



Assembly mechanisms of epiphyte communities  
in a lowland tropical forest (Yunnan, SW China):  
distribution patterns, microclimatic drivers,  
and conservation

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Ting Shen  
April 2023

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Doctor in Sciences at University of Liege, Belgium.





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**Assembly mechanisms of epiphyte communities  
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distribution patterns, microclimatic drivers,  
and conservation**

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Institute of Botany,  
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April 2023

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A tree frog (*Rhacophorus Kio*) is sunbathing  
in the top of a tree (*Parashorea chinensis*).



Dedicated to me, who is engaged in research  
on Canopy Ecology.

by Wen Yang.

*To me,*

*love the life you live,*

*live the life you love.*

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## **Abstract**

Forest canopy, known as the "last frontier of biology", harbours approximately 40% of the world's terrestrial biodiversity, making it one of the most species-rich yet least-known habitats in the biosphere. Forest canopies function as typical examples of habitat islands, characterized by a range of micro-niches that segregate along sharp vertical gradients, the isolation of host trees from each other, and the variation of host trees over time during their ontogenetical development. Epiphytes therefore offer an ideal framework to test the contributions of environmental filters, biotic interactions and dispersal limitations to community assembly and species coexistence at fine spatial scales. While the vertical structures of epiphyte communities and, to a lesser extent, associated variations in microclimatic conditions, have long been documented, no analysis has examined the relationship between microclimatic variation and species composition in a spatially explicit framework due to the unavailability of high-resolution microclimatic data. The development of a network of canopy cranes, coupled with recent advances in microclimatic modelling, opens an avenue of research for an enhanced understanding of the ecological functioning of forest canopies.

In order to examine how environmental variation in time and space impacts the distribution and diversity of epiphytes at different nested spatial scales, I took advantage of a tropical canopy crane to document the distribution of bryophyte and vascular epiphytes, record and model spatiotemporal variation of microclimatic, light and photosynthetically active radiation in a 1.44 ha tropical rainforest, Yunnan, SW China. More specifically, the aims are to: (1) Determine whether variations in light, microclimatic conditions and host tree size affect the variation in species composition and phylogenetic structure of epiphytic communities, and hence, assess the contribution of environmental filtering, phylogenetic constraints and competition to community assembly; (2) Disentangle the contribution of ecological factors, dispersal limitations and biotic interactions to epiphytic species distributions; (3) Integrate these results to determine whether we can evaluate the factors that predict epiphyte species richness and abundance based on site-specific and tree-specific features, in order to provide a scientific basis to identify key drivers for the conservation and management of epiphytes in forest ecosystems.

Generalized Dissimilarity Models implemented to analyse the relationship between taxonomic and phylogenetic turnover among epiphytic communities, host-tree characteristics and microclimatic variation, highlighted the crucial role of microclimates in determining the composition and phylogenetic structure of epiphytic communities. The analyses evidenced the

role of phylogenetic niche conservatism in community assembly, raising concerns about the evolutionary capacity of epiphyte communities to adapt to climate change.

Community modelling analyses revealed that niche preference explains more than 78% of the non-random species pairs formed by epiphytic bryophytes. Biotic interactions contributed less than 20% of the observed co-occurrence patterns, with a strong prevalence of facilitation over competition. The results suggest that epiphytic bryophyte community composition is primarily driven by niche-based processes, whose importance increases with niche complexity and diversity. Biotic interactions play a secondary role, with a very marginal contribution of competitive exclusion. This challenges the idea that competition would be important enough to have a negative impact on the accumulation of species richness on trees following an optimum on middle age trees. The results further suggest that biotic interactions vary depending on lineages and life forms, facilitation prevailing among species from the same lineage and life form and competition among species from different lineages and life forms.

Finally, I integrated these results to evaluate the factors that predict epiphyte species richness and abundance based on site-specific and tree-specific features. The results confirm the utmost importance of large trees with emergent canopies for the conservation of the epiphytic flora, but also indicate that epiphytic diversity assessments in tropical forests must also include small understorey trees, which should be further considered for conservation. The importance of the micro-climatic conditions that prevail at the level of each individual host tree further points to the necessity of maintaining a buffer zone around large host trees targeted for conservation.

## 摘要

林冠被称为“最后的生物学前沿”，蕴含了全球 40% 的陆地生物多样性，是全球生物圈物种丰富度极高却最鲜为人知的生境之一。林冠宿主树之间彼此独立，在功能上类似于“生境岛”；它们在垂直梯度上提供显著分化的微生境，同时，微生境的特征随宿主树个体发育过程的不同而不断变化。因此，附生植物群落提供了一个在精细空间尺度上检验环境过滤、生物相互作用和扩散限制对植物群落构建与物种共存理想框架。尽管相关学者对林冠附生植物群落的垂直结构及其成因已进行初步探究，但由于缺乏有效进入林冠的技术手段和高分辨率的微气候数据，目前尚无法定量解析附生植物群落的三维空间结构及其维持机制。近年来，全球林冠塔吊网络的建立以及微气候模型的快速发展，为增进对森林冠层生态功能的理解提供了新机遇。

为了探究环境要素的时空演变过程如何影响不同嵌套空间尺度上的附生植物的分布格局和多样性，本研究利用在中国西南地区云南省的一个 1.44 公顷热带雨林样地中建立的林冠塔吊，记录了附生苔藓和附生维管植物的分布，收集和模拟了微气候、光照和光合有效辐射的时空变化。具体而言，本研究目的是：(1) 通过验证微气候和宿主树年龄的变化是否影响了附生植物群落的物种组成和系统发育结构，评估了环境过滤、系统发育限制和竞争对群落构建的贡献大小；(2) 分解生物和非生物驱动因子对附生植物物种分布的贡献比率；(3) 整合这些结果确认了基于样地特征和宿主树特点是否可以有效评估附生植物物种多样性和丰度，为森林生态系统中附生植物的保护和科学管理提供理论依据。(本论文的初步结果如下：)

利用广义不相似性模型来分析附生群落之间的物种周转和系统发育周转分别与宿主树特征、微气候变化的关系，揭示了微气候在决定附生群落的组成和系统发育结构中的关键作用，并证实了系统发育生态位保守性在群落构建中的作用。这些结果证实了系统发育的生态位在群落构建中的作用，但也引发了人们对附生植物群落适应气候变化的进化能力的担忧。

群落建模分析表明，环境过滤（生境偏好）解释了超过 78% 的非随机形成的附生苔藓物种对。生物相互作用对观察到的共存模式的贡献低于 20%，其中促进作用优于竞争作用。研究表明，附生苔藓群落组成主要受到环境过滤（非生物）过程的驱动，其重要性随着生态位复杂性和多样性的增加而增加。生物相互作用起到次要作用，其中，竞争排除的贡献非常小。这挑战了竞争对物种丰富度的累积是否会产生负

面影响的观点，而其后果是出现在中龄树上的物种丰富度会增加。该结果进一步表明，生物间的相互作用因门类和生活型的不同而不同，同一门类和生活型的物种之间通常存在促进作用，而不同门类和生活型的物种之间则存在竞争作用。

最后，通过整合这些生物和非生物因子，本研究使用随机森林模型评估了基于该特定样地和宿主树特征预测附生植物物种丰富度和丰度的因素。该研究结果证实了具有突出林冠的大树对于附生植物群落的保护极其重要，但也表明在热带森林中，附生植物多样性的评估和保护需要考虑林下树。该研究进一步表明，由于每一棵宿主树的微气候条件的重要性，有必要在目标保护的大型宿主树周围建立一个缓冲区。

## List of contributions

The thesis is based on the following articles:

**PAPER I Shen, T.**, Corlett, R. T., Collart, F., Kasprzyk, T., Guo, X. L., Patiño, J., Su, Y., Hardy, O. J., Ma, W. Z., Wang, J., Wei, Y. M., Mouton, L., Li, Y., Song, L., & Vanderpoorten, A. (2022). Microclimatic variation in tropical canopies: A glimpse into the processes of community assembly in epiphytic bryophyte communities. *Journal of Ecology*, 110, 3023–3038.

**PAPER II Shen, T.** \*, Song, L., Corlett, R. T., Guisan, A., Wang, J., Ma, W.-Z., Mouton, L., Li, Y., & Vanderpoorten, A. \*, Collart, F. \* (2023). Co-occurrence patterns among epiphytic bryophyte species in a tropical rainforest. (Submission to *PLANT BIOLOGY*)

**PAPER III Shen, T.**, Song, L., Collart, F., Guisan, A., Su, Y., Hu, H.-X., Wu Y, Dong, J.-L. & Vanderpoorten, A. (2022). What makes a good phorophyte? Predicting occupancy, species richness and abundance of vascular epiphytes in a lowland seasonal tropical forest. *Frontiers in Forests and Global Change*, 5, 1007473.

And the contribution of the following articles (in Appendix S1& S2):

**PAPER IV Hu, H.-X.\***, **Shen, T\*.**, Quan, D.-L.\*, Nakamura, A., & Song, L. (2021). Structuring Interaction Networks Between Epiphytic Bryophytes and Their Hosts in Yunnan, SW China. *Frontiers in Forests and Global Change*, 4, 716278.

**PAPER V Hu, H. -X.**, Mo, Y. -X., **Shen, T.**, Wu, Y., Shi, X. -M., Ai, Y. -Y., Lu, H.-Z., Zakari, S., Li, S., & Song, L. (2022). Simulated high-intensity phorophyte removal mitigates the robustness of epiphyte community and destroys commensal network structure. *Forest Ecology and Management*, 526, 120586.

\* These authors contributed equally to the study.





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# 1. General introduction



# 1. General Introduction

Forest canopies, called ‘the last biological frontier’ (Lowman & Rinker, 2004), harbour approximately 40% of the world's terrestrial biodiversity, of which 10% are of canopy-dwelling specialists (Ozanne et al., 2003). This unique biodiversity results from the diverse range of micro-niches that segregate along sharp vertical microclimatic gradients from the tree base to the outer canopy, which are reminiscent, but at much smaller scales, of elevation and latitude gradients (Scheffers et al., 2013; Xing et al., 2023). Such vertical gradients, coupled with the isolation of trees from each other, and the variation of the trees as habitats through time during their ontogenetical development, make trees an ideal model to test the most advanced issues currently in ecology. Despite being a thriving field since the 19th century, the advancement of forest canopy science has been slow, largely due to the limited accessibility of canopies (Nakamura et al., 2017) and forest microclimates (De Frenne et al., 2021). However, the recent development of a network of canopy cranes (Nakamura et al., 2017) and advances in microclimatic modelling have opened up new research avenues to better understand how forest biodiversity is assembled and predict its response to anthropogenic climate change (Spicer & Woods, 2013; Zellweger et al., 2020; De Frenne et al., 2021). It is in this avenue that the present thesis has been engaged.

## 1.1 Epiphyte biodiversity

Epiphytes, including vascular and non-vascular (bryophytes) plants, are inhabited in a unique, three-dimensional space within the canopy and are characteristic and ecological vital components of forest ecosystems, especially in tropical rainforests. They are defined as plants growing structurally and non-parasitically on the surface of other plants (e.g., trees, shrubs, herbs and even other epiphytes), without attachment to the ground (Zotz, 2016). They, therefore, rely on regular water from fog and rainfall as well as atmospheric depositions from dust and litter in the atmosphere. This is particularly notable for epiphytic bryophytes, including mosses, liverworts, and hornworts, which are poikilohydric, meaning that their level of hydration is heavily influenced by the water content of their surroundings. Epiphytic bryophytes vary from boreal forests in the Northern Hemisphere to temperate forests in the Southern Hemisphere (Esseen et al., 1997; Friedel et al., 2006; Mežaka et al., 2008; Díaz et al., 2010), and exhibit a diverse range of life forms (see Figure 1). In a previous study conducted in a tropical canopy crane site in a 1.44-ha lowland rainforest, 90 epiphytic bryophyte species, including 53 mosses and 37 liverworts, were recorded on 69 entire host trees of 14 dominant

tree species across three canopy layers (Shen et al., 2018). These communities of epiphytic bryophytes provide suitable substrates for vascular epiphytes.



Figure 1 Epiphytic bryophyte diversity and their life forms (dendroid, fan, cushion, smooth mat, rough mat, pendant, short turf, tall turf and weft).

Vascular epiphytes, with over 31,000 species, are a highly diverse group of plants and represent approximately 10% of all vascular plant species worldwide (Zotz et al, 2021). In wet montane forests, they may account for up to 50% of the diversity of vascular plants (Kelly et al., 2004). In a mountain cloud forest, up to 195 vascular epiphyte species were found to occur on a single tree (Catchpole & Kirkpatrick, 2010). In the study region of Xishuangbanna, 486 vascular epiphyte species from 29 families and 134 genera were recorded, contributing to nearly 11% of the vascular flora in an area of 19,690 km<sup>2</sup> (Wu et al., 2016; see Figure 2). Despite their significant contribution to forest biodiversity, information on the diversity and

composition of epiphytes in three-dimensional space is still lacking in some parts of the world (Sillett & Antoine, 2004; Sporn et al., 2010), particularly in Southeast Asia.



Figure 2 Epiphyte diversity in a tropical rainforest, Yunnan, SW China  
(Photo: © Liang Song).

## 1.2 Epiphytes in forest canopies

Epiphytes are a notable component of forest canopies, from temperate to tropical rainforests, with the most prominent occurrence in the latter (Gradstein et al., 2001; Acebey et al., 2003). Epiphytes contribute to local and regional biodiversity and play a vital role in maintaining abiotic and biotic processes in forest ecosystems. For instance, they are involved in nutrient cycling (Nadkarni, 1984; Coxson & Nadkarni, 1995; Hsu, 2002), water retention (Van Stan & Pypker, 2015), and water storage from rain and fog, which keeps the canopy humid during dry

seasons (Rhoades, 1995). Epiphytes also provide habitats for canopy-dwelling fauna by offering shelter and food (Cruz-Angón et al., 2009; Gotsch et al., 2016; Sabagh et al., 2017). The dense coverage of epiphytic mosses provides a suitable substrate for vascular epiphytes, leading to an increase in canopy biodiversity (Nieder, 2001; Sporn et al., 2010; see Figure 3). Epiphytes are regarded as effective indicators of environmental quality because of their sensitivity to anthropic disturbance, such as selective logging, deforestation, and habitat loss, and changes in environmental conditions, as they depend on their host trees and microenvironmental conditions (Köster et al., 2009; Larrea & Werner, 2010; Werner et al., 2011; Krömer et al., 2014). Therefore, epiphytic diversity, abundance, and composition can serve as reliable indicators of forest health, succession status, and habitat conservation (e.g., habitat loss, fragmentation, and degradation) (Flores-Argüelles, 2022).



Figure 3 Moss communities as substrates for *Coelogyne suaveolens* communities in a tropical rainforest, Yunnan, SW China (Photo: © Liang Song)

### **1.3 Factors affecting the diversity and distribution of epiphytes**

#### **1.3.1 Micro-climate conditions**

At the interface between atmosphere and forest canopy, epiphytes are exposed to harsh conditions of temperature and humidity, and are physiologically dependent on rainfall for water and nutrient supply. Epiphytes are, hence, extremely sensitive to climatic conditions (Nadkarni, 2010), leading to a succession of communities with increasing levels of stress tolerance due to the stress of light, water, and nutrient. Forest microclimate is, therefore, a significant determinant of the local distribution of vascular epiphytes, as can be deduced from the vertical stratification of species reported (ter Steege & Cornelissen, 1989; Krömer et al., 2007; Zotz & Schultz, 2008; Dias-Pereira et al., 2022).

The microclimates experienced by epiphytes strongly contrast with the climatic conditions that prevail outside forests and determine the composition and structure of their unique biota (Lowman & Schowalter, 2012). Light and microclimatic conditions in local forest ecosystems are influenced by site-specific and tree-specific factors. Site-specific factors include slope steepness, aspect (e.g., north and south slopes), elevation, proximity to the sea or inland water, whether a site is in a valley or on top of a hill, as well as features of forest structure and distance among trees (Bramer et al., 2018). Changes in canopy closure and depreciation in the climax forest interior, particularly the penetration of sunlight, temperature, and humidity, have an impact on orchid existence (Sujalu et al., 2021). Tree-specific factors include tree height and size (Baker et al., 2014), tree density (Von Arx et al., 2013), and tree species (Kovács et al., 2017).

While the vertical structures of epiphyte communities (Mota de Oliveira et al., 2009; Gehrig-Downie et al., 2013; Mota de Oliveira & ter Steege, 2015; Zotz, 2016) and variations in microclimatic conditions (Stuntz et al., 2002; Toivonen et al., 2017; Shen, 2018; Murakami et al., 2022) have been documented, no analysis has examined the relationship between microclimatic variation and species composition in a spatially explicit framework, largely due to the unavailability of fine-scale microclimatic data.

#### **1.3.2 Host tree characteristics**

Trees, characterized by substantial spatiotemporal variations in their characteristics, serve as habitat islands for epiphytes. These characteristics vary depending on the successive ontogenetic stages of the development of trees, during which variations in architecture, phenology, bark characteristics, canopy soil chemistry, and size occur (Taylor & Burns, 2015).



In particular, tree size has been invariably identified as the main driver of epiphytic species richness and abundance (Zotz & Vollrath, 2003; Zotz & Schultz, 2008; Francisco et al., 2021). The complex factor of tree size integrates several ecological processes relevant to epiphyte community assembly (Zhao et al., 2015). It is linked to the exposure time of the host to epiphyte seed rain, but also the greater available space for epiphytes and the increased number of microhabitats available on the tree (Paillet et al., 2019).

Moreover, the characteristics of host trees also differ between tree species due to differences in branching architecture, bark texture, and physico-chemistry (Hidasi-Neto et al., 2019). Host specificity has been reported in many instances (Sáyago et al., 2013; Zhao et al., 2015; Hayward et al., 2017; Wang et al., 2017; Adhikari et al., 2021), indicating that certain epiphytic species are more closely associated with certain tree species than others. Determining the degree of host specificity is important in a conservation context because specialist species are generally more vulnerable to habitat alterations and climate change than generalist species, and host specialists, in particular, are threatened by coextinction with their hosts (Wagner et al., 2015). However, the impact of host tree specificity on epiphytes has been challenged based on the fact that upper canopy branches, where the bulk of orchids occur, may accumulate bryophytes, lichens and dead organic material (Zotz & Vollrath, 2003), potentially homogenizing habitat structure among host tree species.

#### **1.4 Biotic interactions in epiphytes**

Trees are typical examples of habitat islands, which exhibit spatio-temporal variation of biodiversity, similar to that observed in oceanic islands, but at a smaller scale (Taylor & Burns, 2015). In particular, a bell-shaped relationship typically characterizes the variation in epiphytic species richness with tree age (Ellis & Ellis, 2013). During early colonisation stages, species progressively accumulate, with high levels of stochasticity associated with dispersal chance. In line with the idea that, during community succession, niche-based processes (niche preference and biotic interactions) progressively prevail over neutral processes associated with stochastic dispersal events, the contribution of random factors to community composition is expected to decrease on ageing trees (Mežaka et al., 2022). A peak of species richness is expected on mature trees when, in the context of a colonization/competition trade-off, both pioneers and species typical of mature tree stages can be found. Ultimately, species richness is expected to decrease due to increased competition on old trees (Ellis & Ellis, 2013).

Epiphytes thus offer an appealing framework to disentangle the contribution of biotic and abiotic drivers of species distributions. Specific hypotheses can be formulated regarding where and when biotic interactions among epiphyte communities are expected to occur. (Spicer & Woods, 2022).

Biotic interactions play a significant role in epiphytic community composition and are expected to vary greatly along the vertical gradient of the same tree. For epiphytes, the outer canopy is a high stress environment characterized by high exposure to UV radiation and large daily temperature and relative humidity fluctuations, wherein facilitation is expected to prevail (Soliveres et al., 2015). For instance, the likelihood of vascular epiphyte colonization increases with the extent of bryophyte cover thanks to the high water-holding capacities, and hence, the humid microhabitats provided by the latter (Acevedo et al., 2020). The relevance of facilitation by bryophytes for vascular epiphytes is such that bryophyte cover contributed more to models of vascular epiphyte richness than host tree size, which has been identified as the major predictor of epiphyte richness (Francisco et al., 2021; Zotz & Vollrath, 2003; Zotz & Schultz, 2008). As light exposure and daily variations in temperature and relative humidity decrease towards the tree base, interactions are expected to become more competitive (see Spicer & Woods, 2022 for review), especially in saturated epiphyte communities in forests characterized by low-turnover rates (Petter et al., 2021).

Biotic interactions are expected to be more prevalent in non-vascular epiphytes than in vascular ones, with competition playing a more significant role in bryophyte communities (Spicer & Woods, 2022). The role of competition among bryophyte communities has, however, been an area of controversy (Frego & Carleton, 1995; McAlister, 1995; Økland & Økland, 1996; Rydin, 1997; Økland, 2000; Bergamini et al., 2001). Bryophytes species can inhibit one another growth by producing allelopathic substances that prevent the growth of protonema (Whitehead et al., 2018) or by developing a growth strategy oriented towards the fast occupancy of space. Competition has been reported at the juvenile stage, mainly for space (Marino, 1991), light (Van der Hoeven et al., 1998) and nutrients (Twenhöven, 1992). Some studies have suggested that competitive exclusion is rare in bryophyte communities, while others have proposed that certain life forms, such as dendroid forms, are adapted for superior competition (Mälson & Rydin, 2009; Udd et al., 2016; Bates, 1998). In contrast to the bell-shaped relationship between epiphyte species richness and tree age, an unbounded relationship between epiphytic species richness and tree age has been observed in unsaturated communities, where there is no competition (Boudreault et al., 2000; Fritz et al., 2009; Kantvilas & Jarman,

2004).

## **1.5 Aims, research questions, hypotheses, and thesis outline**

The goals of this PhD thesis are to examine how environmental variation in four dimensions impacts the distribution and diversity of epiphytes at different nested spatial scales, at the level of entire trees in vascular epiphytes and among communities from the same tree in bryophytes. I then disentangle the contribution of biotic and abiotic drivers to epiphytic species distributions. Finally, I integrate these results to determine whether we can evaluate the factors that predict epiphyte species richness and abundance based on site-specific and tree-specific features, in order to provide a scientific basis to identify key drivers for the conservation and management of epiphytes in forest ecosystems.

To this end, I studied epiphytic communities in a 1.44-ha tropical forest plot in Xishuangbanna, SW China. This dissertation is based on three research chapters (chapters II–IV) leading to a general discussion (synthesis, chapter V).

In Chapter II, I shifted towards finer scales to examine within-tree variations in community composition. I determined whether variations in light, microclimatic conditions and host tree size affect the variation in species composition and phylogenetic structure of epiphytic bryophyte communities, and hence, assess the contribution of environmental filtering, phylogenetic constraints and competition to community assembly. More precisely, I address the following questions: (1) Is variation in species composition among epiphytic communities more important vertically, reflecting within-tree changes in microhabitat and microclimatic conditions, or horizontally, reflecting differences in age, and hence size and microhabitat diversity, among trees? (2) To what extent are these changes in community composition phylogenetically constrained? (H1) Among communities, I test the hypothesis of an increasingly positive phylogenetic turnover along microclimatic gradients, pointing to phylogenetic niche conservatism; (H2) Within communities, I test the hypotheses that species exhibit increasingly competitive interactions, and hence, increasing phylogenetic overdispersion, from the canopy to the base, and from young to old trees.

In Chapter III, I implement a community analytical framework (D'Amen et al., 2018) to determine the extent to which ecological factors, dispersal limitations, or biotic interactions control the establishment of epiphyte communities. I further test the hypothesis that facilitation prevails over competition in shaping patterns of species distributions and determine how these patterns vary depending on height zone and tree age. I hypothesise that environmental factors

prevail over dispersal limitations and biotic interactions and that, within the latter, competition increases from the canopy top to lower trunk, and from small to large trees, whereas facilitation exhibits the reverse pattern.

In Chapter IV, I conducted a comprehensive census of vascular epiphytes and recorded detailed information on both the intrinsic factors of each individual tree and extrinsic factors describing their environment, to address the following questions: (1) If epiphytes are not randomly distributed among trees, to what extent can we, using a comprehensive description of the characteristics of individual trees and their local environment, predict which trees are likely to host epiphytes and which trees are not, and how epiphytic species richness and abundance vary among individual trees? (2) What are the variables involved? How do these patterns vary between epiphytic ferns and epiphytic spermatophytes? (3) Which management strategies can be accordingly proposed to promote the conservation of vascular epiphytes?

## 1.6 Study area

This study took place in a pristine lowland seasonal rainforest within the core area of Mengla subdistrict (101°35'E, 21°37'N), Xishuangbanna National Natural Reserve in Yunnan, SW China. Mean monthly relative humidity and mean monthly temperature recorded by 12 dataloggers at 2 metres during 2017–2019 were 95.3% (minimum of 90.3% in June and maximum of 98.3% in July) and 20.8°C (minimum of 15.8°C in January and maximum of 25.2°C in June), respectively. This site offers the unique opportunity to explore epiphyte diversity along entire trees, up to 70m, thanks to a canopy crane (TCT7015-10E, Zoomlion Heavy Industry, Changsha, China) whose 60-meter-long arm provides access to the canopy within a 1.1-hectare circle (Figure 4). The crane provides access to 1.1 ha, wherein 8477 healthy individuals of 297 tree species were reported by the Xishuangbanna Station for Tropical Rainforest Ecosystem Studies (XTRES) in 2019. The emergent tree layer (30-70 m high) is dominated by *Parashorea chinensis*, which reaches 45-70 m, and a layer of 30-45 m high trees, such as *Canarium album*, *Pometia tomentosa*, *Sloanea tomentosa*, *Semecarpus reticulata* and *Nephelium chryseum*. The canopy layer (18-30 m high) is mainly comprised of *Barringtonia fuscicarpa*, *Diospyros hasseltii*, *Drypetes hoensis* and *Pseuduvaria indochinensis*. The understorey layer (6-18 m) high is composed of *Cleidion brevipetiolatum*, *Dichapetalum gelonioides*, *Diospyros xishuangbannaensis*, *Garcinia cowa* and *Pittosporopsis kerrii*.

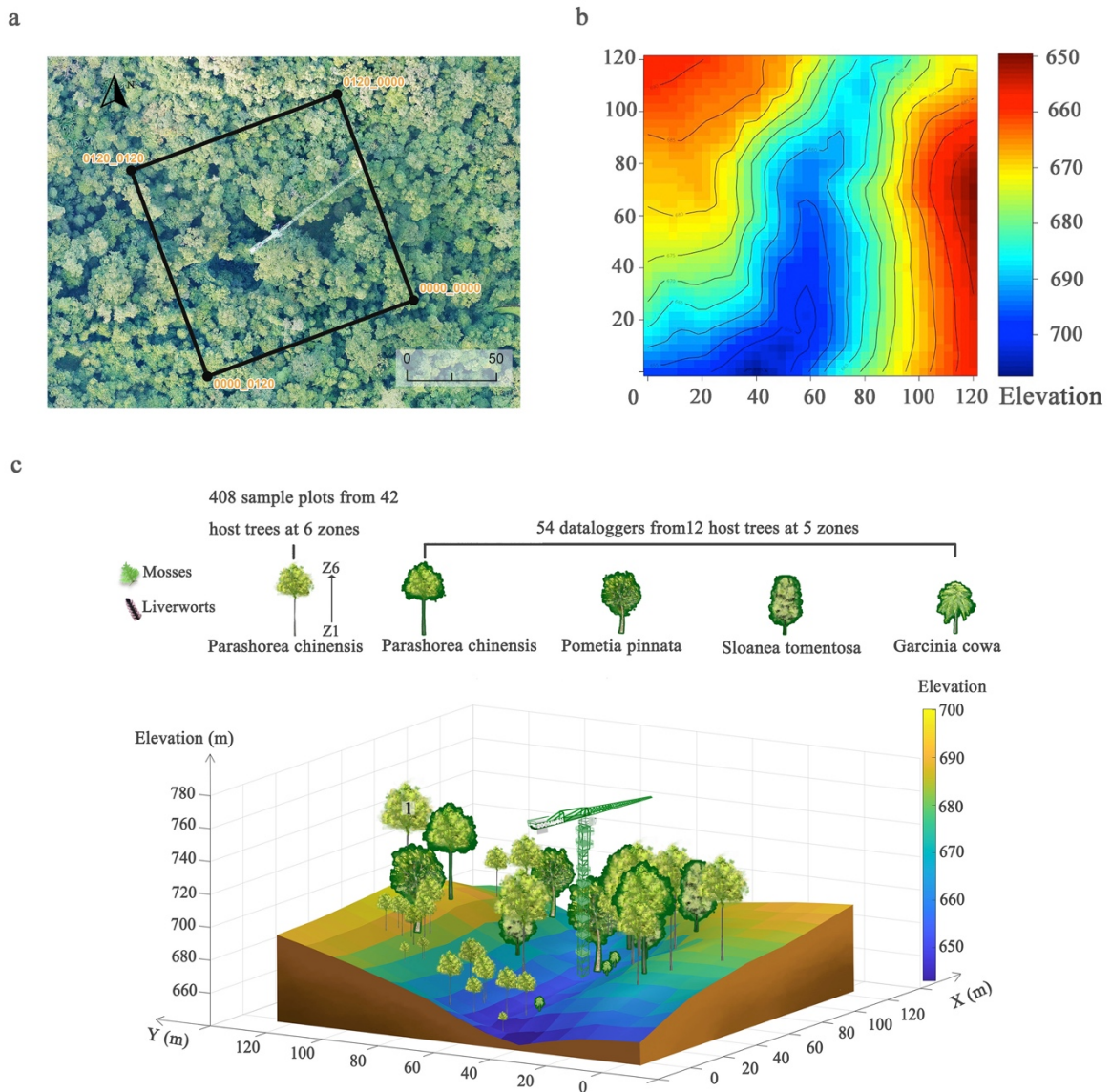


Figure 4 Experimental design (a) Bird's-eye view photograph of the facility (photograph: Yun Deng). (b) Topographic map. (c) Study site implemented in the present thesis in a 1.44 ha tropical canopy crane facility, Yunnan, SW China.

In a 1.1 ha canopy crane site (Figure 4), we focused on investigating the vascular epiphytes and cryptogamic epiphytes. With a diameter at breast height (DBH) of more than 5 cm, we surveyed 1334 individual trees to record all vascular epiphyte individuals. Each individual (or selected leaves or flowers in the case of rare species) of vascular epiphyte was collected and identified in the herbarium of Restoration Ecology Group, CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden.

For cryptogamic epiphytes, we only selected the most dominant and emergent host-tree species, *Parashorea chinensis*, to control for host specificity (Schmitt & Slack, 1990; González-Mancebo, 2003; Guan et al., 2017). *Parashorea chinensis* accounted for 19.5% of all individual trees (DBH  $\geq$  5cm) and offers a large range of microhabitats on the canopy crane site. We excluded trees with DBH less than 5 cm or that were covered by vines and lianas, resulting in a total of 42 individual trees with DBH ranging from 5.4 cm to 135 cm. The three DBH categories were small trees (DBH of 5.4–19.6 cm, n = 16), medium trees (DBH of 20.3–39.6 cm, n = 15), and large trees (DBH of 66.9–135 cm, n = 11), respectively (Figure 4). Each tree was divided into six height zones (Figure 5, Zone 1: tree base is below two meters of trunk, Zone 2: lower trunk is between two meters and middle of trunk, 3: upper trunk is between middle of trunk and bottom of first ramification, 4: inner canopy is the inner third of the canopy crown, 5: middle canopy is the second third of the canopy, 6: outer canopy is the outer-most third of the canopy, modified from Johansson, 1974). Although orientation typically plays a limited role in explaining variation in epiphytic community composition in tropical cloud forests (Song et al., 2011), we controlled for this factor by sampling, within each plot, a subplot of 20 × 20 cm quadrat at each of the four exposures for each trunk zone and four subplots of 20 × 20 cm or the same total area quadrats at the two to four main branches for each crown zone. Four subplots were regarded as a plot representing a zone sample. Two plots were randomly defined for each height zone. Within each sub-plot, a complete species inventory was conducted. Species identification was performed in the laboratory using relevant microscopic techniques and monographs (Shen et al., 2018).