

Microhabitat Preferences of Epiphytic Bryophytes along Host Vertical Gradients in Dipterocarp Tropical Rainforest and Their Indicator Role: Postprint

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Abstract

Epiphytic bryophytes play crucial ecological roles in maintaining water and nutrient cycles within forest ecosystems. However, due to limitations in access technology, the diversity of epiphytic bryophytes and their distribution patterns in the three-dimensional space of forest canopies remain poorly understood. This study, for the first time, employed a canopy crane to investigate epiphytic bryophytes on 69 trees across 13 vertical heights in a dipterocarp tropical rainforest plot of the Xishuangbanna National Nature Reserve. By enumerating bryophyte species and their life forms at different vertical heights, and utilizing canonical correspondence analysis (CCA) and indicator species analysis, we examined the microhabitat preferences and indicator significance of epiphytic bryophytes along the host vertical gradient in this region. The results revealed that a total of 90 epiphytic bryophyte species belonging to 25 families and 60 genera were recorded on the 69 trees in this dipterocarp tropical rainforest, with Lejeuneaceae exhibiting the highest species richness, accounting for 25.6%. Across the 13 vertical heights, three ecological types were delineated: sun-loving bryophytes (at vertical heights >45 m on scattered emergent trees), shade-loving bryophytes (on tree trunks <15 m), and widespread bryophytes (typically distributed broadly across various host vertical heights with wide niches). Furthermore, 17 bryophyte indicator species with special microhabitat preferences were identified ($\text{IndVal} = 0.7$, $P < 0.05$). With increasing host vertical height, the proportions of fan-type and interwoven-type bryophytes decreased, the proportion of pendant-type bryophytes initially increased then decreased, while the proportions of fine-mat and coarse-mat bryophytes increased. Atmospheric humidity, vapor pressure, diameter at breast height (DBH), and bark roughness exerted significant influences on the distribution preferences of epiphytic bryophyte life

forms. In conclusion, epiphytic bryophytes along the host vertical gradient display distinct response patterns to microenvironmental changes in terms of life form and morphological structure, whereas bryophyte communities of the same ecological type share similar adaptation mechanisms. Therefore, epiphytic bryophyte species or life forms with pronounced microhabitat preferences can serve as effective indicator materials for monitoring and managing changes in forest canopy habitats.

Full Text

Habitat Preferences of Epiphytic Bryophytes Along the Vertical Gradient and Their Indicator Functions in the Tropical Dipterocarp Rain Forest

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Abstract: Epiphytic bryophytes play an important role in maintaining water and nutrient cycles in the forest ecosystem. However, diversity and distribution patterns of epiphytic bryophytes in forest canopies are understudied because of the limitations of canopy access techniques. Epiphytic bryophytes and their life-forms were investigated from 69 trees in 13 vertical segments using a canopy crane in the tropical dipterocarp rain forest in Xishuangbanna National Nature Reserve. Canonical correlation analysis (CCA) and the species indicator method were applied to analyze the microhabitat preferences of the epiphytic bryophytes and to find indicators along the vertical gradient of the hosts. The main results are as follows: 90 species were recorded in the study area, belonging to 60 genera and 25 families. Lejeuneaceae was the most species-rich family, representing 25.6% of all bryophyte species recorded. Three special ecological types were extracted from the 13 vertical segments, including sun-loving bryophytes (> 45 m tree trunks), shade-loving bryophytes (< 15 m tree trunks) and generalist bryophytes (usually distributed in various host heights with a broad niche width). Seventeen bryophyte species ($\text{IndVal} > 0.7$, $P < 0.05$) were selected as indicators for specific vertical segments. With the increase in the height sampled, the proportion of species with fan and weft life-forms decreased, the proportion of pendant life-forms increased first and then decreased, while the proportion of smooth mat and rough mat life-forms increased. The relative humidity, vapor pressure, tree size and bark roughness have significant

influences on the distribution preferences of epiphyte life forms. In conclusion, epiphytic bryophytes show different life-form compositions and morphological structures in response to changes in the microenvironment along the vertical gradient of hosts, while bryophytes assembled in the same microhabitat usually have similar adaptation mechanisms. The epiphytic species or life-forms with obvious preferences for specific microhabitats can be used as indicators during the monitoring and management of habitat changes in the forest canopy.

Key words: canopy, epiphytes, vertical distribution, habitat preference, indicator species

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Introduction

The tropical forest canopy represents one of the most species-rich habitats in the biosphere (Stork, 2007). Its unique environmental conditions nurture extremely rich epiphytic plants, particularly epiphytic bryophytes. Epiphytic bryophytes, defined as bryophytes growing on the bark of trees or shrubs (Smith, 1982), play crucial ecological roles in maintaining water and nutrient cycles in forest ecosystems (Ah-Peng, 2017; Shi, 2017) and make substantial contributions to the formation and maintenance of canopy biodiversity and habitat diversity, thus holding high ecological conservation value. Due to their diminutive size, lack of cuticle, and direct exposure to air, epiphytic bryophytes are extremely sensitive to habitat changes and can serve as bio-indicators of forest ecosystem health (Glenn et al, 1988; Wu et al, 2002).

The complexity of tropical canopies and diversification of microhabitats have fostered abundant epiphytic bryophytes, with tropical canopies hosting approximately 25-30% of global bryophyte species (Gradstein & Pócs, 1989). Current research on tropical epiphytic bryophytes has primarily focused on tropical America and Africa (Gradstein & Pócs, 1989; Frahm & Gradstein, 1991; Wolf, 1993; Kürschner & Parolly, 1998; Holz et al, 2002), with fewer studies conducted in tropical Asia (Kürschner, 1990; Frey et al, 1990; Ariyanti et al, 2008; Sporn et al, 2009, 2010). Asian tropical rainforests not only harbor bryophyte flora distinct from those of tropical America and Africa but also contain the most

families and genera (Buck & Thiers, 1898; Gradstein & Pócs, 1989). Among these, dipterocarp tropical rainforests represent the tallest tropical forest plant communities in the world (Raes et al, 2014). The dipterocarp tropical rainforest in Xishuangbanna was not discovered until 1975, attracting considerable attention from botanists (Zhu, 2000). This forest is dominated by the nationally protected plant *Parashorea chinensis*.

As scattered giant trees, *P. chinensis* reaches heights of 40-70 m (Tang et al, 2008), nearly twice the height of lowland rainforests in tropical America (Dislich & Mantovani, 2016), providing ample substrate and living space for epiphytic plants (Engemann et al, 2016). Moreover, light, temperature, and water availability change dramatically along the vertical gradient within the forest (Szarzynski & Anhuf, 2001), creating heterogeneous microhabitats for epiphytes (Woods et al, 2015). Morphologically diverse bryophytes can retain moisture through various adaptations such as reducing air resistance, increasing thickness of leaf margin cells, providing capillary systems, and mutual protection (Glime, 2013), thereby adapting to the gradient microhabitat changes from tree base to canopy top. However, studies on epiphytic bryophyte preferences along host vertical heights and their indicator functions for canopy habitats remain scarce.

Due to limitations in canopy access techniques, surveys of epiphytic bryophytes have been largely restricted to trunk areas below 2 m (Slack, 1976; Song et al, 2011; Lowman & Schowalter, 2012). In recent years, the application of canopy cranes has broken through research bottlenecks (Mitchell et al, 2002), greatly advancing understanding of canopy habitats and their biodiversity. By the end of 2016, 11 canopy cranes had been established abroad, covering approximately 11.7 hm² of forest area, with five located in tropical forests (Wu et al, 2016). Under the “Canopy Biodiversity Monitoring Network” of the China Biodiversity Monitoring and Research Network (Sino BON) (Ma, 2015, 2016), China has built seven canopy cranes in different forest types (six completed, two under construction) (Nakamura et al, 2017). Among these, the world’s tallest canopy crane has been constructed in the dipterocarp tropical rainforest of Xishuangbanna, providing solid hardware support for canopy epiphyte diversity research (Wu et al, 2016). Although canopy cranes have been deployed across temperate, subtropical, and tropical forests worldwide, only the Wind River crane in the United States has been used to study non-vascular plant diversity and spatial distribution (Wu et al, 2016).

This study represents the first systematic investigation of epiphytic bryophyte composition and distribution patterns in the canopy crane plot of Xishuangbanna dipterocarp tropical rainforest. We examined epiphytic bryophyte preferences along host vertical gradients and their potential influencing factors, revealed response and adaptation mechanisms to microenvironmental changes, and identified indicator species for special microhabitats, providing scientific basis for bryophyte conservation and forest resource management.

1. Study Area

The Xishuangbanna National Nature Reserve (101°35 E, 21°36 N), located on the northern edge of Southeast Asian tropical rainforests, possesses China's largest and most concentrated tropical rainforest and belongs to the Indo-Burma biodiversity hotspot (Mittermeier et al, 2004). Within this region, the Chinese Academy of Sciences established a canopy crane in 2014 at the foot of Zebra Mountain in Bubeng Village, Mengla County, Xishuangbanna Dai Autonomous Prefecture. The crane covers approximately 1 hectare of forest area, with a tower height of 81 m and an arm length of approximately 60 m. The central coordinates are 101°34 56.154 E, 21°37 4.467 N, occupying a circular forest plot with a radius of 56.4 m.

The region belongs to the northern tropical monsoon climate zone, primarily controlled by the southwest monsoon, with an average annual temperature of approximately 21°C, high temperatures year-round without frost, annual rainfall of approximately 1500 mm, average annual relative humidity of 86%, and distinct wet and dry seasons (Cao et al, 2006; Zhu et al, 2006).

The tropical *Parashorea chinensis* forest can be divided into upper, middle, and lower layers (Zhu, 2000). In this tropical plot, upper canopy trees (height >30 m) receive the strongest light conditions, mainly including *Parashorea chinensis*, *Sloanea tomentosa*, *Canarium album*, and *Pometia tomentosa*. Phanerophytes with heights between 40-60 m are called scattered giant trees (Zhu, 2000). Middle canopy trees (16-30 m) form the community's closed canopy layer under moderate light conditions, primarily composed of *Diospyros atrotricha*, *Ficus langkokensis*, *Litsea dilleniifolia*, and *Barringtonia fuscarpa*. Lower canopy trees (6-16 m) receive the weakest light intensity, mainly including *Pittosporopsis kerrii*, *Baccaurea ramiflora*, *Diospyros xishuangbannaensis*, and *Cleidion brevipetiolatum*.

2.1 Methods

Field surveys of epiphytic bryophytes were conducted from April to May 2017. We investigated 69 trees in the plot, including 20 upper canopy trees, 25 middle canopy trees, and 24 lower canopy trees. Host characteristics are shown in Table 1. This study primarily utilized the canopy crane in the dipterocarp tropical rainforest plot and specially designed telescopic tools to collect bryophytes on middle and upper canopy trees taller than 10 m, while using long ladders to assist in collecting bryophytes on trunks below 10 m. Within each plot, we randomly selected tree species without severe damage from each canopy layer.

For each selected lower (U1-U4) and middle (S1-S4) canopy tree, we divided the trunk from base to canopy top into four vertical zones: U1(S1), trunk base to 2 m below trunk; U2(S2), lower trunk; U3(S3), upper trunk; U4(S4), entire canopy from the first main fork to canopy top (Sporn et al, 2010). Upper canopy trees were divided into six vertical zones due to their complex branching structure: C1, trunk base to 2 m below trunk; C2, lower trunk; C3, upper trunk; C4, inner

canopy; C5, middle canopy; C6, outer canopy (Johansson, 1974). A 20 cm × 20 cm sampling frame was used to collect samples on the windward (southwest) and leeward (northeast) sides of each vertical zone, with two samples taken from upper and lower positions each, totaling four samples per vertical zone on each trunk (sampling area of 4 × 400 cm² per vertical zone). Each zone in the canopy was sampled 4-6 times using different sized frames according to branch diameter class, selecting branches on upper and lateral sides in each cardinal direction as much as possible (total sampling area of 1600 cm² per zone).

Table 1 Description of host traits

Host type	Number	DBH (cm)	Tree height (m)	Bark roughness
Upper trees				
Middle trees	25			
Lower trees				

Host DBH data were provided by the Xishuangbanna Forest Ecosystem National Observation and Research Station. Tree height (HT) and canopy height (HC) were measured using a 100-meter tape. The height of each vertical zone on a tree refers to the distance from ground to the middle position of each zone, calculated using the following equations: $H_{base} = 2$, $H_{trunk} = HT - HC - 2$, $H_{lower_trunk} = 1/4(HT - HC - 2) + 2$, $H_{upper_trunk} = 3/4(HT - HC - 2) + 2$, $H_{inner_canopy} = (HT - HC) \times 1/3 \times 1/2$, $H_{middle_canopy} = (HT - HC) \times 1/2$, $H_{outer_canopy} = (HT - HC) \times 5/6$. To compare and quantify tree zone heights, we transformed vertical zone height values into 13 vertical heights ($H1=1-5$ m, $H2=6-10$ m, $H3=11-15$ m, $H4=16-20$ m, $H5=21-25$ m, $H6=26-30$ m, $H7=31-35$ m, $H8=36-40$ m, $H9=41-45$ m, $H10=46-50$ m, $H11=51-55$ m, $H12=56-60$ m, $H13=61-65$ m). Bark roughness was classified using the 1-9 scale of Male and Roberts (2005) (Figure 4 [Figure 4: see original paper]: 1 = very smooth; 3 = smooth with cracks; 5 = shallow folds; 7 = deep cracks; 9 = surface with numerous uneven fissures; while 2, 4, 6, 8 represent intermediate levels between adjacent grades).

Microclimate data including air temperature (°C, model HMP155A), relative humidity (%RH, model HMP155A), photosynthetically active radiation (PAR, $\mu\text{mol}/\text{m}^2 \cdot \text{s}$, model SQ-311), wind speed (m/s, model CSAT3), and air pressure (kPa, model CS106) were monitored in real-time and recorded hourly by eight microclimate systems along the crane's vertical gradient. However, due to anomalies in some data during the experimental period, we only used microclimate data from June-July 2017 (61 days) at heights of 1.4 m, 23.6 m, 47.2 m, 55.2 m, and 62.1 m on the Bubeng crane. Since vapor pressure is more meaningful for explaining bryophyte community distribution, air pressure was converted to vapor pressure using the Goff-Gratch equation.

Bryophyte life forms in this region can be classified into seven types: fan, smooth mat, rough mat, pendant, short turf, tall turf, and weft (modified from Mägde-

frau 1982). All bryophyte specimens in this study were identified by the authors, except for a few difficult specimens that were identified with expert assistance. Voucher specimens are stored in the Laboratory of Biodiversity Research Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

2.2 Data Processing

All statistical analyses were performed using R version 3.4.3 (<http://www.r-project.org>) and OriginPro 9.0. We calculated the frequency of each species in each vertical zone. To ensure reliable results, low-frequency occasional species (41 species) were excluded, meaning bryophyte species that appeared only once or twice in each of the 13 vertical heights were not included in the statistics. Our dataset consisted of vertical zone-bryophyte data (each row representing a vertical zone, each column representing a bryophyte species or life form) and vertical zone-environmental factor data (each row representing a vertical zone, each column representing an environmental factor). Environmental factors included climatic factors (air temperature, relative humidity, PAR, wind speed, and vapor pressure) and host characteristic factors (DBH, zone height, and bark roughness).

Spearman correlation analysis was used to compare correlations among environmental factors (Table 2). Atmospheric humidity was significantly correlated with air temperature, PAR, wind speed, and tree height (correlation coefficient >0.6 , $P < 0.05$). Since atmospheric humidity is most closely related to bryophyte physiology, it was retained while other correlated factors were removed. Finally, atmospheric humidity, vapor pressure, DBH, and bark roughness were selected as environmental factors for ordination analysis. We used canonical correspondence analysis (CCA) in the vegan package (Oksanen et al, 2017) to analyze relationships between epiphytic bryophytes and their life forms with potential driving factors. The only tall turf life form distributed in H6 and H7 was not shown in the CCA diagram due to its low frequency.

Based on the CCA diagram showing bryophyte community preferences in vertical zones (H1-H3 zones, H4-H8 zones, and H9-H13 zones), we used the `indval` function in the `labdsv` package (Roberts, 2016) in R to calculate `IndVal` values (Duf rene & Legendre, 1997) for each epiphytic bryophyte to identify indicators for special habitats, using `IndVal` >0.7 as the criterion for indicator species (Li, 2001).

Table 2 Spearman correlation matrix among the eight environmental factors

Atmospheric temperature	PAR	Wind speed	Vapor pressure	Bark roughness	DBH	Tree height
Atmospheric humidity	0.997	PAR	Wind speed	Vapor pressure	Bark roughness	DBH
Tree height						

Note: Correlation coefficients with $P < 0.01$ are shown in bold.

Table 3 The vertical segment preference, life form, habitat type, and indicator values (IndVal) of epiphytic bryophytes

[Table content showing species names, life forms, vertical distribution preferences, and IndVal values]

Note: H1-H13 represent the heights of the 13 vertical segments; species with IndVal 0.7 were selected as indicator species; $P < 0.05$ indicates statistical significance of IndVal.

3.1 Taxonomic Distribution of Epiphytic Bryophytes

A total of 90 epiphytic bryophyte species belonging to 60 genera and 25 families were recorded from 316 vertical zones across 13 vertical heights on 69 trees in the study plot. Among these, liverworts comprised 37 species, 19 genera, and 6 families, while mosses comprised 53 species, 41 genera, and 19 families. Lejeuneaceae was the dominant family, with its species accounting for 25.6% of all bryophyte species recorded, followed by Meteoriaceae (8.9%) and Frullaniaceae (6.7%).

3.2 Composition of Liverworts and Mosses and Bryophyte Life Forms

Figure 1 [Figure 1: see original paper] Percentage of liverworts and mosses in the 13 vertical segments

Figure 2 [Figure 2: see original paper] **Percentage of life forms in the 13 vertical segments**

The proportion of liverworts showed a trend of first increasing (H1-H5), then decreasing (H5-H10), and finally increasing again (H11-H13) with increasing vertical height (Figure 1). Seven life forms of epiphytic bryophytes were recorded in this forest plot (Figure 2). With increasing host vertical height, fan life forms gradually decreased (all >0.5 between H1-H3 zones), pendant life forms first increased (H1-H8, reaching maximum at H8) then decreased (H9-H13), while mat life forms (both smooth and rough) showed a pattern of gradual increase (H1-H6), decrease (H7-H8), and then increase again (H9-H13).

3.3 Microhabitat Preferences of Epiphytic Bryophytes Along Vertical Gradients

The CCA analysis of environmental factors and bryophyte species (Figure 3 [Figure 3: see original paper]) revealed that epiphytic bryophyte communities could be divided into three distinct groups: H1-H3 zone communities, H4-H8 zone communities, and H9-H13 zone communities. The H1-H3 trunk zones were highly correlated with atmospheric humidity and mainly comprised 20 epiphytic bryophyte species including *Rhynchosegium inclinatum*, *Claopodium prionophyllum*, *Isopterygium minutirameum*, *Pinnatella ambigua*, *Fissidens holianus*, *Homaliodendron microdendron*, and *Exostratum blumii* (Table 2). Vertical zones higher than 45 m (>H9) were negatively correlated with atmospheric humidity and mainly comprised six bryophyte species: *Frullania ericoides* and *F. fuscovirens* from Frullaniaceae, *Acrolejeunea sandvicensis* and *Mastigolejeunea auriculata* from Lejeuneaceae, and *Groutiella tomentosa* and *Erythrodonium julaceum* from other families (Table 2). The 24 epiphytic bryophyte species in H4-H8 zones showed no obvious preference for atmospheric humidity.

Seventeen epiphytic bryophyte species were identified as indicators for different vertical zones (Table 1). Among them, 16 indicator species were found in H1-H3 zones: *Claopodium prionophyllum*, *Homaliodendron microdendron*, *Plagiochila trabeculata*, *Plagiochila nitens*, *Haplohymenium triste*, *Radula javanica*, *Caduciella mariei*, *Trichosteleum sitgmosum*, *Pinnatella ambigua*, *Isoclatiella surcularis*, *Leucophanes octoblepharioides*, *Cheilolejeunea trapezia*, *Plagiochila parviramifera*, *Mitthyridium flavum*, *Plagiochila furcifolia*, and others. *Groutiella tomentosa* was the only indicator species for H9-H13 zones.

3.4 Main Driving Factors Influencing Bryophyte Preferences Along Vertical Gradients

CCA results indicated that the four environmental factors collectively explained 16.98% of the variation in the distribution patterns of the seven bryophyte life forms. Monte Carlo permutation tests showed that the effects of these four environmental factors on bryophyte life form distribution patterns were significant ($P = 0.011$), confirming the reliability of the CCA results. Atmospheric

humidity, vapor pressure, DBH, and bark roughness all significantly influenced bryophyte life form distribution ($P = 0.001$).

The CCA ordination results (Figure 4 [Figure 4: see original paper]) showed that weft, fan, and short turf life forms were highly positively correlated with atmospheric humidity and vapor pressure, mainly distributed in H1-H3 zones. Rough mat life forms were positively correlated with DBH and bark roughness, concentrated in zones higher than H9. Pendant life forms were mainly distributed between H6-H8 zones, while smooth mat life forms were widely distributed in zones above H4.

4. Conclusion and Discussion

Similar to early studies by Gradstein and Pócs (1989), the families we surveyed—Lejeuneaceae, Frullaniaceae, Plagiochilaceae, Radulaceae, Meteoriaceae, Pterobryaceae, Neckeraceae, Orthotrichaceae, Fissidentaceae, Calymperaceae, Hypnaceae, and Sematophyllaceae—dominate typical tropical rainforest families. Lejeuneaceae held absolute dominance as the most species-rich family in this tropical forest plot, consistent with findings from other tropical regions (Cornelissen & Streege, 1989; Sporn, 2010; Oliveira et al, 2016).

The proportion of liverworts showed a pattern of first increasing, then decreasing, and increasing again with vertical height, indicating that liverworts are more abundant on upper trunks and outer canopy regions, suggesting a preference for better-lit vertical zones. Some liverworts have small lobed ventral leaves that help store water (Kelly, 2004), and closely imbricate lateral leaves can reduce water evaporation under strong light. Some sun-loving moss species from the Orthotrichaceae family distributed on canopy branches also tend to be imbricate under high temperature and light conditions to slow water loss and protect stems from damage (Scott, 1982).

Bryophytes distributed above H9 zones were negatively correlated with humidity (Figure 4), while PAR was highly correlated with humidity, meaning these bryophytes were highly positively correlated with PAR. Most bryophytes in this region showed red or reddish-brown leaves, with these pigments providing photoprotection through photochemical pathways (Krinsky, 1968). For example, *Frullania ericoides* from Frullaniaceae, mainly distributed in the upper canopy (>H9), appears reddish-brown, while *F. musciola* appears reddish. Furthermore, the higher the vertical zone where colored bryophytes occur, the darker their color (Cornelissen & Streege, 1989); for instance, the reddish-brown color of *F. ericoides* in H12 and H13 zones is darker than that of the same species in H6 or H4 zones.

In tropical rainforests, cryptogamic epiphytes are extremely important as ecological indicators (Gradstein et al, 2001). Holz and Gradstein (2005) noted that their distribution patterns in forests reflect differences in microhabitat light, temperature, moisture, and substrate conditions. This aligns with our findings: bryophytes such as *Claopodium prionophyllum*, *Homaliodendron microdendron*,

and *Plagiochila trabeculata* frequently occur in tree base and lower trunk regions, indicating shady, humid understory habitats, while *Groustiella tomentosa* prefers the canopy crowns of scattered giant trees, serving as an optimal indicator for bright, dry canopy habitats.

Previous studies by Holz and Gradstein (2005) used bryophyte indicator species to indicate three different forest types. We pioneered the application of the species indicator method to epiphyte habitat preferences along host vertical heights, which is more statistically meaningful and reflects the indicator functions of epiphytic bryophytes for special microhabitats.

Based on the ecological adaptation characteristics of epiphytic bryophytes along vertical heights, we classified epiphytic bryophyte communities into three ecological types: sun-loving bryophytes, shade-loving bryophytes, and generalist bryophytes. Sun-loving bryophytes (mainly distributed in zones above H9, i.e., >45 m on scattered giant trees) dominate the upper canopy and adapt to strong sunlight. Shade-loving bryophytes (restricted to zones below H3, i.e., <15 m on lower canopy trees) inhabit lower trunk regions and lower canopy trees, preferring humid, cool habitats. Generalist bryophytes (typically distributed across 0-70 m, i.e., in more than three discontinuous height zones) have broad niches along vertical trunks. This classification is similar to previous results based on frequency distribution in Johansson zones (Cornelissen & Streege, 1989; Acebey, 2003), but our study provides more direct evidence for classifying ecological types of epiphytic bryophytes in dipterocarp tropical forests using quantitative height data.

With increasing host vertical height, weft and fan life forms decreased, while smooth mat and rough mat life forms increased, reflecting gradient changes in light and moisture conditions along the vertical axis. The compact, closely appressed structure of small, flat smooth mat life forms helps reduce water loss to cope with dry, bright microenvironments, thus these bryophytes mainly occur on trunks above 20 m (>H4). Fan and weft life forms mainly inhabit humid lower zones (H1-H3) (Bates, 1998). Short and tall turf life forms showed different microhabitat preferences: short turf life forms mainly occurred on trunks in H2 and H3 zones, while tall turf life forms mainly occurred on horizontal or forked canopy branches in H6 and H7 zones (Sporn et al, 2010). Pendant life forms mainly occurred on trunks in H7 and H8 zones, possibly because the middle canopy layer at these heights has wind and fog, facilitating direct absorption of rainwater and fog moisture (Glime, 2013), while dense leaves of middle canopy trees block some sunlight to avoid direct light damage. Additionally, pendant bryophytes typically have papillose structures on cell walls that help reflect intense sunlight to reduce water loss (Yang, 2008). Rough mat life forms were positively correlated with DBH and bark roughness, likely because these bryophyte communities tend to form compact cushions on trunks with larger surface areas and rougher bark, effectively reducing water evaporation and improving water retention capacity to adapt to dry, hot microenvironments (Wu, 1998). The changes in bryophyte life form composition along host vertical gradi-

ents are consistent with findings from tropical forests in Indonesia by Sporn et al (2010), reflecting bryophyte response and adaptation strategies to hydrothermal conditions.

In summary, epiphytic bryophyte life forms and morphological structures show different response patterns to microenvironmental changes along host vertical gradients (e.g., differentiation between sun-loving and shade-loving species), while bryophytes assembled in the same microhabitat share similar adaptation mechanisms (e.g., water retention and strong light resistance mechanisms in sun-loving species). The distribution patterns of epiphytic bryophytes along vertical gradients and their microhabitat preferences likely result from long-term adaptation and evolution to heterogeneous canopy habitats. Therefore, epiphytic bryophyte species or life forms with obvious preferences for specific microhabitats can serve as effective indicator materials for monitoring and managing forest canopy habitat changes.

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