of host DBH and bark roughness on the distribution patterns of epiphytic bryophyte species and life forms. The species data matrix consisted of plots as rows and bryophyte species or life form coverage as columns, while the environmental factor matrix comprised plots as rows and host characteristic factors as columns. Spearman correlation analysis using the `corr` function in the psych package was applied to host characteristic factors, retaining only the most strongly related factor when collinearity existed. Results showed no significant collinearity between the two host factors in this study.

Before ordination, Detrended Correspondence Analysis (DCA) was performed using the `decorana` function in the vegan package (Jari et al., 2019) to determine whether Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA) was appropriate. If the maximum gradient length among the first four

DCA axes was <3, RDA was selected; if >4, CCA was used; and if between 3–4, both were suitable. DCA results indicated CCA for species-host characteristics and RDA for life form-host characteristics. Monte Carlo permutation tests using the `permutest` function assessed the significance of explained variance, while the `envfit` function evaluated the significance of each host characteristic factor.

2.1 Species Composition of Epiphytic Bryophytes in the Two Vegetation Types

The survey recorded 60 epiphytic bryophyte species belonging to 39 genera and 20 families, including 48 species (33 genera, 19 families) in tropical rain forest and 19 species (14 genera, 9 families) in tropical mountain evergreen broad-leaved forest, with six shared species. Species accumulation curves (Figure 1 [Figure 1: see original paper]) showed that tropical rain forest species richness continued to increase, while the curve for tropical mountain evergreen broad-leaved forest approached an asymptote, indicating that sample size was adequate for the latter but additional sampling is needed to fully capture tropical rain forest bryophyte diversity.

Based on Important Values, the top three dominant families, genera, and species are shown in Table 3 . The three dominant families accounted for over 66% of total epiphytic bryophyte frequency and coverage, exceeding 86% in tropical mountain evergreen broad-leaved forest. Dominant families comprised 17 species (35.42% of total) in tropical rain forest and 10 species (52.63% of total) in tropical mountain evergreen broad-leaved forest, representing the main species groups. The top three dominant genera in tropical rain forest all belonged to the dominant family Neckeraceae, comprising five species (10.42% of total), while those in tropical mountain evergreen broad-leaved forest corresponded to its dominant families, comprising seven species (36.84% of total). Dominant species in both vegetation types fell within their respective top three families and genera, demonstrating strong representativeness.

2.2 Life Form Composition of Epiphytic Bryophytes

Tropical rain forest epiphytic bryophytes exhibited all seven life forms, with fan (15 species, 31.25% of total) and smooth mat (10 species, 20.83%) being most abundant. Tropical mountain evergreen broad-leaved forest had only five life forms, lacking fan and rough mat types, with smooth mat (9 species, 47.37%) and turf (4 species, 21.05%) being dominant. Across all DBH classes (Figure 2 [Figure 2: see original paper]) and bark roughness levels (Figure 3 [Figure 3: see original paper]), fan types were optimal in tropical rain forest, while smooth mat types dominated in tropical mountain evergreen broad-leaved forest.

2.3 Comparison of Species, Life Forms, and Host Characteristics

The Shannon diversity index was 1.538 for tropical rain forest and 1.357 for tropical mountain evergreen broad-leaved forest. Comparative analysis (Table 4) revealed significant differences in species richness ($P = 0.017$), Margalef index ($P = 0.003$), and bryophyte coverage across different DBH classes ($P = 0.007$) and bark roughness levels ($P = 0.005$).

2.4 Ordination Analysis Results

CCA ordination of bryophyte species and host characteristics (Figure 4 [Figure 4: see original paper]) showed that the first two axes explained 26.29% of species distribution variance ($P = 0.001$), indicating significant relationships with host DBH and bark roughness, with the latter having greater influence. Partial analyses revealed that DBH and bark roughness individually explained 13.15% ($r^2 = 0.950$, $P = 0.001$) and 13.10% ($r^2 = 0.855$, $P = 0.001$) of variance, respectively, suggesting roughly equal influence on species distribution.

RDA ordination of life forms and host characteristics (Figure 5 [Figure 5: see original paper]) showed that the first two axes explained 46.18% of life form distribution variance ($P = 0.001$), with the first axis accounting for 40.81%—five times more than the second axis (5.37%). Partial analyses indicated that DBH explained 2.78% ($r^2 = 0.612$, $P = 0.001$) while bark roughness alone explained 47.65% ($r^2 = 0.782$, $P = 0.001$), demonstrating that life form distribution was primarily controlled by bark roughness. Plot points clearly separated by vegetation type, with life forms showing distinct preferences: pendant, fan, weft, and rough mat types aggregated in tropical rain forest, while turf, cushion, and smooth mat types clustered in tropical mountain evergreen broad-leaved forest.

3.1 Diversity, Distribution Patterns, and Driving Factors

Bryophyte species richness in different forest types is closely related to air humidity and canopy density (Gradstein & Sporn, 2010). The dense canopy, high understory humidity, and low light conditions in tropical rain forests favor epiphytic bryophytes that rely on surface water absorption (Song et al., 2015b). The availability and heterogeneity of different microsites constitute the primary factors influencing forest bryophyte diversity and composition (Tina et al., 2009). Ódor et al. (2013) studied epiphytic bryophyte composition patterns and drivers in managed temperate forests, demonstrating high sensitivity to microclimate continuity (light, temperature, and humidity).

The higher and diversity in tropical rain forest indicates more variable community composition, reflecting greater habitat diversity that supports richer epiphytic bryophyte assemblages. Generally, larger host DBH and greater bark roughness support more epiphytic species and individuals (Wagner et al., 2015; Zhao et al., 2015; Wang et al., 2016). This study found significant relationships between host DBH, bark roughness, and bryophyte distribution, with significant coverage differences across DBH classes and bark roughness levels, but no significant differences in species richness. One possible explanation is that pioneer species establish dominant populations on limited bark surfaces, restricting colonization by other species. While species richness may not increase on large-diameter or rough-barked trees, these dominant populations accumulate over time, resulting in significant coverage differences. Gradstein & Culmsee (2010) similarly found that some bryophyte species prefer large DBH and rough bark, but species richness was not correlated with DBH and only weakly with bark roughness. Beyond DBH and roughness, other host characteristics including bark pH, water-holding capacity, and texture also influence epiphyte establishment (Ma et al., 2009; Song et al., 2011). Like other plants, epiphytic community composition and diversity patterns are shaped by combined effects of environmental factors, biotic interactions, and neutral processes (Götzenberger et al., 2012; Ovaskainen et al., 2017). Patiño et al. (2018) found that dispersal limitation (a neutral process) creates high community similarity at small spatial scales, with epiphytic species composition being very similar among nearby trees. Biotic interactions may also influence community assembly and species coexistence, though competition and coexistence mechanisms among epiphytes remain poorly understood (Rydin, 2009) and require further investigation.

3.2 Life Form Composition and Relationship with Host Characteristics

Bryophyte life forms represent adaptive responses to environmental conditions, and analyzing life form characteristics across habitats can reveal bryophyte-environment relationships (Kürschner, 2004). The RDA ordination clearly separated life forms between the two vegetation types: dendroid, weft, pendant, and fan types were more abundant in tropical rain forest, while cushion and turf types dominated in tropical mountain evergreen broad-leaved forest. Dendroid, weft, pendant, and fan types typically occur in shaded, moist environments, whereas cushion and turf types prefer well-lit, relatively dry conditions (Gradstein & Sporn, 2010; Glime, 2017), consistent with the understory microclimates of the two forest types and validating life forms as environmental indicators.

Several explanations have been proposed for these life form-environment relationships. Mat types' close substrate contact helps them withstand dry environments (Bates, 1998). In cushion types, peripheral shoots experience greater desiccation risk than central shoots, often growing less and creating the hemispherical profile (Bates, 1998). Turf types reduce shoot-atmosphere contact area and air movement between shoots, effectively decreasing water loss and adapting to relatively dry habitats (Wu, 1998). Physiologically, papillose leaf cells represent an evolutionary adaptation to dry conditions, occurring in 36.2% of turf species and conferring strong drought tolerance (Bates, 1998). Fan types create flat photosynthetic surfaces ideal for intercepting atmospheric moisture in humid environments, with characteristics including high cell wall elasticity, drought-resistant osmotic adjustment, low light saturation, and low photosynthetic compensation points that adapt them to shaded, moist conditions (Song et al., 2015b). Bryophyte life forms are strongly correlated with survival strategies (During, 1979; Bates, 1998; Kürschner et al., 1999), and analyzing dominant life forms across environments can improve understanding of community habitat conditions (Kürschner et al., 1999; Oishi, 2009; Glime, 2017).

RDA results also demonstrated that host characteristics, particularly bark roughness, significantly influence life form composition and distribution. Culberson (1955) considered bark factors the most important determinant of forest epiphytic community composition. Since epiphytic communities are primarily controlled by moisture and bark represents a dry substrate with low water content, bark roughness—which directly affects water-holding capacity—plays a decisive role and is a key factor explaining epiphytic composition and distribution (Barkman, 1958). As functional traits for environmental adaptation, life forms exhibit different adaptive characteristics on bark of varying roughness. Gradstein & Sporn (2010) found that smooth bark predominantly supported mat types, suggesting this is a successful strategy for establishment on smooth substrates. Life form composition and distribution effectively reflect microhabitat moisture and temperature conditions. Given that different forest types and host characteristics support distinct life form assemblages, bryophyte life forms should be considered an important indicator for forest monitoring.

Acknowledgments

We thank Dr. Ma Wenzhang from Kunming Institute of Botany, Chinese Academy of Sciences, for assistance with specimen identification; the Xishuangbanna Forest Ecosystem National Observation and Research Station for fieldwork support; and the CAS-Queensland Biotechnology Cooperation Project (GJHZ1130) for providing background data for some sample plots (Table 2).

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Appendix

Epiphytic Bryophyte Species, Life Forms, and Occurrence Frequency Information for Two Typical Vegetation Types in Xishuangbanna

[The appendix table content would be preserved here with the same structure as in the original, showing species names, life forms, occurrence frequencies, diameter classes, and bark roughness values for each taxon.]

Note: Figure translations are in progress. See original paper for figures.

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